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EFFECTS OF HARVEST TREATMENTS ON SPRUCE BUDWORM, *Choristoneura fumiferana* (Clem.) (*Lepidoptera: Tortricidae*), DISPERSAL WITHIN FOREST STANDS

by

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in Partial Fulfillment of the Requirements
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ABSTRACT

Dang, Z. 1996. Effects of Harvest Treatments on Spruce Budworm, *Choristoneura fumiferana* (Clem.) (*Lepidoptera: Tortricidae*), Dispersal within Forest Stands.

Key words: balsam fir, black spruce, branch sampling, dispersal, harvest, pheromone trap, sticky trap, spruce budworm [*Choristoneura fumiferana* (Clem.)], water trap, white spruce.

Dispersal is a critical trait during the life history of the spruce budworm, *Choristoneura fumiferana* (Clem.), which leads to its widespread infestation and damage. Budworm dispersal study is of importance for protecting and regenerating valuable white spruce, preferred by the forest industry. One factor that influences dispersal is forest density. The objectives of this project were to investigate: 1. the effects of harvest treatments on the larval dispersal of spruce budworm; 2. the effects of harvest treatments on the responses of budworm male moths to pheromone traps.

Harvest treatments were set up in two plots near Black Sturgeon Lake in the late fall of 1993 as follows: one uncut treatment, one partial cut with white and black spruce left, one partial cut with white spruce and birch and aspen left, and one strip clearcut. Spruce budworm egg-mass and larval densities were determined by branch sampling. Sticky traps were deployed for small larval dispersal, water traps for large larval dispersal, and pheromone traps for the responses of male moths to them in the above treatments during 1994 and 1995.

Spruce budworm densities (egg masses or larvae per 150-g branch tip) were always greater on white spruce than on balsam fir and black spruce. In most cases, the number of small larvae falling to the forest floor was significantly (α

$\leq$ 0.05) greater in the two partial cuts and strip clearcut than in the uncut treatment. This result can be explained by the lateral dispersal of the small larvae and by the filtering effect of the plentiful overstory crowns in the uncut treatment on dispersing small larvae. The small larvae falling to the forest floor have difficulties with survival there.

However, the number of large larvae falling to the forest floor was not influenced by the harvest treatments. This is the result of insignificant differences in large larval densities between the uncut treatment and two partial cuts. Large larvae drop down vertically and cannot be filtered as easily as small larvae. Large larvae falling to the forest floor rarely damage young seedlings there.

The number of male moths caught by pheromone traps was significantly ($\alpha \leq 0.10$) greater in the two partial cuts, but significantly ($\alpha \leq 0.10$) lower in the strip clearcut when compared with the uncut treatment. Possible reasons for these results were less competition between female moths and pheromone traps and stronger air currents in the two partial cuts. Pheromone traps should be set up away from natural openings in forests. Forest stands can be stratified according to their basal area before trap catch data are pooled to improve the correlation between trap catch and egg mass or larval density.

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INTRODUCTION

Spruce budworm, *Choristoneura fumiferana* (Clem.), is an insect native to North America's boreal forest and feeds mainly on white spruce, *Picea glauca* (Moench) Voss, balsam fir, *Abies balsamea* (L.) Mill., and black spruce, *Picea mariana* (Mill.) B.S.P. (Greenbank 1963b; Miller 1963; Sanders 1991). The budworm's geographical distribution covers most of the range of its major host trees (Sanders 1991). The boreal forest occupies 61% of the total Canadian land area and about 80% of the total forested lands (Bickerstaff *et al.* 1981). In Ontario, 73% of its total commercially productive forest area is boreal forest (Smyth and Campbell 1987).

In Canada, the estimated average annual mortality and growth loss caused by the spruce budworm from 1982 to 1987 was 8.7 million m^3 (Hall and Moody 1994). For Ontario in 1991, 9.1 million ha were moderately to severely defoliated by the spruce budworm (Canadian Council of Forest Ministers 1993). As a result of this large economic impact, much research effort has been dedicated to the spruce budworm.

The volume of valuable white spruce, preferred by the forest industry, has diminished in the boreal forest (MacLean 1984; Gordon 1985; Zoladeski and Maycock 1990). The possible reasons for this decline are the weak regeneration capability of white spruce in natural forests, human activities and spruce budworm damage (Eis 1965; Gordon 1985). It costs more to plant white spruce than to regenerate it naturally;

therefore, techniques to regenerate it naturally are of great interest.

In order to consider regenerating white spruce more successfully, it is essential to consider the negative influence of a continuous carpet of thick moss or lichen and non-decomposed organic matter in the Boreal Forest (Bonan and Shugart 1989; Baldwin 1991). It is believed that white spruce seeds cannot efficiently germinate and penetrate the moss layer (Frank 1990; Nienstaedt and Zasada 1990). Recently-exposed mineral soils are the most favourable sites for white spruce regeneration (Nienstaedt and Zasada 1990), and canopy openings reduce the moss cover on these soils (Baldwin 1991). Germination and seedling establishment are common on organic substrate after harvest in both clearcuts and shelterwoods although they are not as efficient as on mineral soil (Putman and Zasada 1986; Wurtz and Zasada 1986). Canopy opening or clearcutting, and leaving white spruce seed trees would benefit white spruce regeneration. Part of the long-term plans is to determine how the harvesting treatments will influence the establishment of white spruce.

Controlling budworm populations to protect existing white spruce and increase its seed production is also of importance to spruce regeneration. A first step in controlling budworm is to be familiar with critical areas of the budworm's life history and biology that may be important to white spruce regeneration. One such life-history trait of the spruce

budworm is dispersal. It is dispersal that spreads budworm from one forest stand to another, which in turn leads to infestation and damage.

Spruce budworm disperse as small larvae (first and second instars), as large larvae (third to sixth instars) and as adults (Jennings *et al.* 1983; Miller 1963; Morris and Mott 1963; Mott 1963; Sanders 1991; Shaw and Little 1973). However, successful dispersal (landing on host trees) is the key to budworm survival and damage to trees. Successful dispersal is influenced by forest density (Batzer 1976; Kemp and Simmons 1979; Morris and Mott 1963; Mott 1963), by strong sunlight and high temperatures (Wellington 1948; Shaw and Little 1973), and by disturbance (Sanders 1991).

My hypothesis is that thinning the forest canopy would increase larval dispersal to the forest floor.

The pheromone monitoring system is an economic and convenient tool for understanding the spruce budworm geographical distribution and population densities. This in turn helps forest managers make rational spruce budworm management decisions. It requires a good correlation between trap catches and larval or egg mass densities. Good correlations had been obtained in a single plot program (McDougall 1973; Sanders 1988). However, correlations between

catches and larval densities are poor if data from heterogeneous forest stands are pooled together (Allen *et al.* 1986; Sanders 1988). The same precision in larval and egg mass densities for single plot program can be obtained for pooling data from heterogeneous forest stands. Therefore, it is of importance to understand how different forest stands influence pheromone trap catches. Male moth catches by each pheromone-baited trap are presumed to represent the relative density of moths in a given area (Sanders 1988).

A second hypothesis is that male moth catch per trap should be reflected in both the large larval densities and host tree basal area after thinning.

To test my two hypotheses, different harvest treatments were set up in two plots near Black Sturgeon Lake, Ontario during the late fall of 1993. Harvest treatments were: one uncut treatment, one partial cut with only white and black spruce left, one partial cut with white spruce and birch and aspen left, one strip clearcut. The following activities were conducted in the plots in 1994 and 1995:

1. branch samples for budworm density (egg masses, second-instar and large larvae) and defoliation were taken in the uncut treatment and two partial cuts;
2. understorey regeneration and defoliation were examined;
3. sticky traps were set up in all treatments to sample small

larval dispersal;

4. water traps were deployed in all treatments to examine large larval dispersal;

5. pheromone traps were set up in all treatments to investigate response differences of male moths to traps.

LITERATURE REVIEW

LIFE CYCLE AND DISPERSAL PERIODS

Life Cycle

The spruce budworm has only one generation per year (Mattson *et al.* 1988; Sanders 1991). Overwintered second-instar larvae emerge from hibernaculae in early May until late May (Miller 1963). After migrating to suitable feeding sites, second-instar larvae start to mine old needles or unopened vegetative buds. With the development of buds, the budworm begins to feed on current, succulent foliage (Mattson *et al.* 1988). Following the second instar, the spruce budworm molts 4 times to reach the sixth instar. They pupate in late June to mid July (Miller 1963). Pupal development lasts from 8 to 14 days (Mattson *et al.* 1988; Miller 1963).

Adults appear in the field from late June to early August. Mating occurs shortly thereafter (Mattson *et al.* 1988; Miller 1963). Females lay about 200 eggs in clusters in late July and early August (Miller 1963). Each egg mass contains about 20 eggs on average (Mattson *et al.* 1988; Miller 1963). Eggs hatch within 8 to 14 days (Mattson *et al.* 1988; Miller 1963). Emergence of first-instar larvae is usually completed by mid August (Miller 1963). After dispersal, first-instar larvae spin hibernaculae in overwintering sites without feeding, molt to second-instar larvae and overwinter (Mattson *et al.* 1988; Miller 1963).

Dispersal Periods

There are four dispersal periods in the life cycle of the spruce budworm. The first instar disperses in the late summer when the larvae search for overwintering sites (Jennings *et al.* 1983; Miller 1958; Mott 1963). Another ecological role for first instar dispersal is to redistribute themselves because eggs are laid in masses. The second instar disperses, following emergence from hibernaculae, in spring when the larvae seek feeding sites in needles or new buds and again to thin themselves (Jennings *et al.* 1983; Miller 1958; Mott 1963; Shaw and Little 1973). First and second instar dispersal is often called the small larval dispersal (Jennings *et al.* 1983; Morris and Mott 1963; Mott 1963). The third period is the large larval dispersal (third to sixth instar) when the larvae look for new feeding sites or are disturbed by environmental factors such as overheating and winds (Miller 1963; Morris and Mott 1963; Sanders 1991). Finally, the fourth period is adult dispersal which is both local and long range. Local dispersal is mainly to seek mates and oviposition sites (Greenbank *et al.* 1980; Miller 1963; Outram 1971; Sanders 1969; Sanders and Lucuik 1975). Long range dispersal involves the long distance displacement of moths (Greenbank *et al.* 1980) to seek new habitats for subsequent generations. Redistribution of spruce budworm populations within and between forest stands primarily results from the small larval and moth dispersal (Jennings *et*

al. 1983; Morris and Mott 1963).

Numerous factors affect the dispersal of spruce budworm larvae (Jennings *et al.* 1983). They can be divided into two groups: the conditions of the spruce budworm themselves and environmental factors. The former are factors such as larval weight, length of silken threads, nutritional levels and population densities (Batzer 1968; Mott 1963). The latter are factors such as air temperatures, sunshine, wind velocity, turbulence and forest structure (Batzer 1976; Greenbank *et al.* 1980; Kemp and Simmons 1979; Mott 1963).

SMALL LARVAL DISPERSAL

First Instar Dispersal

New hatchlings (first-instar larvae) are positively phototactic during their dispersal (Wellington and Henson 1947). This positive phototactic property is reversed at body temperatures greater than 28°C (Wellington 1948). But, Eidt (1969) argued that the dispersal of first-instar larvae occurs over a wide range of temperatures irrespective of the direction of light sources. New hatchlings drop on silken threads and may land on a lower branch. The threads often detach or break, and then the larvae are carried away by winds (Batzer 1968; Henson 1950), sometimes for long distances (Morris and Mott 1963). The dispersal of first-instar larvae happens mostly within host tree crowns, but to some extent between tree crowns (Régnière and Fletcher 1983).

After dispersal first-instar larvae may find overwintering sites in an infested or uninfested host tree or non-host tree or even on the forest floor. The result is population redistribution within and between tree crowns and forest stands (Morris and Mott 1963; Mott 1963).

Second Instar Dispersal

Second-instar larvae start to emerge from hibernaculae in the spring after enough heat is accumulated (Bean and Wilson 1964; Miller *et al.* 1971). The emerged larvae also are positively phototactic, but it is reversed at high body temperatures of about 36 °C and over (Wellington 1948). However, this temperature is rarely reached during the spring dispersal. Most second-instar larvae disperse during the hottest period of a day, but rainfall markedly inhibits dispersal (Shaw and Little 1973). Thus, to a great extent, light and reasonably high temperatures are beneficial to spring dispersal. Like new hatchlings, most second-instar larvae spin silken threads and the threads often detach and break. Then, the spinning larvae are dispersed by winds (Batzer 1968; Henson 1950). The dispersal of second-instar larvae is significantly greater between than within host tree crowns (Jennings *et al.* 1983; Régnière and Fletcher 1983).

Effect of Harvest Treatments

Harvest treatments change the characteristics of forest stands, and this in turn influences the small larval dispersal. The following results were obtained by Jennings *et*

al. (1983) in 19 to 30 m wide clearcut strips, 23 to 50 m wide uncut residual strips, and dense stands. The number of first instar dispersing to the forest floor decreased in the order: uncut residual strips, clearcut strips and dense stands. Significantly more first-instar larvae dispersed to the forest floor in uncut residual strips than in dense stands. The number of second instar dispersing to the forest floor was remarkably greater in clearcut strips than in uncut residual strips or in dense stands (Jennings *et al.* 1983). The difference between first and second instar may be explained by Régnière and Fletcher's (1983) observation that the dispersal of second-instar larvae is significantly greater between than within host tree crowns. It also may result from the size of the clearcut strips. Fellin (1985) reported that the catches in ground sticky traps for small larvae of western spruce budworm are lower in clearcut stands than in uncut stands when clearcuts are 50 ha or larger, but the catches in the clearcut are higher than in the uncut stands when clearcuts are about 6 ha. Additionally, removal or thinning of nonmerchantable understorey substantially increased the catches of ground sticky traps for small larvae of western spruce budworm (Fellin 1985).

Climbing Back

Régnière and Fletcher (1983) wrapped the trunks of host trees with sticky girdle traps to find out if the small larvae which had fallen on the forest floor during the

dispersal could climb back up the host trees. They concluded that first-instar larvae cannot climb back onto host trees. They overwinter or die on the forest floor. In contrast, some second-instar larvae falling to the forest floor can climb back onto the host trees during the spring dispersal (Régnière and Fletcher 1983). Some of these larvae may have been from the spring dispersal and some from overwintering sites on the forest floor. Second-instar larvae in the spring are attracted to volatiles of current-year or two-year-old growth of the host trees (Ascoli and Albert 1985). But similar research for first-instar larvae has not been undertaken. This may partially explain why second instar in the spring dispersal can climb back to host trees even though light, temperature and other factors may affect the small larvae climbing back.

Host Tree Crown Closure and Non-Host Tree Species

Stand density and composition influence larval survival (Batzer 1976; Mott 1963). Kemp and Simmons (1979) calculated the primary survival rate of second-instar larvae during the spring dispersal by dividing the post-dispersal population densities (third instar) sampled after the spring dispersal by corresponding pre-dispersal densities sampled in the fall of the previous year. Crown closure and the diameters at breast height (DBH) and crown diameters of host trees were positively correlated with spruce budworm survival in the spring dispersal. However, the percentage of non-host trees

is inversely related to the survival of second instar during the spring dispersal (Kemp and Simmons 1979). Morris and Mott (1963) reported similar results: dispersal losses were relatively low in dense stands of preferred host trees and relatively high in opened or mixed wood stands.

Buoyant Effect of the Silken Threads

The length of threads spun by a small larva is one of the factors which affect small larval dispersal. Batzer (1968) examined the buoyant effect of these threads. The falling velocity of the small larvae decreased exponentially with increasing thread length. This result implies that thread length may influence small larvae landing on host trees and their dispersal distances.

Small Larval Losses During Dispersal

Early studies on fall and spring dispersal losses were undertaken by Miller (1958) in mature and middle-aged stands in the Green River Watershed, New Brunswick from 1952 to 1957. Fall dispersal losses were based on the difference between hatched egg (first-instar) density before the fall dispersal and second- instar larval density sampled in the fall after the dispersal. Spring losses were based on the difference between the second-instar larval density sampled in early May before the spring dispersal and the third-instar larval density after the dispersal. Estimated mortality in hibernaculae was deducted. The fall dispersal losses ranged from 48 to 82% and averaged 64.1%; the spring dispersal

losses ranged from 18 to 71%, and averaged 53.7%. Factors influencing Miller's (1958) estimates were predation, failure to spin hibernaculae, non-diapause development, the loss of hibernaculae and failure to establish a feeding site. Mortality caused by these factors is difficult to estimate in a natural population. However, Miller (1958) claimed that these mortality factors accounted for a very small proportion of mortality when compared with dispersal. Kemp and Simmons (1979) used almost the same methods as Miller (1958) to calculate primary survival rates of the spring dispersal. The spring dispersal survival rates averaged 32.5%. Compared with Miller's (1958) method, Kemp and Simmons (1979) did not estimate overwintering mortality in hibernaculae.

More recently, a different method for dispersal loss estimates was used by Régnière and Fletcher (1983). They converted first- and second-instar larvae trapped with ground sticky traps into the number of larvae per m^2. The unit for expressing egg and second-instar larval (before the spring dispersal) densities was the number of larvae per m^2 of branch surface area. Fall dispersal losses were calculated by dividing ground-trapped first-instar larval density by the egg density. Spring dispersal losses were estimated by dividing ground-trapped second-instar larval density by larval density from branch sampling in early May. The fall dispersal loss was about 4.95%, and the spring dispersal loss 3.95%. *Jennings et al.* (1983) used almost the same method to

estimate dispersal losses. The dispersal loss of first-instar larvae was 0.2%, and that of second-instar larvae 1.2%. The major failure of these estimates was that the number of small larvae which landed on non-host trees during dispersal were not counted.

It is difficult to compare the small larval dispersal losses estimated by the two methods mentioned above. The small larval losses estimated by Miller (1958) and Kemp and Simmons (1979) are the larval density decrease in host tree crowns during dispersal, which is expressed as the percentage of the larval density before dispersal. But the estimates made by Régnière and Fletcher (1983) and Jennings *et al.* (1983) are the ratio of larval density trapped on the ground to larval density in host tree crowns before dispersal. Therefore, comparing the results from the two methods is not meaningful.

LARGE LARVAL DISPERSAL

Direct damage caused by the spruce budworm includes growth loss, top kill, cone and seed mortality, widespread tree mortality and scenic impairment (Bible 1985; Mattson *et al.* 1988). This damage is initiated by the emerged second-instar larvae and continued to the sixth instar. Second, third and fourth instars together consume only 4% of the total amount of food taken during the whole larval stage. The fifth instar consumes 9% and the sixth instar 87% (Miller 1977). Similar

consumption results were obtained by Retnakaran (1983) with artificial diet incorporating amaranth dye.

After one- and two-year-old needles, expanding vegetative buds and staminate flowers on feeding sites established by second-instar larvae are consumed, the large larvae move to the expanding foliar shoots of host-tree species (Atwood 1944; Blais 1952; Greenbank 1963a; Mattson *et al.* 1988; McGugan 1954; Miller 1963). Then they feed on current foliar shoots, and occasionally on developing female cones (Miller 1963; Sanders 1991). As the large larvae feed on foliar shoots, two or more shoots are webbed together to form a silken tunnel as shelter (Miller 1963; Miller 1977; Sanders 1991). The large larvae feed either in the tunnel (Miller 1963), or reach out of the tunnel to feed and quickly retreat into the tunnel when disturbed (Sanders 1991). Many needles are partially eaten and later turn reddish brown due to desiccation. These needles together with some dried frass remain in the twigs by the silk. At high population densities, the aggregation of these needles and dried frass gives a characteristic reddish colour of spruce budworm outbreaks (Miller 1977; Sanders 1991).

Under most conditions the large larvae are photopositive to both diffuse and direct light (Wellington 1948). This biological characteristic probably keeps the large larvae in the tips of host-tree branches and the tops of host tree crowns and increases the probability of their feeding on

current foliage (Sanders 1991).

However, high temperatures and starvation induce and maintain their photonegativity (Wellington 1948). If air temperature is at about 28°C under full sunshine or the large larvae are heated to about 36°C, the larvae begin to perform photonegatively (Wellington 1948). If temperatures continually increase, they may leave the feeding tunnels for shade and readily drop with silken threads (Sanders 1991).

At high population densities, all current foliage is easily consumed (Miller 1963; Morris and Mott 1963). With the destruction of current foliage, the large larvae begin to starve, which triggers them to behave photonegatively (Wellington 1948). Under these conditions, many large larvae are forced to move downwards to the lower branches and search for new feeding sites (Sanders 1991). Their photopositive reaction to diffuse or indirect light brings them outwards again to the tips of the lower branches (Sanders 1991). The probability of their encounter with fresh foliage is again increased. During this whole process, a number of the large larvae drop with silken threads from the heavily defoliated overstory to lower vegetation or the ground (Miller 1963; Morris and Mott 1963; Sanders 1991).

These fallen larvae may land and feed on advanced tree regeneration or young seedlings, climb up host trees, die on the ground, be eaten by ground predators or pupate on the ground (Gordon 1985; Miller 1963; Sanders 1991).

MOTH DISPERSAL

Moth dispersal are local and long range movements. Local dispersal involves both male and female moths. Its main purpose is for mate seeking and oviposition. After emergence, females mostly remain sedentary on the foliage close to their pupal cases. While extending their pheromone glands after sunset, they start to call or release sex pheromone (Sanders 1969). Females usually call until dawn under suitable temperatures (Palaniswamy and Seabrook 1985). Calling is affected by temperature and females do not start to call at temperatures of 7°C or lower (Sanders and Lucuik 1975). Females are fully capable of flight after 50% of their eggs are laid (Greenbank *et al.* 1980; Miller 1963). Males mainly respond to calling females to mate on the second and third nights after emergence (Outram 1971; Sanders and Lucuik 1975). Males buzz around peripheral branches from dawn until shortly after midnight following the second day after emergence, and stop buzzing flight at around 13°C (Greenbank *et al.* 1980). Generally, moths in the forest canopy are more active during the evening and at night than during the day (Greenbank *et al.* 1980).

Large numbers of moths may disperse over considerable distances especially during an outbreak. It was believed in the 1950's that thunderstorms which precede typical cold fronts were responsible for the initiation of mass flights, and the mass deposition of moths in towns or on lakes was

caused by the passage of cold fronts and downdrafts of storm cells (Henson 1951; Greenbank 1957; Wellington 1954). Large gains or losses observed in egg densities are too frequent to be explained by occasional cold fronts (Greenbank 1963c). In addition, egg losses are consistently high in severely defoliated stands (Morris 1963). This led to the following understanding at long-range dispersal (Greenbank 1973).

A relatively complete story about long-range dispersal was told by Greenbank *et al.* (1980) by means of canopy, radar and aircraft observations. Three stages are inherent in the long-range dispersal process: emigration (takeoff and departure from a stand), displacement, and immigration (descent and landing). Both male and female moths are involved in long-range dispersal, but egg-carrying females are predominant. Takeoff starts 1 or 2 hours before sunset and peaks shortly thereafter. Favourable temperatures for takeoff are from 18 to 23°C. The distances of displacement range from about 10 to 600 km. Duration of flights varies from less than a hour to several hours. The distances and duration are influenced by temperatures and wind speeds. During the final stage, moths close wings to drop vertically, and very often land in forests. This complete story provides a better understanding of the effects of long-range moth dispersal on the initiation and spread of infestations.

RESPONSES TO PHEROMONE TRAPS

Importance

Reliable estimates of spruce budworm geographic distribution and population densities will assist forest managers in making rational management decisions. To meet this purpose, spruce budworm densities have been monitored using the traditional branch sampling method of examining foliage for larvae and egg masses. But the traditional method is costly in time and money.

It was a breakthrough in methodology when the major component of the spruce budworm sex pheromone (attractant) was identified as trans-11-tetradecenal in 1971 (Weatherston *et al.* 1971). Subsequently, Sanders and Weatherston (1976) reported that the optimum blend of the sex pheromone is 95-97% E-11-tetradecenal to 3-5% Z-11-tetradecenal. The development of synthetic sex pheromone offered a more cost effective method for forecasting population trends and estimating larval and egg mass densities (Grant 1991; Sanders 1978).

Lures

Before 1976, virgin female moths were used as lures in traps (Miller and McDougall 1973; Sanders 1988). Lures widely used in the 1980's were polyvinyl chloride pellets (PVC) containing 0.03% synthetic pheromone (w/w) (Allen *et al.* 1986; Sanders 1981; Sanders 1986a; Sanders 1988). The PVC pellet has a release rate close to that of a female moth

(Silk *et al.* 1980). Later, Sanders and Meighen (1987) demonstrated that Biolures (Consep Membranes Inc.) and polyethylene vials (International Pheromone System) showed high stability in attractiveness over time and catches among individual lures when compared with PVC and other lures.

Trap Selection

Trap selection is mainly dependent on catch-capacity, cost and convenience. Sticky traps were used in early monitoring programs because of the ease in counting trapped moths by visual inspection. However, the trapping surfaces of sticky traps became saturated when a relative small number of moths were caught (Houseweart *et al.* 1981). With saturation, the catch no longer had a quantitative relationship with population densities or changes (Grant 1991). A limited trap surface area, therefore, prevents the use of sticky traps over a wide range of population densities (Houseweart *et al.* 1981).

The use of large-capacity, nonsaturating traps is recommended. Nonsaturating, liquid-filled traps are less of a problem than sticky traps. But they are messy and inconvenient for counting large number of moths killed in the liquid reservoir. Liquid-filled traps are also more expensive and bulkier than sticky traps (Grant 1991; Sanders 1986a).

Recent attention has focused on the use of non-sticky, high-capacity bucket or funnels traps (Ramaswamy and Cardé 1982; Sanders 1986a). In these traps, moths are killed with

plastic resin strips impregnated with insecticides. Sanders (1986a) recommended the use of Multi-Pher® and Uni-Trap® traps in the pheromone monitoring system for the spruce budworm. Multi-Pher and Uni-Trap traps are equipped with internal funnel-shaped baffles that prevent moths from escaping.

Trap Placement

Trap placement initially involves trap height. The highest trap catches occur in the upper canopy of host trees (Miller and McDougall 1973). However, the deployment of traps at upper canopy heights is impractical for any extensive monitoring program. Therefore, pheromone traps are hung on branches of host trees at about 1.5 to 2.0 m above the ground, an appropriate height for operational use, and about 0.5 m or farther from the tree trunk for both eastern and western spruce budworms (Allen *et al.* 1986; Houseweart *et al.* 1981; Miller and McDougall 1973; Ramaswamy *et al.* 1983; Sanders 1978; Sanders and Meighen 1987; Sanders 1986b; Sanders 1988; Sweeney *et al.* 1990).

The other aspect of trap placement is trap spacing. Houseweart *et al.* (1981) reported that traps closer than 20 m apart can significantly interfere with each other. When compared with trap distances of 5, 10, 20 and 30 m, the least interference exists when traps are spaced at 40 m (Houseweart *et al.* 1981). Allen *et al.* (1986) also reported that 40 m is a good distance to avoid interference between traps. Traps can be deployed in a cluster of 3 or in a cluster of 5 (Allen

et al. 1986; Sanders 1988). In a cluster of 3, traps 40 m apart were positioned in an equilateral triangle. In a cluster of 5, 4 traps were positioned in a square and the fifth in the centre, and the distance between traps was not less than 40 m. However, a 3-trap cluster is as efficient as the 5-trap cluster (Allen *et al.* 1986; Sanders 1988).

Monitoring Population Trends and Estimating Population Densities

The possibility of following local population trends and predicting a local outbreak with pheromone traps is very appealing. Changes in pheromone trap catch have reflected similar trends in larval densities at Black Sturgeon Lake, Ontario even though different lures and traps had been used for a 20-year trapping program in the same plot (Sanders 1988). Within 20 years, the r^2 value for the regression relationship between annual trap catch and larval density in the same year was 66%, and for larval density in the following year was 81% (Sanders 1988). If either an increase in annual catch in three consecutive years or an annual catch threshold of about 50 moths per trap had been adopted, the spruce budworm outbreak at Black Sturgeon Lake in 1983 could have been predicted six years in advance (Sanders 1988). A similar 12-year program was carried out by Miller and McDougall (1973) in one plot in New Brunswick. The r^2 value for the regression relationship between annual trap catch and large larval density in the following year where was 98%

(Miller and McDougall 1973). It is clear that pheromone baited traps can be used to forecast the transition of local populations from endemic to epidemic levels (Miller and McDougall 1973; Sanders 1988).

In order to use pheromone traps to estimate population densities for a large area, a good relationship between trap catches and larval or egg-mass densities from multiple plots is required. Allen *et al.* (1986) conducted a 3-year program in six states in the U. S. A. and two provinces in Canada for monitoring sparse to medium budworm populations. When data were pooled, r^2 value for the regression of larval population densities on trap catches was not significant. When data are stratified by state or province, trap catches in several locations are significantly correlated with larval densities for the same or subsequent generations (Allen *et al.* 1986). Sanders (1988) deployed pheromone traps in 53 plots within Ontario from 1982 to 1984. Relatively good r^2 values were only obtained in low population locations (Sanders 1988). For a one-year program in 12 stands in Keweenaw County, Michigan, a good correlation was obtained by Ramaswamy *et al.* (1983) in low to moderate population levels. Therefore, pheromone trapping can be a promising tool for estimating local population densities which range from low to medium.

Correlation between moth catches and larval densities obtained from multiple plots in a single year is poorer than that from a single plot over a long term (Miller and

McDougall 1973; Sanders 1988). Possible reasons given by Allen *et al.* (1986) and Sanders (1988) include: 1. trap catches in different plots or even plots in different states and provinces are affected by local climate, topography and stand composition; 2. spruce budworm populations in different plots are not independent. This mainly results from moth movement. But moth movement may not be expressed in larval densities. For these reasons the sex pheromone monitoring system may be limited for use in locally sparse to moderate populations.

ECOLOGICAL ROLE

The ecological role of spruce budworm in spruce-fir forests was first proposed by Swaine *et al.* (1924). In their view, spruce budworm outbreaks result in more dead fir than spruce, increase spruce representation in the stand and accelerate the conversion of spruce-fir to pure spruce forests. Later, contrary to the contention that spruce budworm outbreaks accelerate the conversion of spruce-fir to pure spruce forests, de Gryse (1947) reported that in some stands spruce budworm outbreaks do not result in any remarkable increase in spruce component. Indeed, fir content actually increases under some conditions (Baskerville 1975a; 1975b; MacLean 1984; Prebble and Morris 1951).

Spruce budworm outbreaks result in more dead balsam fir than white or red spruce or cause more severe damage to

balsam fir than to spruce when the height of spruce and fir is over 45 cm (Gordon 1985). If the height is under 45 cm, the defoliation is slight and almost the same for spruce and fir (Gordon 1985). In spruce-fir forests, the fir component tends to increase during growth competition. However, the spruce budworm plays an important role in maintaining spruce content in spruce-fir forests (Gordon 1985).

Blais (1985) and MacLean (1984) commented that the relationship between spruce budworm outbreaks and forests observed under one set of conditions will not necessarily be suitable for others. Miller and Rusnock (1993) hypothesized that the ecological role of the spruce budworm in forests varies remarkably under different forest and climatic conditions.

MATERIALS AND METHODS

PLOT DESCRIPTION

This project was conducted in two 10-ha plots, B1 and 4, located near Black Sturgeon Lake, northwestern Ontario (Figure 1). The two plots were about 2 km apart. Plots B1 and 4 were mixed-wood stands consisting mainly of balsam fir, white spruce, black spruce, birch and aspen. Plot B1 was divided by Bichon (1996) into 64 subplots, in a 40 m by 40 m grid pattern during the early summer of 1993 (Figure 2). During the late fall of 1993 in plot B1, an 160-m wide strip was left uncut, an 80-m wide strip was partially cut and an 80-m wide strip was clearcut (Figure 2). Only white and black spruce and a few birch trees were left in the partial cut of plot B1. Meanwhile, plot 4 was partially harvested throughout the whole plot leaving white spruce, birch and aspen.

During the late summer of 1993, before the harvest treatments, all stations in the partial cut and strip clearcut treatments of plot B1 had been marked by painting the bases of station trees and by burying aluminum cans at these stations. The marking was conducted by Bichon (1996). All these stations were relocated using a metal detector during the spring of 1994. Each station was marked again with a 183 cm long by 5 cm square wooden stake. The wooden stakes, with tops painted pink, were driven into the ground leaving about 150 cm above ground.

Twelve subplots from each treatment of plot B1 were

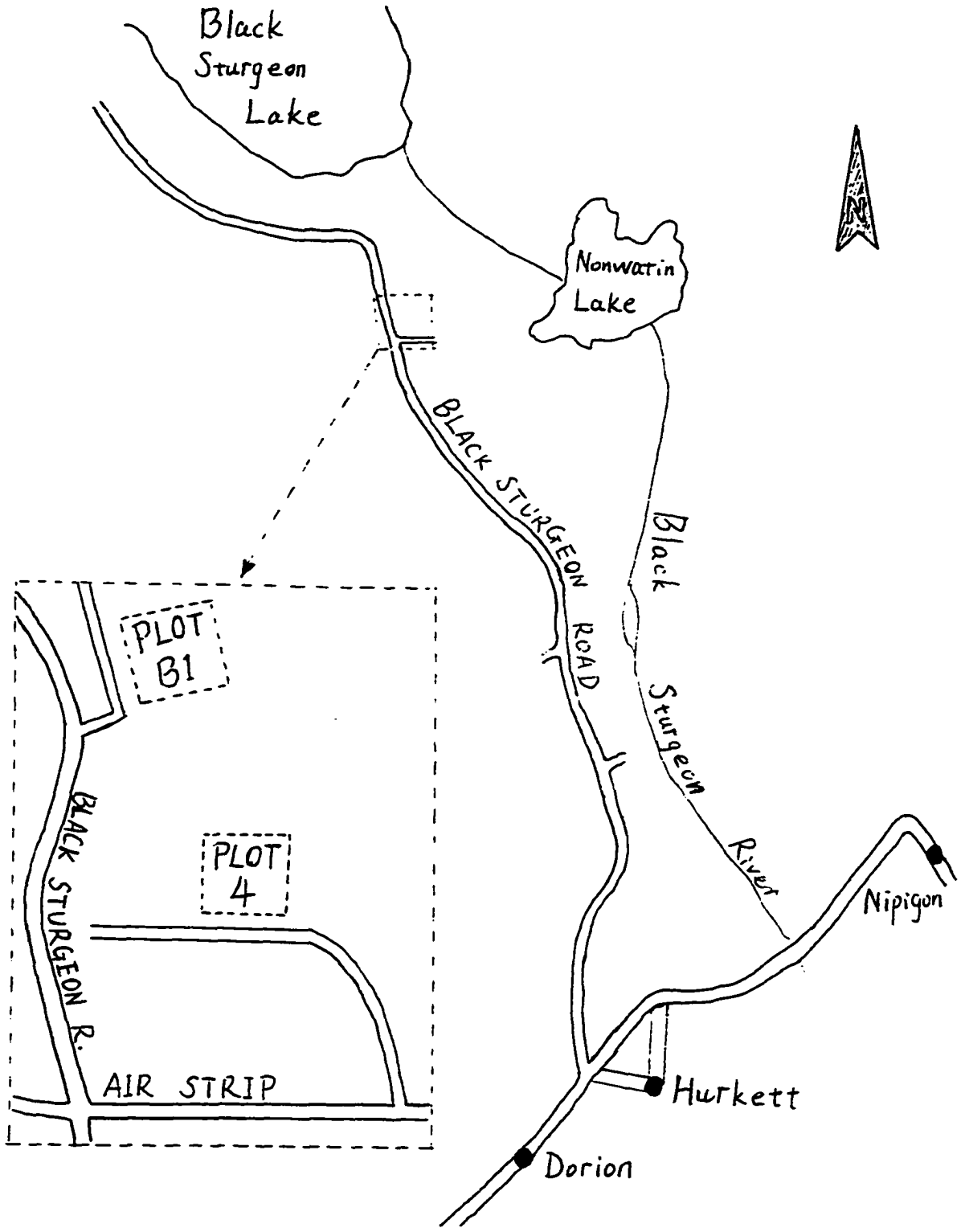
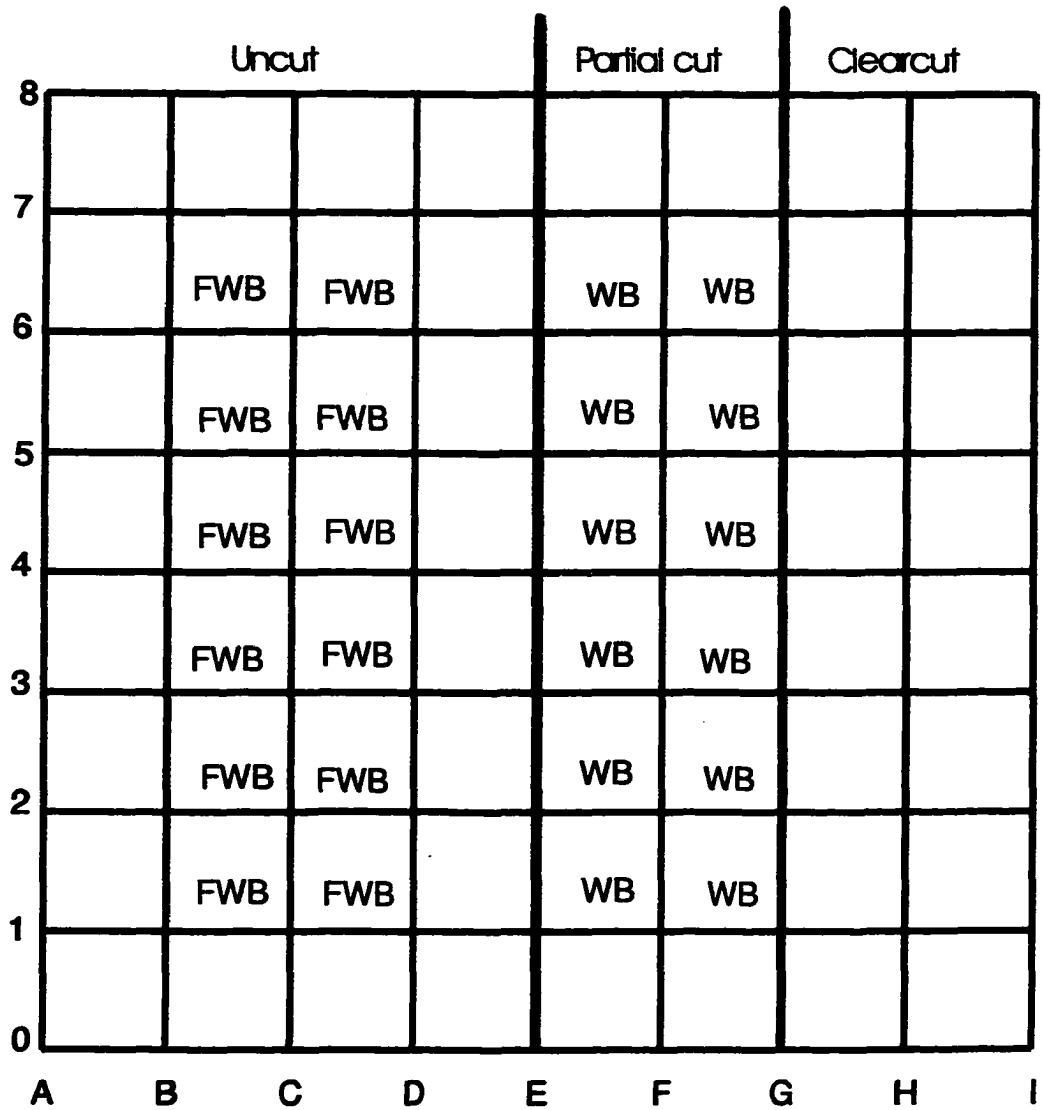


Figure 1 Sketch map showing the relative position of Black Sturgeon Lake in northwestern Ontario to the field plots.



LEGEND:
F = balsam fir; W = white spruce; B = black spruce

Figure 2 Layout of sampled trees for larval and egg mass densities and overstory defoliation within selected subplots of plot B1 near Black Sturgeon Lake in 1994 and 1995.

selected systematically for dispersal observation (Figure 2). Only 12 subplots were selected in the same way in the middle of plot 4 (Figure 3).

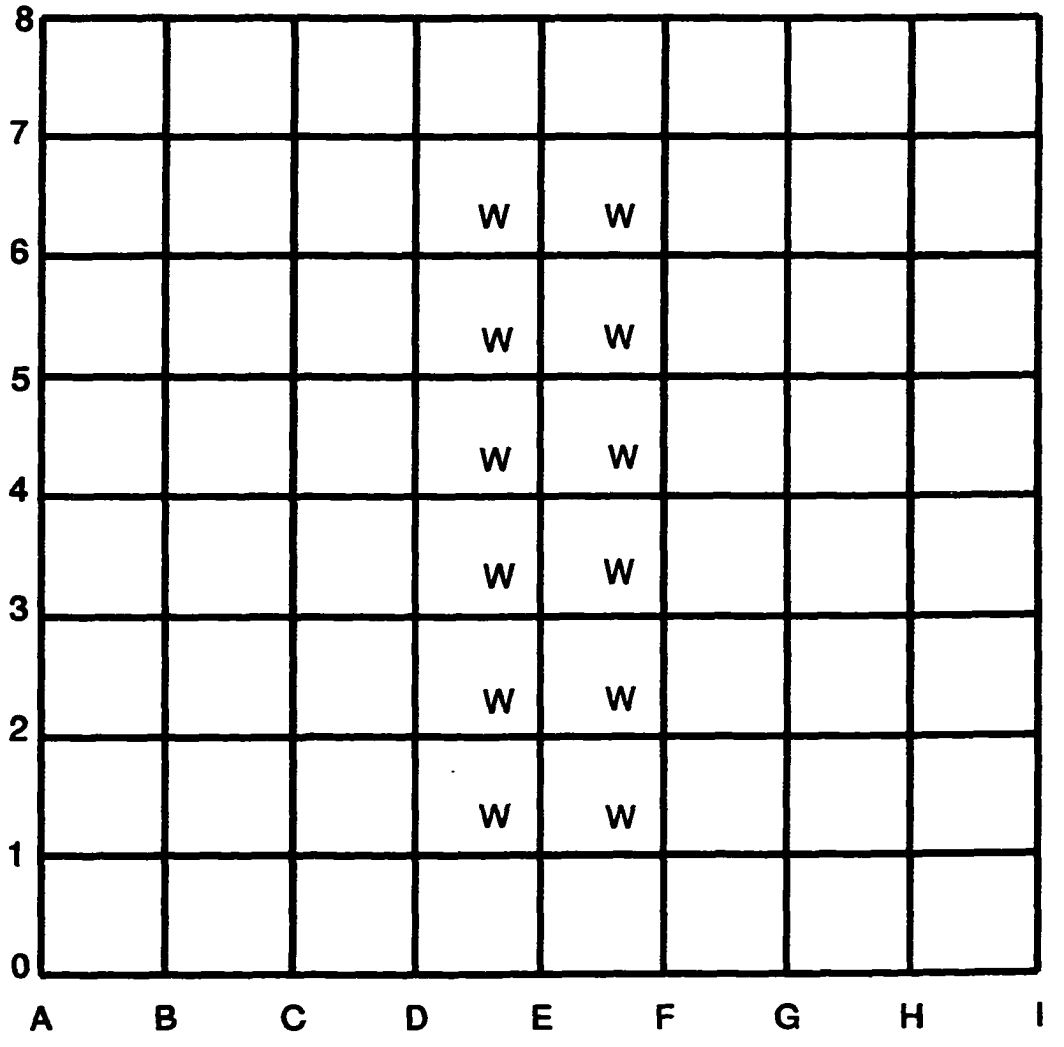
The diameters at breast height (DBH) were measured for all trees with DBH greater than 4 cm in sampled subplots in 1995. Crown closure was estimated from infrared aerial photographs taken by Sureway Company, Thunder Bay, Ontario in the summer of 1994.

BRANCH SAMPLING

One healthy codominant tree per species of balsam fir, black and white spruce in each selected subplot of the uncut treatment of plot B1 were marked for sampling. Marked trees in the partial cut of plot B1 were black and white spruce, and in plot 4 white spruce only (Figures 2 and 3). Due to the mortality of a few marked trees in the winter and the damage of consecutive sampling to host trees, dead and low-vigour trees were replaced during the sampling of 1995.

Egg Mass Densities

Branch sampling to determine egg mass densities on each marked tree was conducted using pole-pruners on 11 August 1994, and on 29, 30 July, and 1 August 1995 (Figures 2 and 3). All branch tips pruned from the upper mid-crown were trimmed to a branch tip at 45 cm in length (Régnière *et al.* 1989; Régnière and Sanders 1983; Sanders 1980). Each branch tip was placed in a brown paper bag marked by sampling date,



LEGEND:
W = white spruce.

Figure 3 Layout of sampled trees for larval and egg mass densities and overstory defoliation within the selected subplots of plot 4 near Black Sturgeon Lake in 1994 and 1995.

tree species and location. All filled bags were immediately sealed by folding their tops and stapling them. Branch samples were stored in a cool basement and processed within three days after pruning. Processing branch samples involved recording the sampling date, tree species and location, and fresh weight, and visually examining foliage for egg-mass bearing needles which were removed and number of egg masses was counted. Needles fallen inside each bag were also visually examined.

Second Instar Densities

Miller (1958) indicated that an insignificant number of second-instar larvae overwinter on host tree trunks. Therefore, a 45-cm branch tip was an acceptable unit for sampling second-instar larval densities. The process of obtaining branch tips was similar to that used for egg mass densities (Figures 2 and 3). Sampling days were 10 and 11 May 1995. Sampling date, tree species and location, and fresh weight were recorded.

Second-instar larvae were forced to emerge from hibernaculae by the paper cone method (Sanders 1980) in a laboratory at Lakehead University since diapause had been completed under field conditions. After branch tips were taken out from the bags, the inside of each paper bag was searched for emerged second-instar larvae. In the paper cone method a branch tip was placed upright in a jar holding water and covered with a piece of brown paper to form a cone. Each

paper cone with a branch was set up on a sheet of brown paper on a table and was circled with a Tanglefoot® ring to prevent the larvae from escaping. Lights in the laboratory were left on for 24 hours each day during the emergence period. The branches were sprayed daily with water during the emergence period.

Second-instar larvae were collected daily as they crawled on the outsides of the paper cones and the paper sheets or were entrapped by the Tanglefoot® rings. The inside of the paper cones were also checked carefully to count dead or living larvae at the end of the emergence period.

Large Larval Densities

Branch sampling for large larval density on each marked tree was conducted on 7, 8 and 9 June 1994 and on 2, 3, 5 and 8 June 1995 (Figures 2 and 3). Most steps were the same as for egg mass density sampling, but pole pruners with baskets were used. The difference in sample processing was that foliage was visually examined for larval instar and number of each sampled branch. A search for larvae inside bags was also carried out.

Overstory Defoliation

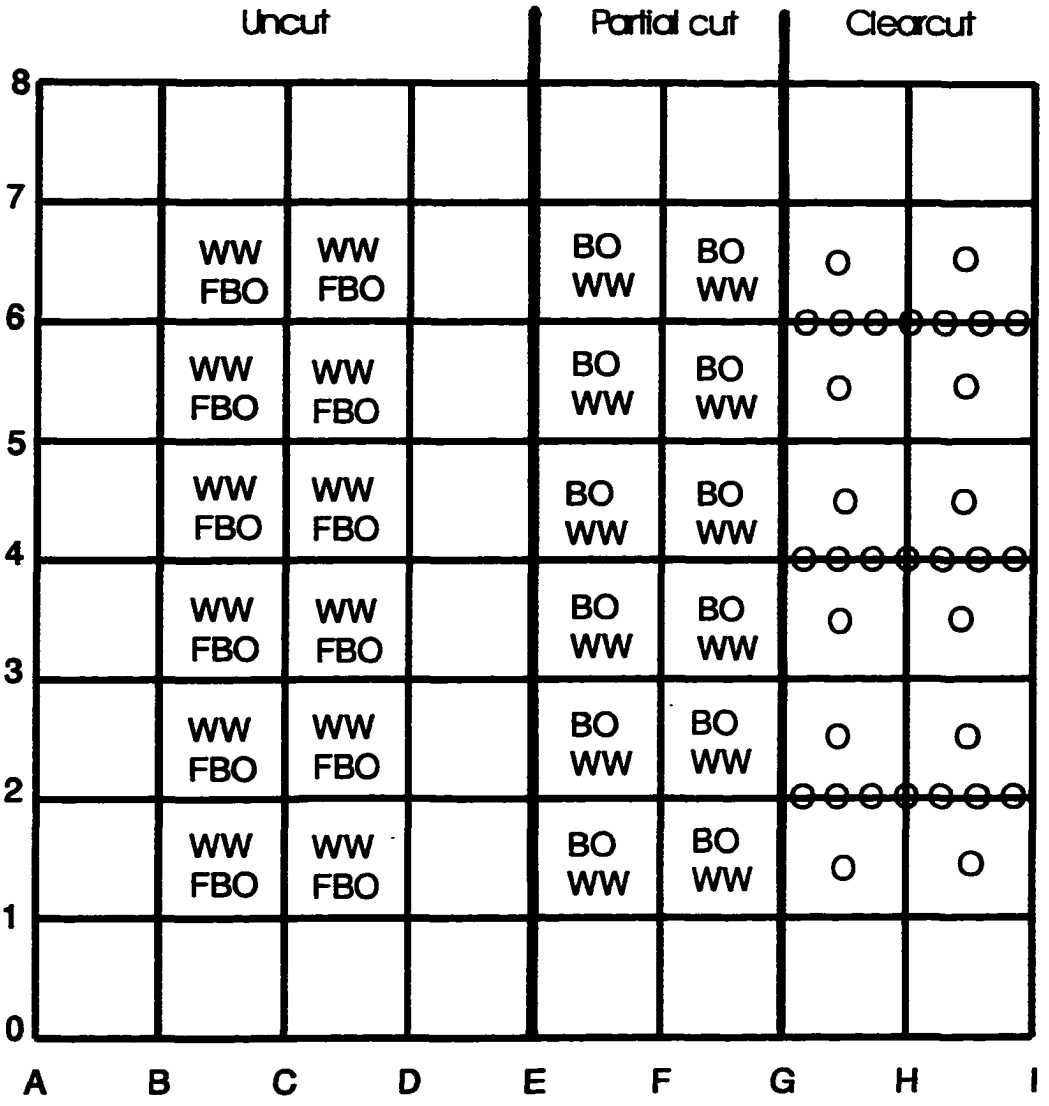
On 7, 10 and 11 July 1994, all the marked trees were sampled again with pole pruners in a way similar to that described above to estimate the indices of the spruce budworm defoliation (Figures 2 and 3). The defoliation index of each branch sample was obtained by observing its 25 most distal

shoots one by one. A number from 0 to 12 corresponding to defoliation intensity was given to each shoot according to the Fettes' method (Sanders 1980). Finally, the mean defoliation index of all the 25 shoots was determined. Defoliation sampling in 1995 was combined with egg-mass sampling on 29, 30 July, and 1 August.

STICKY TRAP SAMPLING

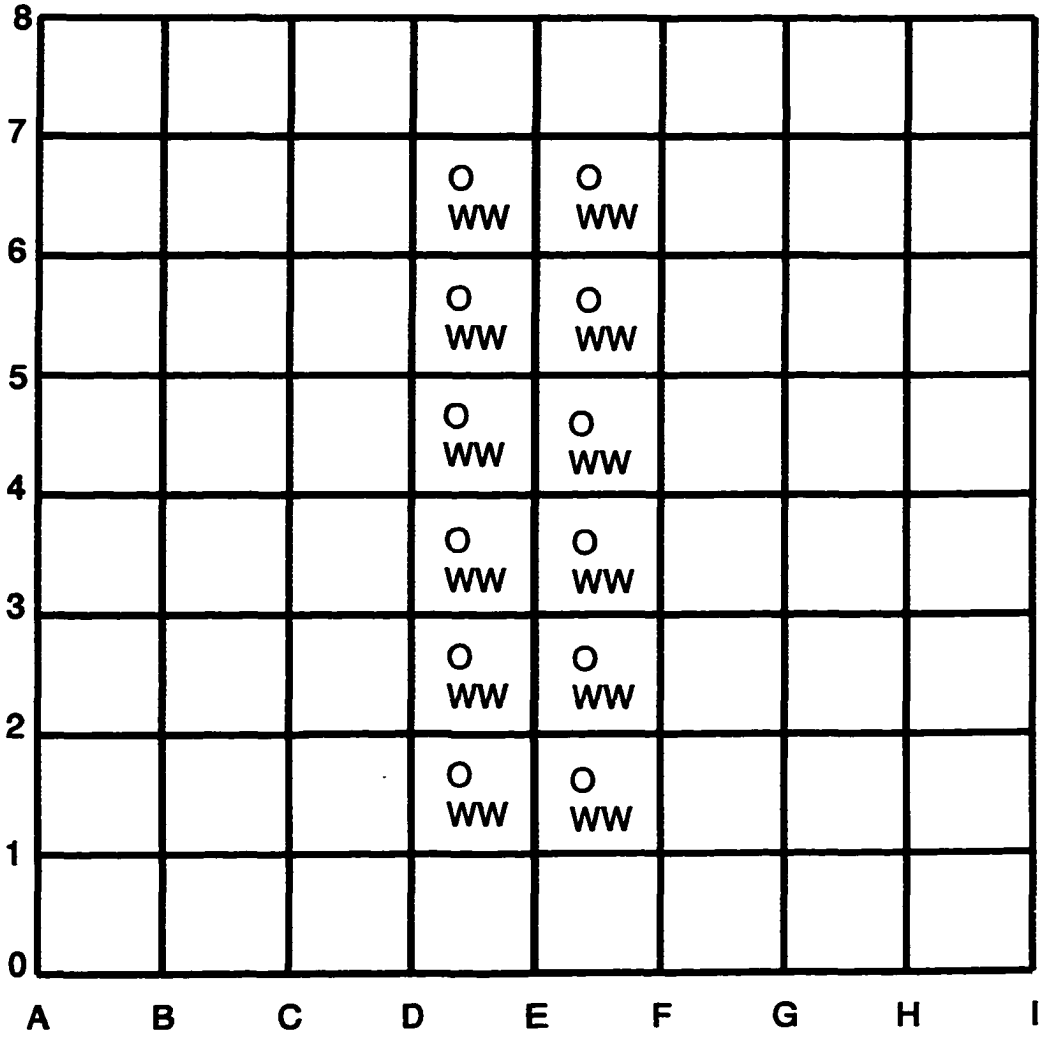
Sticky traps were used for surveying the dispersal differences of first and second instars onto the forest floor in different cutting treatments. A platform was made using 3 wooden stakes measuring 117 cm long by 3.8 cm by 2.2 cm and topped with a 1 cm thick piece of plywood measuring 40 cm by 40 cm. This platform which was used as a support for a sticky trap was positioned horizontally about 90 cm above the ground, but sloped slightly to drain rain. A piece of waxed paper measuring 38 cm by 32 cm was cut from a 2-l milk carton. The waxed paper was stapled to the top of the platform and covered with a thin layer of Tree Tanglefoot®.

Sticky traps were placed under the crown dripline of each marked host tree. Two traps were placed under each white spruce (north and south sides), one under each black spruce (south side), one under balsam fir (south side), and one in the open or under non-host trees about 5 m away from host tree crowns in each selected subplot of the uncut treatment and the two partial cuts (Figures 4 and 5). The layout of



LEGEND:
WW = 2 traps under white spruce;
F = 1 trap under balsam fir;
B = 1 trap under black spruce;
O = 1 trap in open or under non-host tree;
No water trap in the centre of each selected subplot of the clearcut.

Figure 4 Layout of sticky and water traps for sampling small and large larval dispersal on the forest floor in plot B1 near Black Sturgeon Lake in 1994 and 1995.



LEGEND:
WW = 2 traps under white spruce;
O = 1 trap in open.

Figure 5 Layout of sticky and water traps for sampling small and large larval dispersal on the forest floor in plot 4 near Black Sturgeon Lake in 1994 and 1995.

sticky traps in the strip clearcut was 7 traps 10 m away from each other on each gridline of 3 gridlines: from G2 to I2, G4 to I4 and G6 to I6 (Figure 4). These traps were numbered from 1 to 7 from gridline G to gridline I. As well, a sticky trap was placed in the centre of each selected subplot of the strip clearcut of plot B1. Shrubs above sticky traps were removed to maintain a clear path for the dispersal of first- and second-instar larvae.

All the sticky traps were checked by counting the small larvae and by replacing the milk cartons and the Tree Tanglefoot® at a 2-day interval for first-instar larvae and at a 4-day interval for second-instar larvae. Carlson *et al.* (1988) and Jennings *et al.* (1983) deployed their sticky traps at the beginning of the small larval dispersal and retrieved them at the end of the dispersal. Then the sticky paper was examined in a laboratory. However, our sticky traps were checked at 2 or 4 day intervals to avoid miscounting the small larvae caused by shrinking and moulding. Sticky trap sampling for first-instar dispersal was conducted from 7 July to 9 August 1994 and from 1 to 30 July 1995. Second- instar larval dispersal was sampled with the same sticky trap stations from 13 May to 1 June 1995.

WATER TRAP SAMPLING

A plastic tray measuring 52 cm long, 25 cm wide and 6 cm deep was employed as a water trap to sample the large larvae

dispersing downwards from the overstory in the different cut treatments. Except for the fact that there was no water trap in the centre of each selected subplot in the strip clearcut, other locations were the same as described for the sticky traps (Figures 4 and 5). Herbs and shrubs immediately above the traps were cleared away to maintain the dispersal larvae falling into the traps. Water traps were not deployed in the strip clearcut in 1995 because of the zero catch result in 1994.

Water trap sampling was conducted from 15 June to 3 July 1994 and from 12 June to 27 June 1995. Each trap was checked at 2-day intervals to record the number and instars of spruce budworm larvae that had dropped. Water in each trap was cleaned by filtering and the volume was topped up with fresh water at each visit. Two or four drops of Kodak Photo-Flo 200® solution were added during each visit. The Photo-Flo solution decreased the surface tension of water in each trap to ensure that large larvae sink to the bottom of each trap.

Coniferous seedling defoliation and density assessment were conducted after water trap sampling on 3 July 1994 and on 27 June 1995. The middle of the south side of each water trap was considered as the central point of a small circular subplot with a 1.128 m radius. All seedlings of white spruce, black spruce and balsam fir within the small circular subplot were measured for crown widths and heights and for defoliation intensity by using the Fettes methods.

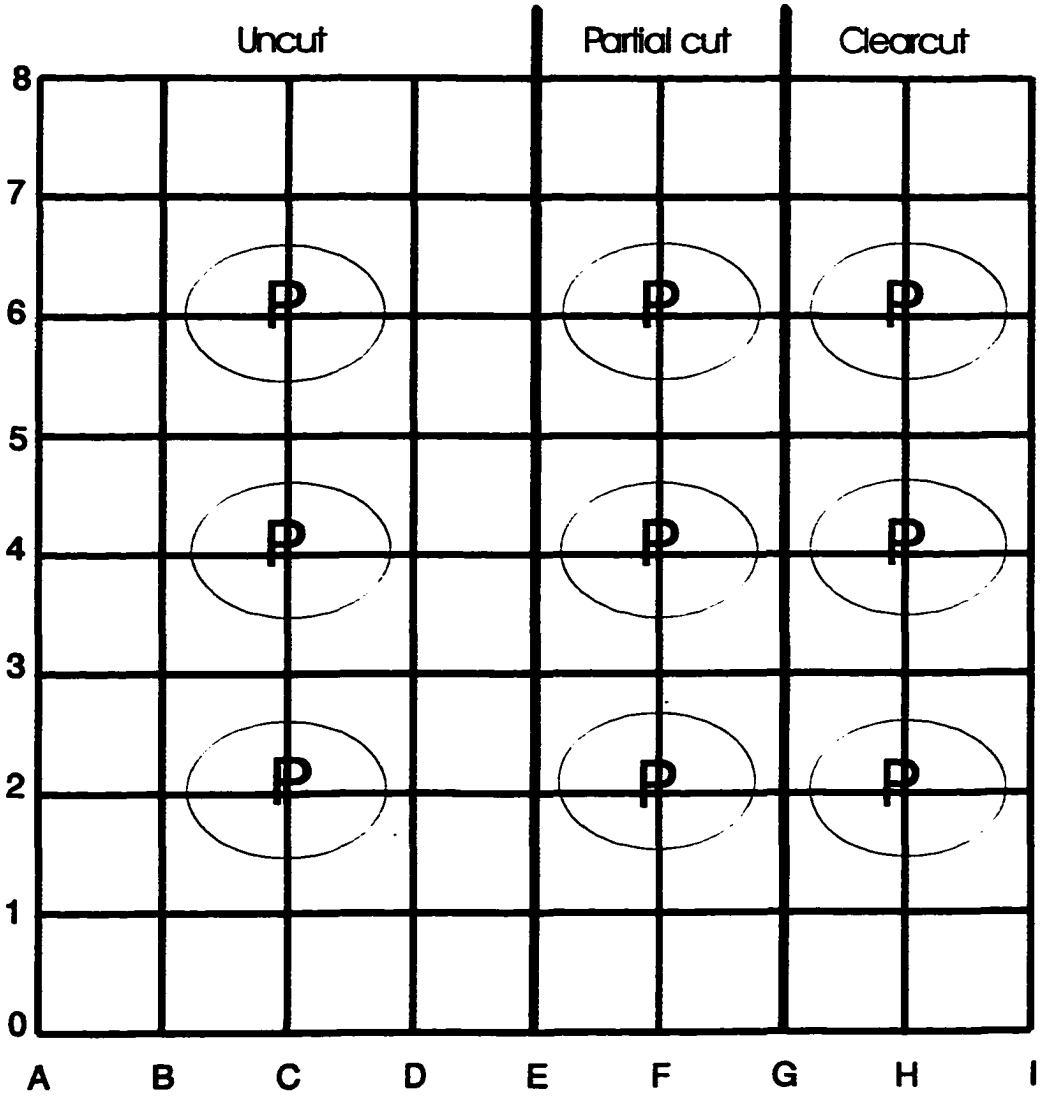
PHEROMONE TRAP SAMPLING

Male moth responses to pheromone traps in different cut treatments were observed. Three Multi-pher® traps were placed systematically within each treatment in plot B1 and 4 for a total of 12 pheromone traps (Figures 6 and 7). A trap was hung at a height of about 190 cm and 50 cm away from the tree trunk in a central host tree of each designed location in the uncut treatment and the two partial cuts in plots B1 and 4. The traps in the strip clearcut of plot B1 were hung at a height of about 150 cm on a wooden stake and about 50 cm away from the grid stake. Traps were 80 m away from each other. The trap nearest the road in each cut treatment was also 80 m away from the forest edge.

A Biolure® lure (Consep Inc., Bend, OR) containing 2.8 mg of 95:5 blend of E:Z-11- tetradecenal was used as bait in each trap. A VAPORTAPE II® insecticidal strip (Hercon Environmental, Emigsville, PA) containing 10% dichlorvos was placed in each trap. Pheromone traps were checked daily from 2 July to 9 August 1994 and from June 24 to July 31 1995. Daily trap checks were carried out to reduce the repellency of accumulated dead moths inside traps on trap catches (Sanders 1986b).

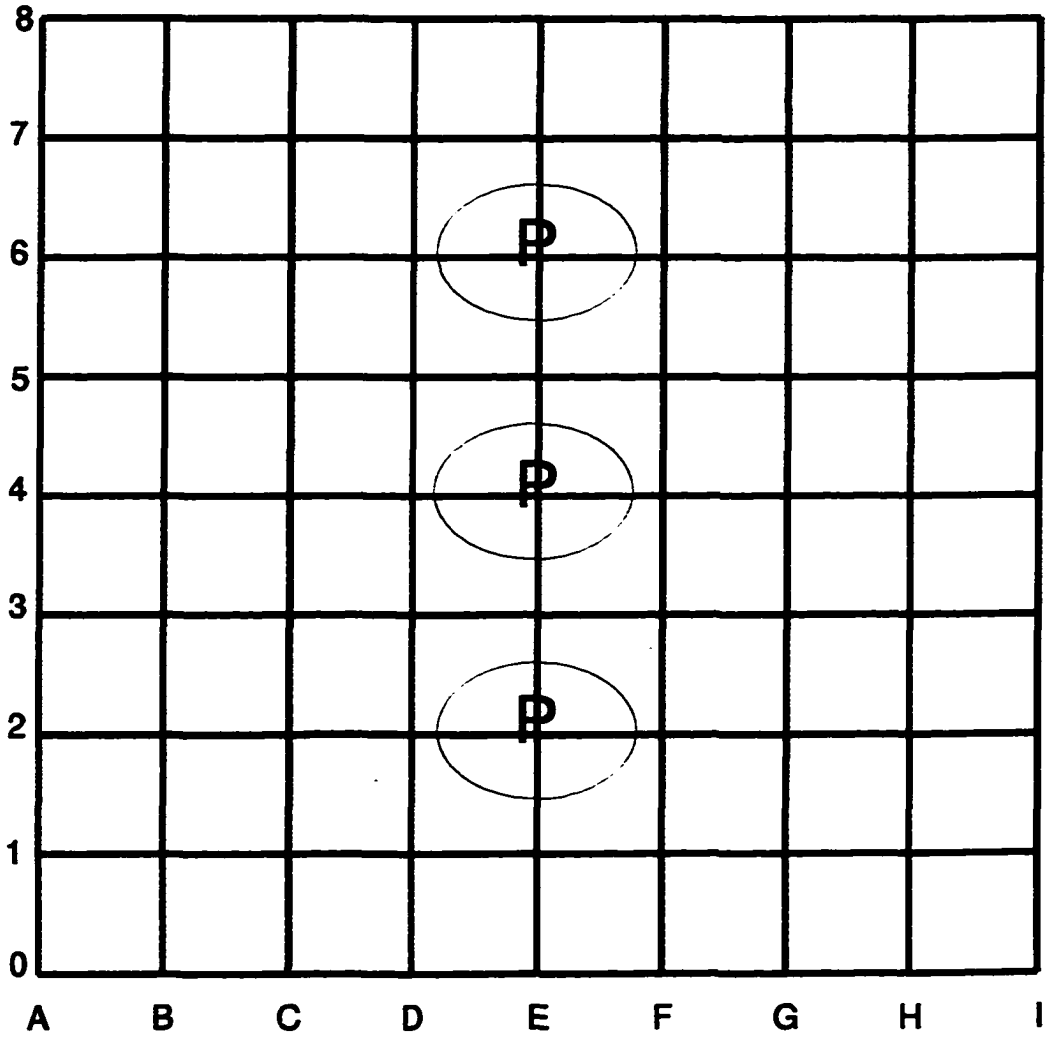
DATA ANALYSIS

Branch sample-units were standardized to make samples from different host-tree species more comparable. Compared



LEGEND:
P = 1 pheromone trap.

Figure 6 Layout of pheromone traps for sampling moth flight in plot B1 near Black Sturgeon Lake in 1994 and 1995.



LEGEND:
P = 1 pheromone trap.

Figure 7 Layout of pheromone traps for sampling moth flight in plot 4 near Black Sturgeon Lake in 1994 and 1995.

with surface area (Morris 1955) and bud count (Miller *et al.* 1972), fresh weight is the more appropriate unit to express density of all immature stages of the spruce budworm, especially when samples from different host tree species and locations are compared (Régnière *et al.* 1989). It is also easy to measure fresh weight objectively. Therefore, branch sample-units for egg mass and larval densities were standardized again at 150-g even though branch tips were trimmed at 45-cm long in field.

Budworm counts of individual sticky, water and pheromone traps at each observation time were pooled respectively for each trapping season. This led to one trap with just one total catch for a whole trapping season.

Finally, independent-sample *t*-tests (Norusis 1993) were used to test the discrepancies of larval and egg mass densities within and between treatments. The same *t*-tests were also applied to examine the catch differences of sticky, water and pheromone traps within and between treatments.

RESULTS

PLOT DESCRIPTION

After the harvest treatments, the basal area of each host and all non-host tree species and crown coverage in the uncut treatment of plot B1 were the highest when compared with the two partial cuts (Table 1). The basal area of hardwood in the partial cut of plot 4 was greater than that of all host trees, but it was not so in the uncut treatment and partial cut of plot B1 (Table 1).

Table 1. Basal area and crown closure in the uncut treatment and two partial cuts of plots B1 and 4 near Black Sturgeon Lake.

Treatment/ plot	Tree	Basal area 1995 (m^2/ha)	Crown closure 1994 (%)
Uncut/B1	balsam fir	6.29	
	black spruce	0.51	
	white spruce	5.04	
	hardwood	11.78	
	total	23.62	65 - 75
Partial cut/B1	black spruce	0.29	
	white spruce	3.96	
	hardwood	0.34	
	total	4.59	15 - 25
Partial cut/4	white spruce	3.50	
	hardwood	7.50	
	total	11.00	35 - 45

BRANCH SAMPLING

Egg Mass Densities

Within the uncut treatment, egg mass density on white spruce was significantly greater than on balsam fir and on

black spruce during both 1994 and 1995 (Table 2). However, there were no significant differences in egg mass densities between balsam fir and black spruce during the same years. Similarly, in the partial cut of plot B1 in 1994 and 1995, egg mass density on white spruce was significantly greater than on black spruce.

Table 2. Egg mass density for each host tree species in the uncut treatment and two partial cuts of plots B1 and 4 near Black Sturgeon Lake in 1994 and 1995.

Treatment/ plot	Host tree (n = 12)	Egg masses per 150-g branch tip 1994 (SE)	1995 (SE)
Uncut/B1	balsam fir	3.0a (1.07)	1.4a (0.53)
	black spruce	2.4a† (0.74)	1.5a† (0.59)
	white spruce	8.8b* (1.31)	5.6b† (1.01)
Partial cut/B1	black spruce	2.3a† (0.53)	1.4a† (0.27)
	white spruce	4.4b† (0.64)	7.2b† (1.11)
Partial cut/4	white spruce	4.9 † (0.99)	2.0 * (0.34)

Means followed by the same letter within a treatment in each year are not significantly different as determined by *t*-tests at $\alpha \leq 0.05$; means followed by the same symbol for a tree species between treatments in each year are not significantly different as determined by *t*-tests at $\alpha \leq 0.05$.

Egg mass density on black spruce in the uncut treatment was not significantly different from that in the partial cut of plot B1 in both 1994 and 1995 (Table 2). In contrast in 1994, egg mass density on white spruce in the uncut treatment was significantly greater than that in the two partial cuts which were almost the same. However, in 1995, egg mass density on white spruce in the uncut treatment was not

significantly different from that in the partial cut of plot B1, but both were significantly greater than that in the partial cut of plot 4 (Table 2).

Second Instar Densities

Within the uncut treatment, second-instar larval density on white spruce was significantly greater than that on balsam fir and black spruce. The difference in larval density between balsam fir and black spruce was not significant (Table 3). In the partial cut of plot B1, larval density on white spruce was significantly greater than on black spruce (Table 3).

The larval density on white spruce in the uncut treatment was not significantly different from that in the partial cut of plot B1 in 1995, but both were significantly greater than that in the partial cut of plot 4 (Table 3). The larval density on black spruce in the uncut treatment was significantly lower than that in the partial cut of plot B1 in 1995.

Large Larval Densities

Within the uncut treatment in 1994, the large larval density on black spruce was significantly lower on white spruce and balsam fir. The difference in larval densities between white spruce and balsam fir was not significant (Table 4). In 1995 the large larval density on white spruce was significantly greater than on both balsam fir and on black spruce which in turn were not significantly different

Table 3. Second-instar larval density for each host tree species in the uncut treatment and two partial cuts of plots B1 and 4 near Black Sturgeon Lake in 1995

Treatment/ plot	Host tree (n = 12)	Larvae per 150-g branch tip 1995 (SE)
Uncut/B1	balsam fir	4.4a (0.77)
	black spruce	5.5a* (1.29)
	white spruce	15.4b† (2.61)
Partial cut/B1	black spruce	11.0a† (1.81)
	white spruce	16.3b† (1.83)
Partial cut/4	white spruce	9.7 * (1.42)

Means followed by the same letter within a treatment are not significantly different as determined by *t*-tests at $\alpha \leq 0.10$; means followed by the same symbol for a tree species between treatments are not significantly different as determined by *t*-tests at $\alpha \leq 0.10$.

Table 4. The large larval density for each host tree species in the uncut treatment and two partial cuts of plots B1 and 4 near Black Sturgeon Lake in 1994 and 1995.

Treatment/ plot	Host tree (n = 12)	Larvae per 150-g branch tip 1994 (SE)	1995 (SE)
Uncut/B1	balsam fir	8.9b (1.86)	12.4a (2.62)
	black spruce	2.5a* (0.81)	7.3a* (1.61)
	white spruce	12.7b* (1.87)	22.5b* (3.09)
Partial cut/B1	black spruce	2.1a* (0.77)	7.0a* (2.04)
	white spruce	18.1b* (2.54)	24.5b* (3.53)
Partial cut/4	white spruce	11.5 * (2.04)	20.0 * (3.71)

Means followed by the same letter within a treatment in each year are not significantly different as determined by *t*-tests at $\alpha \leq 0.05$; means followed by the same symbol for a tree species between treatments in each year are not significantly different as determined by *t*-tests at $\alpha \leq 0.05$.

from each other (Table 4). Within the partial cut of plot B1 in both 1994 and 1995, the large larval density on black spruce was significantly lower than on white spruce (Table 4).

Between treatments, there were no significant differences in the large larval density on white and black spruces during 1994 and 1995 (Table 4).

Large larval densities on white spruce and balsam fir in the uncut treatment and two partial cuts were significantly greater than overwintering second-instar larval densities in 1995, but the same significance was not seen on black spruce (Table 5).

Table 5. Comparison of overwintering second-instar and large larvae densities for each host tree species in the uncut treatment and two partial cuts of plots B1 and 4 near Black Sturgeon Lake in 1995.

Treatment/ plot	Host tree (n = 12)	Larvae per 150-g branch tip L 2 (SE)	LL (SE)
Uncut/B1	balsam fir	4.4a (0.77)	12.4b (2.62)
	black spruce	5.5a (1.29)	7.3a (1.61)
	white spruce	15.4a (2.61)	22.5b (3.09)
Partial cut/B1	black spruce	11.0a (1.81)	7.0a (2.04)
	white spruce	16.3a (1.83)	24.5b (3.53)
Partial cut/4	white spruce	9.7a (1.42)	20.0b (3.71)

L2 = second instar and LL = large larvae.
Means followed by the same letter for the same tree species within a treatment are not significantly different as determined by *t*-tests at $\alpha \leq 0.10$.

Overstory Defoliation Indices

Within the uncut treatment, defoliation on white spruce was significantly greater when compared with balsam fir and black spruce in both 1994 and 1995 except in 1994 when defoliation on white spruce was not significantly greater than on balsam fir (Table 6). Defoliation on balsam fir was significantly greater than on black spruce in 1994 while it was not significantly different in 1995 (Table 6). Within the partial cut of plot B1 in 1994 and 1995, defoliation on white spruce was significantly greater than on black spruce (Table 6).

Between treatments, defoliation on white spruce was not significantly different in 1994, whereas in 1995 defoliation on white spruce in the uncut treatment was significantly greater than in the two partial cuts which in turn were not significantly different from each other (Table 6). Defoliation on black spruce in the uncut treatment was not significantly different from that in the partial cut of plot B1 during both 1994 and 1995 (Table 6).

Defoliation indices of individual branch tips were plotted against the large larval number of corresponding individual branch tips when data in 1994 and 1995 were pooled for each host tree species. There was no positively increasing trend (Figure 8).

Table 6. The overstory defoliation index determined by the Fettes' method for each host tree species in the uncut treatment and two partial cuts of plots B1 and 4 near Black Sturgeon Lake in 1994 and 1995.

Treatment/ plot	Host tree (n = 12)	Mean defoliation index 1994 (SE)	1995 (SE)
Uncut/B1	balsam fir	2.3b (0.38)	0.9a (0.19)
	black spruce	0.8a* (0.24)	1.0a* (0.25)
	white spruce	3.4b* (0.42)	4.2b* (0.44)
Partial cut/B1	black spruce	0.8a* (0.22)	0.8a* (0.24)
	white spruce	4.0b* (0.52)	2.6b† (0.34)
Partial cut/4	white spruce	2.8 * (0.39)	2.3 † (0.45)

Means followed by the same letter within a treatment in each year are not significantly different as determined by *t*-tests at $\alpha \leq 0.05$; means followed by the same symbol for a tree species between treatments in each year are not significantly different as determined by *t*-tests at $\alpha \leq 0.05$.

STICKY TRAP SAMPLING

Within Treatments

Within the uncut treatment and two partial cuts in 1994 and 1995, there were no significant differences in trap catch of first and second instars between the south and north side of white spruce except for second instar in 1995 when a significant difference was obtained in the partial cut of plot 4 (Table 7).

Within the uncut treatment for first and second instars in 1994 and 1995, none of the trap catches in five locations was significantly different (Table 7).

Within the partial cut of plot B1, there were no

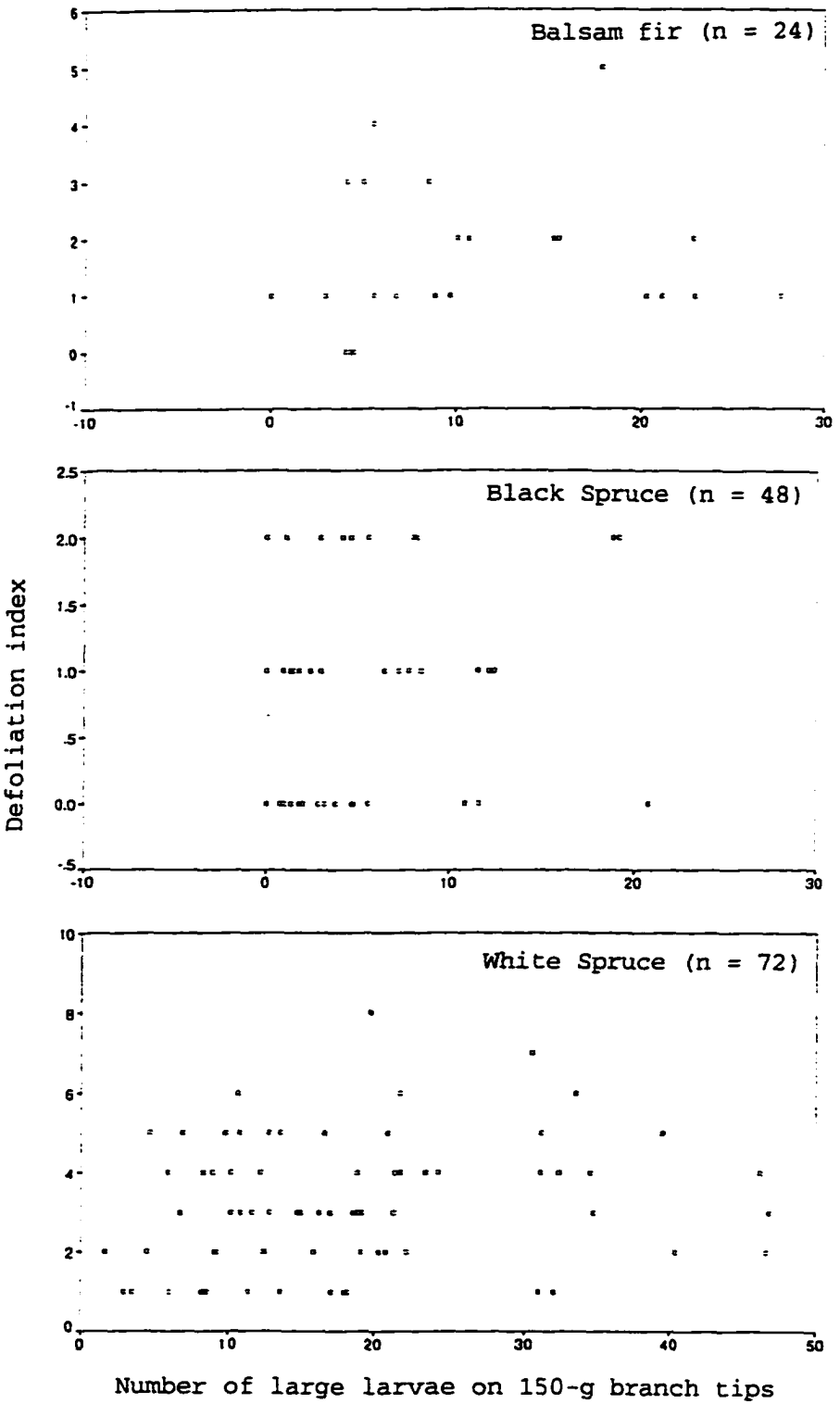


Figure 8. Overstory defoliation indices (determined by Fettes' method) of individual branch tips plotted against the number of large larvae on corresponding individual 150-g branch tips from plots B1 and 4 near Black Sturgeon Lake in 1994 and 1995.

significant differences in the number of first and second instars caught between the open and the north side of white spruce in 1994 and 1995 (Table 7). However, significant differences were seen in 1995 between the number of first and second instars caught in the south side of white spruce and in the open. There were no significant differences in first and second instars caught from black spruce and the south and north sides of white spruce except in 1994 when the number caught on the north side was significantly greater (Table 7). Catches of first instar in 1994 and second instar in 1995 in the open were significantly greater than those from black spruce whereas for first instar in 1995, there was no significant difference (Table 7).

Within the partial cut of plot 4, there were no significant differences for first and second instars caught from three locations in 1994 and in 1995, except the number of second instar caught on the south side of white spruce was significantly less in 1995 (Table 7).

Between Treatments

For first instar in 1994, trap catch in the uncut treatment was significantly lower than that under each corresponding location in the other three treatments which in turn were not significantly different from each other (Table 7). One exception is that there was no significant difference in catch under black spruce, and also no significant difference in catch in the open between the uncut treatment

and the partial cut of plot 4 (Table 7). The other exception is that trap catch in the open in the strip clearcut was significantly greater than that in the two partial cuts (Table 7).

For first instar in 1995, there were no significant differences among all treatments except that the trap catch under the southern side of white spruce in the partial cut of plot B1 was significantly greater than that in the partial cut of plot 4 (Table 7).

For second instar in 1995, the number of larvae caught in the uncut treatment was significantly less than from the other three treatments which were in turn not significantly different from each other (Table 7). The exception is that the trap catch under the south side of white spruce in the uncut treatment was not significantly lower than that in the partial cut of plot 4 which in turn was significantly lower than that in the partial cut of plot B1.

The small larval catch (larvae per 3 sticky traps during a whole season) on the three gridlines in the strip clearcut of plot B1 was low in the middle and high at both sides in 1994 and 1995 (Table 8).

Table 7. Sticky trap catch in all treatments of plots B1 and 4 near Black Sturgeon Lake in 1994 and 1995.

Treatment/plot Trap location (n = 12 traps)	larvae per trap during the entire season L1 1994(SE)	 L1 1995(SE)	 L2 1995(SE)
Uncut/B1			
balsam fir	2.4a (0.60)	0.9a (0.31)	1.8a (0.72)
black spruce	1.5a† (0.26)	0.9a* (0.26)	1.6a* (0.34)
N. white spruce	1.6a* (0.38)	2.1a* (0.61)	2.2a* (0.32)
S. white spruce	1.4a* (0.36)	1.9a*‡ (0.53)	2.3a* (0.54)
open or nonhost	2.5a* (0.56)	1.2a* (0.37)	2.5a* (0.47)
Partial cut/B1			
black spruce	2.6a† (0.47)	2.1ac* (0.60)	6.1a† (0.80)
N. white spruce	4.1c† (0.50)	2.5ac* (0.60)	6.3ac† (0.99)
S. white spruce	4.3ac† (0.75)	3.3a†‡ (0.50)	5.1a† (0.56)
open	4.3c‡ (0.68)	1.3bc* (0.31)	8.6bc† (0.86)
Clear cut/B1			
open	8.1 † (1.15)	0.7 * (0.22)	7.7 † (0.90)
Partial cut/4			
N. white spruce	3.8a† (0.77)	1.6a* (0.31)	6.0a† (1.02)
S. white spruce	3.5a† (0.53)	1.3a* (0.43)	3.6b* (0.43)
open	3.3a*‡ (0.62)	1.0a* (0.33)	6.1a† (0.88)

L1 = first instar, L2 = second instar, N. = north side and S. = south side.
Means followed by the same letter within a treatment in each year are not significantly different as determined by *t*-tests at $\alpha \leq 0.05$; means followed by the same symbol for the same trap location among treatments in each year are not significantly different as determined by *t*-tests at $\alpha \leq 0.05$.

Table 8. Total catch of three sticky traps during the entire season on the gridlines of the strip clearcut in plot B1 near Black Sturgeon Lake in 1994 and 1995.

Instar/year	Trap on gridline G to I 1	2	3	4	5	6	7
				(larvae)			
L1/1994	24	21	16	18	18	14	17
L1/1995	4	4	1	3	3	2	4
L2/1995	24	24	30	21	17	19	21

WATER TRAP SAMPLING

Within the uncut treatment and two partial cuts during 1994 and 1995, there was no significant difference in water trap catch between the north and the south side of white spruce (Table 9).

Within the uncut treatment in 1994 and 1995, trap catch under either the north or south side of white spruce was significantly greater than that under the other three locations, except in 1994 when trap catch under the north side of white spruce was not significantly greater than under balsam fir (Table 9). There were no significant differences in trap catch among balsam fir, black spruce and in the open during the same years.

Within the partial cut of plot B1 in 1994 and 1995, trap catch decreased significantly from either the north or south side of white spruce to black spruce and with the lowest catch found in the open (Table 9). Within the partial cut of plot 4 in 1994 and 1995, trap catch from the north or south sides of white spruce was significantly greater than in the open (Table 9).

Between treatments, there were no significant differences in water trap catch in both 1994 and 1995 when a comparison was made among the corresponding trap locations (Table 9).

Water traps in the strip clearcut of plot B1 caught no budworm in 1994 even though the traps nearest the host trees were just 10 m away.

Table 9. Water trap catch in the uncut treatment and two partial cuts of plots B1 and 4 near Black Sturgeon Lake in 1994 and 1995.

Treatment/plot Trap location (n = 12 traps)	larvae per trap during the entire season 1994 (SE)	 1995 (SE)
Uncut/B1		
balsam fir	1.9ac (0.53)	1.8a (0.53)
black spruce	1.3at (0.33)	1.4at (0.47)
N. white spruce	3.1cdt (0.58)	6.0bt (1.17)
S. white spruce	4.9bdt (0.93)	7.1bt (2.08)
open or nonhost	0.8at (0.22)	0.5at (0.42)
Partial cut/B1		
black spruce	1.5at (0.42)	2.1at (0.43)
N. white spruce	4.7bt (0.87)	4.8bt (0.99)
S. white spruce	4.5bt (0.91)	5.7bt (1.05)
open	0.3ct (0.19)	0.3ct (0.14)
Partial cut/4		
N. white spruce	3.3bt (0.62)	3.3bt (0.63)
S. white spruce	3.2bt (0.61)	4.0bt (0.70)
open	0.8at (0.39)	0.1at (0.08)

N. = north side and S. = south side.
Means followed by the same letter within a treatment in each year are not significantly different as determined by *t*-tests at $\alpha \leq 0.05$; means followed by the same symbol for the same trap location among treatments in each year are not significantly different as determined by *t*-tests at $\alpha \leq 0.05$.

Within all treatments in 1994 and 1995, seedling density of balsam fir was much higher than that of white and black spruce (Table 10). Seedling densities in the uncut treatment were much higher than in the strip clearcut and two partial cuts in 1994 and 1995 (Table 10). All coniferous seedlings surveyed around water traps were lower than 45 cm. Generally, budworm defoliation on coniferous seedlings in all the treatments was invisible in 1994 and 1995 (Table 10).

Individual water trap catches were plotted against the number of large larvae of corresponding individual branch tips when data in 1994 and 1995 were pooled for each host tree species. There was no positively increasing trend (Figure 9).

Table 10. Coniferous seedling density (seedlings per 4 m^2 circular subplot) and defoliation index determined by Fettes' method in all treatments of plots B1 and 4 near Black Sturgeon Lake in 1994 and 1995.

Treatment/plot	Balsam fir		White spruce		Black spruce	
Year	DEN	DEF	DEN	DEF	DEN	DEF
Uncut/B1 (n = 60 circular subplots)						
1994	4.62	0.3	0.05	0.3	0.00	0.0
1995	5.05	0.0	0.08	0.0	0.02	0.0
Partial cut/B1 (n = 48 circular subplots)						
1994	1.13	0.1	0.00	0.0	0.00	0.0
1995	1.52	0.1	0.02	0.0	0.00	0.0
Clearcut/B1 (n = 21 circular subplots)						
1994	0.43	0.0	0.00	0.0	0.00	0.0
Partial cut/4 (n = 36 circular subplots)						
1994	0.94	0.0	0.03	0.0	0.00	0.0
1995	1.67	0.0	0.03	0.0	0.00	0.0

DEN = seedling density; DEF = defoliation index.

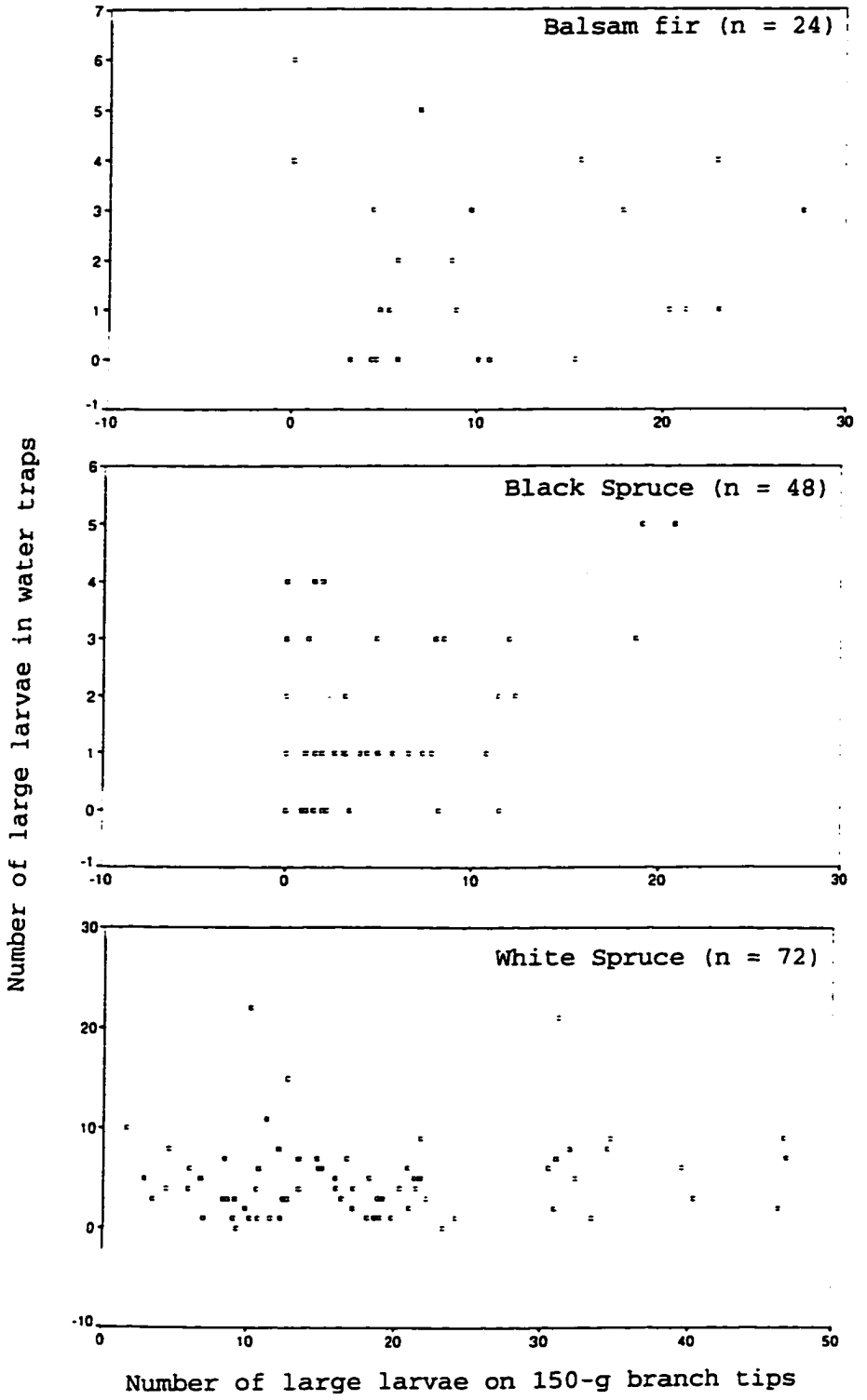


Figure 9. Individual water trap catches plotted against the number of large larvae on corresponding individual 150-g branch tips from plots B1 and 4 near Black Sturgeon Lake in 1994 and 1995.

PHEROMONE TRAP SAMPLING

Trap catch significantly decreased from the two partial cuts to the uncut treatment and then to the strip clearcut in both 1994 and 1995 except in 1994 when trap catch in the partial cut of plot B1 was not significantly greater than in the uncut treatment (Table 11). There was no significant difference between the two partial cuts in both 1994 and 1995 (Table 11).

Table 11. Pheromone trap catch in all treatments of plots B1 and 4 near Black Sturgeon Lake in 1994 and 1995.

Treatment/plot	Moths per trap during the entire season			
(n = 3 traps)	1994	(SE)	1995	(SE)
Uncut/B1	763.7c	(141.96)	285.0c	(9.50)
Partial cut/B1	1091.3ac	(79.18)	412.3a	(20.33)
Clearcut/B1	288.3b	(29.20)	139.0b	(16.64)
Partial cut/4	1342.7a	(91.20)	381.7a	(26.77)

Means followed by the same letter between treatments in each year are not significantly different as determined by *t*-tests at $\alpha \leq 0.10$.

DISCUSSION

SMALL LARVAL DISPERSAL

Filtering Effect

The hypothesis that thinning forest canopy would increase larval dispersal to the forest floor is generally supported by the results for small larval dispersal. In most cases, the number of small larvae dispersing to the forest floor in the two partial cuts or the strip clearcut were significantly greater than in the uncut treatment in 1994 and 1995. The results in the strip clearcut are similar to those obtained by Jennings *et al.* (1983). In 8 of 9 cases, egg mass or second-instar larval densities in the two partial cuts were not greater than in the uncut treatment in 1994 and 1995. Furthermore, considering the basal area of host trees in the uncut treatment and the two partial cuts, total numbers of egg masses and second-instar larvae in the uncut treatment were much greater than in the two partial cuts. Therefore, opening up the stand leads to more small larvae falling to the forest floor.

This dispersal can be explained by the stand properties of the uncut treatment and two partial cuts. A progressive filtering effect of plentiful host and non-host tree crowns on the dispersing small larvae largely diminishes the number that would be expected on sticky traps. This filtering effect may be a function of stand density and air currents within the stands (Beckwith and Burnell 1982). Stand densities can

be represented by the basal area of all tree species. The basal area of all tree species in the uncut treatment was much greater than in the two partial cuts. Thus, there were plenty of host and non-host tree crowns in the uncut treatment to act as a filter. Similarly, crown closure in the uncut treatment was much greater than in the two partial cuts. It is likely that air currents in the two partial cuts or in the strip clearcut would be stronger than in the uncut treatment. The strong filtering effect in the uncut treatment explains why a significantly lower number of the small larvae was trapped there.

Abnormal Result for First Instar in 1995

Trap catch for first instar in the strip clearcut and two partial cuts in 1995 was expected to be significantly higher than in the uncut treatment, but it was not. Thus the hypothesis that thinning forest canopy would increase larval dispersal to the forest floor was not supported for the first instar dispersal in 1995. The shrubs, mainly young aspen suckers, in the strip clearcut and the two partial cuts were much taller than the sticky traps in late summer 1995. Their closure was about 90%. The shrubs around the sticky traps were trimmed to some extent in the two partial cuts and the strip clearcut. However, the filtering effect of those dense shrubs and the aerial dispersal of the small larvae reduced the number of first-instar larvae which would be expected on the sticky traps in the strip clearcut and the two partial

cuts in 1995. Lower egg mass density in 1995 may have contributed to the abnormal result, together with first instar dispersal mainly within host tree crowns as reported by Régnière and Fletcher (1983). As a result, sticky trap catch in the two partial cuts and the strip clearcut was not significantly greater than in the uncut treatment.

Aerial Dispersal

Sticky trap catches under different host tree species and in the open were similar within the uncut treatment or within any one of the two partial cuts in 1994 and 1995. This suggests that the small larvae disperse in a combination of horizontal and vertical movements in the air within the uncut treatment and within each of the two partial cuts. Morris and Mott (1963) also reported that the dispersal of the small larvae is aerial and gives rise to lateral exchanges from crown to crown. Therefore, small larval dispersal is a major factor in the redistribution of budworm population within and between forest stands (Jennings *et al.* 1983; Morris and Mott 1963).

Overwintering Second Instar Density in 1995

After the spring dispersal, large larval density should be generally lower than overwintering second-instar larval density before the spring dispersal. However, most large larval densities sampled in June 1995 were significantly greater than overwintering second-instar larval densities sampled in May 1995. This anomaly may be explained by

reference to the results obtained by Régnière *et al.* (1989) who found that fewer than half (40.2%) of the overwintering second-instar larvae is within a 45-cm tip section of a balsam fir branch while 74.5 to 83% of third to sixth instars is within the tip section. This result suggests that a whole branch or branch section longer than 45 cm should be used to sample overwintering second-instar larval density, especially when a comparison is made with the large larval density after dispersal.

LARGE LARVAL DISPERSAL

Mass Dropping

The hypothesis that thinning forest canopy would increase larva dispersal to the forest floor is not supported by the results for large larval dispersal. Water trap catches in the two partial cuts were not significantly different from that in the uncut treatment in 1994 and 1995. This was the result of the large larval densities which were not significantly different among the uncut treatment and the two partial cuts in 1994 and 1995.

The similarity in the water trap catches for the large larvae can be explained by the weight of the mature larvae, which is at least 1500-fold that of second-instar larvae (Mattson *et al.* 1988). As a result, the large larvae drop down vertically and cannot be filtered by tree crowns as easily as the small larvae. The lowest water trap catch in

the open within the uncut treatment or in any one of the two partial cuts as well as a complete zero catch in the strip clearcut also support the contention that there is little lateral dispersal for the large larvae. Additionally, dispersal leading to inter-tree redistribution of large larvae is much less common than for the small larvae (Morris and Mott 1963).

Water trap results suggest that sunlight and air current contributed little to the mass dropping of the large larvae in spite of their increases in the partial cuts. As well, the suggestion is supported by nonsignificant difference in water trap catches between the south and north side of white spruce.

Effect on Young Seedlings

The budworm defoliation on young seedlings under 45 cm in all the treatments was undetectable as Gordon (1985) reported. There are many unfavourable factors on the ground such as less food available, abundant ground predators, and temperature and sunlight differences. These may prevent the large larvae from feeding much on young seedlings, induce early pupation or mortality.

The densities of coniferous seedlings were very low in the two partial cuts and strip clearcut. This indicates that the harvesting process destroyed the young seedlings that had existed there.

RELATIONSHIP BETWEEN LARGE LARVAL DENSITY AND OVERSTORY DEFOLIATION OR WATER TRAP CATCH

For each host-tree species, there should have been a positively increasing trend between defoliation indices and large larval number on individual branch tips. But this pattern was not seen even though data in 1994 and 1995 was pooled by tree species.

The abnormality may be explained by the large larval distribution. The larval distribution is almost random at densities below 0.1 larva per branch tip, but is aggregated at higher densities (Régnière and Sanders 1983). The large larval densities ranged from 2.1 to 24.5 larvae per 150-g branch tip in 1994 and 1995. The aggregation may vary over the season such that larval aggregation intensity on a branch tip sampled in early June for large larval density may not represent the defoliation produced on another branch tip sampled in late July or early August even though they were from the same tree. There were also other factors such as predators in tree crowns, large larval movement within a tree crown and large larval dropping. All these factors together may flatten the expected positive relationship between large larval density and defoliation.

Similarly, there was no discernable pattern in the relationship between individual water trap catches and the number of large larvae on individual branch tips. Aggregated distribution can result in large numbers of the large larvae

within a sampled branch tip, but the sample may not be representative of all the other branches of the same tree. Conversely, the water trap catch represents large larvae dropping from several branches of the same tree and therefore the distributions are less aggregated. The conclusion can be drawn that more than one branch should be sampled to find the relationship between water trap catches and large larval densities. Other factors affecting this pattern are predators in the trees and on the ground, large larvae escaping from water traps and drifting during large larval drop.

PHEROMONE TRAP SAMPLING

Except in the strip clearcut, the hypothesis that male moth catch in the uncut treatment should be greater than in the two partial cuts was not supported. The larval numbers of the spruce budworm in a given area depend to a great extent on the quantity of foliage available. The final moth count in an area is determined by the number of large larvae. Therefore, the number of moths in an area is influenced largely by the quantity of host tree foliage (Allen *et al.* 1986). Due to the greater basal area of host tree species in the uncut treatment than in any of the two partial cuts and to the nonsignificant difference in large larval densities between the uncut treatment and the two partial cuts, the number of large larvae and moths in the uncut treatment would be greater than that in the two partial cuts. However, a

greater trap catch for male moths in the uncut treatment relative to the two partial cuts was not observed.

This can be explained by two influences. First, pheromone amount per Biolure is equivalent to that of a virgin female. The attraction of pheromone traps to male moths in the uncut treatment was weakened by the competition between the pheromone traps and the large number of female moths in the uncut treatment when compared with the number of females in the two partial cuts. This probably resulted in lower trap catches in the uncut treatment and higher trap catches in the two partial cuts. Second, reduced canopy density in the two partial cuts might carry pheromone plumes more efficiently in the stand and attract more male moths to the traps.

Two suggestions can be made from the results of this study to improve the estimation of spruce budworm larval density indirectly through a pheromone monitoring system. First, forest stands can be classified into different strata according to the basal area of all tree species and all host tree species before pheromone trap catches and larval or egg-mass densities from multiple plots are pooled. Only then can data within each stratum be pooled. Correlations between moth catches and larval or egg-mass densities should be improved significantly by using this stratification. Second, there are many openings in natural forests. Pheromone traps should be set up away from those openings in natural forest stands. If pheromone traps were set up within the openings or on the

edge of openings, trap catches might be increased disproportionately.

WHAT ABOUT WHITE SPRUCE REGENERATION

With the view of regulating budworm population density, thinning stands could result in greater mortality of small larval population because these fallen larvae rarely climb back to the host trees (Régnière and Fletcher 1983). Thus, the possibility of spruce budworm damage on seed trees left for seed production might be decreased.

It appeared that regenerating white spruce seedlings in the two partial cuts and strip clearcut would not be damaged much by spruce budworm if the spruce regenerates abundantly. This is suggested from the observations that large larvae do not drop in large number from the trees in a more open stand and budworm rarely damage young seedlings.

Furthermore, the moss or lichen layer was wiped out. Without moss or lichen, white spruce may regenerate more abundantly. A field survey will be necessary to investigate white spruce regeneration in the two partial cuts and strip clearcut. It is hoped that white spruce seedling establishment will be common in the two partial cuts and strip clearcut as reported by Putman and Zasada (1986) and Wurtz and Zasada (1986).

CONCLUSIONS

Results from field survey, branch sampling, and sticky, water and pheromone trap samplings near Black Sturgeon Lake during 1994 and 1995 indicate:

1. the harvesting process destroyed most coniferous seedlings that existed before harvest treatments. It is still too early to conclude if more white spruce will regenerate within a partial cut where the stand was thinned and white spruce was left as seed trees or within a strip clearcut;
2. budworm (egg masses, second instar and large larvae) density on white spruce is always higher when compared with that of balsam fir and black spruce;
3. in most cases, the number of small larvae falling to the forest floor in the partial cuts and strip clearcut were significantly higher during spring and fall dispersal when compared with the uncut treatment;
4. harvest treatments did not increase the number of large larvae falling to the forest floor during their dispersal. Large larvae falling to the forest floor rarely damaged young seedlings under 45 cm, of which most are balsam fir, with a few white and black spruce seedling;
5. male moth responses to pheromone traps were significantly greater in the partial cut, but significantly lower in the strip clearcut when compared to the uncut treatment. This suggests that the traps should be set up away from natural openings in forest stands. Furthermore, forest stands can be

stratified according to their basal area before pheromone trap catch data are pooled. Then the correlation between trap catch and egg mass or larval density may be improved.

REFERENCES CITED

Allen, D. C., L. P. Abrahamson, G. N. Lanier, S. R. Swier, R. S. Kelley and M. Auger. 1986. Monitoring spruce budworm (*Lepidoptera: Tortricidae*) populations with pheromone-baited traps. Environmental Entomology. 15:152-165.

Ascoli, A. and P. J. Albert. 1985. Orientation behaviour of second-instar larvae of eastern spruce budworm *Choristoneura fumiferana* (Clem.) (*Lepidoptera: Tortricidae*) in a Y-type olfactometer. Journal of Chemical Ecology. 11:837-845.

Atwood, C. E. 1944. The feeding habits of young spruce budworm larvae. The Canadian Entomologist. 76:64-66.

Baldwin, K. A. 1991. An introduction to the boreal forest in Ontario. Proceedings of the Entomological Society of Ontario. 122:73-86.

Baskerville, G. L. 1975a. Spruce budworm: super silviculturalist. The Forestry Chronicle. 51:138-140.

Baskerville, G. L. 1975b. Spruce budworm: the answer is forest management: or is it? The Forestry Chronicle. 51:157-160.

Batzer, H. O. 1968. Hibernation site and dispersal of spruce budworm larvae as related to damage of sampling balsam fir. Journal of Economic Entomology. 61:216-220.

Batzer, H. O. 1976. Silviculture control techniques for the spruce budworm. pp 110-116 *in* Chansler, J. F. and W. H.

Klein, Proceedings of a Symposium on the Spruce Budworm, November 11-14, 1974, Alexandria, Va. USDA Miscellaneous Publication No.1327. 188pp.

Bean, J. L. and L. F. Wilson. 1964. Comparing various methods of predicting development of spruce budworm *Choristoneura fumiferana* in northern Minnesota. Journal of Economic Entomology. 57:925-928.

Beckwith, R. C. and D. G. Burnell. 1982. Spring larval dispersal of the western spruce budworm (*Lepidoptera: Tortricidae*) in North-Central Washington. Environmental Entomology. 11:828-832.

Bible, T. D. 1985. Economic considerations for spruce budworm management in North America. pp. 176-187 *in* Sanders, C. J., R. W. Stark, E. J. Mullins and J. Murphy, Recent Advances in Spruce Budworms Research. Proceedings, CANUSA Spruce Budworms Symposium, Bangor, ME, 16-20 September 1984. Canadian Forestry Service, Ottawa. 527 pp.

Bichon, R. T. 1996. Spruce Budworm (*Choristoneura fumiferana* Clem.) Late-instar Dispersal and Impact on Host-Species Natural Regeneration in a Boreal Mixedwood Forest of Ontario. Thesis for the Master of Science in Forestry. Lakehead University, Thunder Bay, Ontario. 204 pp.

Bickerstaff, A., W. L. Wallace and F. Evert. 1981. Growth of Forest in Canada, Part 2: a Quantitative Description

of the Land Base and the Mean Annual Increment. Environment Canada, Canadian Forestry Service, Petawawa, Ontario. Information Report PI--X-1. 136 pp.

Blais, J. R. 1952. The relationship of the spruce budworm (*Choristoneura fumiferana* Clem.) to the flowering condition of balsam fir (*Abies balsamea* [L.] Mill.). Canadian Journal of Zoology. 30:1-19.

Blais, J. R. 1985. The ecology of the eastern spruce budworm: a review and discussion. pp 45-49 *in* Sanders, C. J., R. W. Stark, E. J. Mullins and J. Murphy, Recent Advances in Spruce Budworms Research. Proceedings, CANUSA Spruce Budworms Symposium, Bangor, ME, 16-20 September 1984. Canadian Forestry Service, Ottawa. 527 pp.

Bonan, G. B. and H. H. Shugart. 1989. Environmental factors and ecological processes in boreal forests. Annual Review of Ecology and Systematics. 20:1-28.

Canadian Council of Forest Ministers. 1993. Compendium of Canadian Forestry Statistics. Canadian Council of Forest Ministers, Ottawa.

Carlson, C. E., W. W. McCaughey and L. J. Theroux. 1988. Relations among stand structure, dispersal of second-instar western spruce budworm, defoliation, and height growth of young conifers. Canadian Journal of Forest Research. 18:794-800.

de Gryse, J. J. 1947. Noxious forest insects and their

control. Canada Year Book, 1947. Dominion Bureau of Statistics, Ottawa, Canada.

Eidt, D. C. 1969. Orientation of spruce budworm hatchlings. The Canadian Entomologist. 101:1005-1006.

Eis, S. 1965. Development of white spruce and alpine fir seedlings on cut-over areas in the central interior of British Columbia. The Forestry Chronicle. 41:419-431.

Fellin, D. G. 1985. Dispersal of western spruce budworm larvae and adults as related to silvicultural treatments. pp 116-117 *in* Sanders, C. J., R. W. Stark, E. J. Mullins and J. Murphy, Recent Advances in Spruce Budworms Research. Proceedings, CANUSA Spruce Budworms Symposium, Bangor, ME, 16-20 September 1984. Canadian Forestry Service, Ottawa. 527pp.

Frank, R. M. 1990. *Abies balsamea* (L.) Mill. Balsam fir. pp 26-35 *in* Burns, R. M. and B. H. Honkala, Silvics of North America. Vol.1, Conifers. Agriculture Handbook 654. Forest Service, United States Department of Agriculture. Washington, DC. 675pp.

Gordon, A. 1985. Budworm! What about the forest? Spruce-Fir Management and Spruce Budworm. Society of American Foresters, Region VI Technical Conference. Forest Service, U. S. Dept. of Agriculture, Northeastern Forest Experiment Station, Broomall, PA. GTR-NE-99:3-29.

Grant, G. G. 1991. Development and use of pheromones for monitoring lepidopteran forest defoliators in North

America. Forest Ecology and Management. 39:153-162.

Greenbank, D. O. 1957. The role of climate and dispersal in the initiation of outbreaks of the spruce budworm in New Brunswick. II. the role of dispersal. Canadian Journal of Zoology. 35:385-403.

Greenbank, D. O. 1963a. Staminate flowers and the spruce budworm. In Morris, R. F., The Dynamics of Epidemic Spruce Budworm Populations. Memoirs of the Entomological Society of Canada. 31:202-218.

Greenbank, D. O. 1963b. Host species and the spruce budworm. In Morris, R. F., The Dynamics of Epidemic Spruce Budworm Populations. Memoirs of the Entomological Society of Canada. 31:219-223.

Greenbank, D. O. 1963c. The analysis of moth survival and dispersal in the unsprayed area. In Morris, R. F., The Dynamics of Epidemic Spruce Budworm Populations. Memoirs of the Entomological Society of Canada. 31:87-99.

Greenbank, D. O. 1973. The dispersal process of spruce budworm moths. Canadian Forest Service Information Report M-X-39. 25 pp.

Greenbank, D. O., G. W. Schaefer and R. C. Rainey. 1980. Spruce Budworm (*Lepidoptera: Tortricidae*) Moth Flight and Dispersal : New Understanding from Canopy Observations, Radar and Aircraft. Memoirs of the Entomological Society of Canada. No.101. 49 pp.

Hall, P. J. and B. Moody. 1994. Forest depletions caused by

insects and diseases in Canada, 1982-1987. Forest Insect and Disease Survey Information. Report ST-X-8. Natural Resources Canada, Canadian Forestry Service, Ottawa.

Henson, W. R. 1950. The means of dispersal of the spruce budworm. Ph. D. Thesis. Yale University, New Haven, Connecticut. 102 pp.

Henson, W. R. 1951. Mass flights of the spruce budworm. The Canadian Entomologist. 83:240.

Houseweart, M. W., D. T. Jennings and C. J. Sanders. 1981. Variables associated with pheromone traps for monitoring spruce budworm populations (*Lepidoptera*: *Tortricidae*). The Canadian Entomologist. 113:527-537.

Jennings, D. T., M. W. Houseweart, and J. B. Dimond. 1983. Dispersal losses of early instar spruce budworm *Choristoneura fumiferana (Lepidoptera*: *Tortricidae)* larvae in strip clearcut and dense spruce-fir forests of Maine. Environmental Entomology. 12:1787-1792.

Kemp, W. P. and G. A. Simmons. 1979. Influence of stand factors in survival of early instar spruce budworms. Environmental Entomology. 8:993-996.

MacLean, D. A. 1984. Effects of spruce budworm outbreaks on the productivity and stability of balsam fir forests. The Forestry Chronicle. 60:273-279.

Mattson, W. J., G. A. Simmons and J. A. Witter. 1988. The spruce budworm in eastern North America. pp. 309-330 *in* Berryman, A. A., Dynamics of Forest Insect Population,

Patterns, Causes, Implications. Plenum Press. New York. 603 pp.

McGugan, B. M. 1954. Needle-mining habits and larval instar of the spruce budworm. The Canadian Entomologist. 86:439-454.

Miller, C. A. 1958. The measurement of spruce budworm populations and mortality during the 1st and 2nd larval instar. Canadian Journal of Zoology. 36:409-422.

Miller, C. A. 1963. The spruce budworm. In Morris, R. F., The Dynamics of Epidemic Spruce Budworm Populations. Memoirs of the Entomological Society of Canada. 31:12-19.

Miller, C. A. 1977. The feeding impact of spruce budworm on balsam fir. Canadian Journal of Forestry Research. 7:76-84.

Miller, C. A., D. C. Eidt and G. A. McDougall. 1971. Predicting spruce budworm development. Canadian Forest Service Bi-monthly Research Notes. 27:33-34.

Miller, C. A., E. G. Kettela and G. A. McDougall. 1972. Sampling methods in spruce budworm surveys. Canadian Forest Service Bi-monthly Research. Notes 28:31.

Miller, C. A. and G. A. McDougall. 1973. Spruce budworm moth trapping using virgin females. Canadian Journal of Zoology. 51:853-858.

Miller, A. and P. Rusnock. 1993. The rise and fall of the silvicultural hypothesis in spruce budworm (*Choristoneura fumiferana*) management in eastern Canada. Forest Ecology

and Management. 61:171-189.

Mitchell, R. G. 1979. Dispersal of early instar of the Douglas-fir tussock moth. Annals of the Entomological Society of America. 72:291-297.

Morris, R. F. 1955. The development of sampling techniques for forest insect defoliators with particular reference to the spruce budworm. Canadian Journal of Zoology. 33:225-294.

Morris, R. F. 1963. Introduction. In Morris, R. F., The Dynamics of Epidemic Spruce Budworm Populations. Memoirs of the Entomological Society of Canada. 31:7-12.

Morris, R. F. and D. G. Mott. 1963. Dispersal and the spruce budworm. In Morris, R. F., The Dynamics of Epidemic Spruce Budworm Populations. Memoirs of the Entomological Society of Canada. 31:180-189.

Mott, D. G. 1963. The analysis of the survival of small larvae in the unsprayed area. In Morris, R. F., The Dynamics of Epidemic Spruce Budworm Populations. Memoirs of the Entomological Society of Canada. 31:42-52.

Nienstaedt, H and J. C. Zasada. 1990. *Picea glauca* (Moench) Voss, white spruce. pp 204-226 *in* Burns, R. M. and B. H. Honkala, Silvics of North America. Vol.1, Conifers. Agriculture Handbook 654. Forest Service, United States Department of Agriculture. Washington, DC. 675pp.

Norusis, M. J. 1993. SPSS For Windows: Base System User's Guide, Release 6.0. SPSS Inc. 828 pp.

Outram, I. 1971. Aspects of mating in the spruce budworm *Choristoneura fumiferana* (Lepidoptera: Tortricidae). The Canadian Entomologist. 103:1121-1128.

Palaniswamy, P. and W. D. Seabrook. 1985. The alteration of calling behaviour by female *Choristoneura fumiferana* when exposed to synthetic sex pheromone. Entomologia Experimentalis et Applicata. 37:13-16.

Prebble, M. L. and R. F. Morris. 1951. The spruce budworm problem. The Forestry Chronicle. 27:14-22.

Putman, W. and J. Zasada. 1986. Direct seeding techniques to regenerate white spruce in interior Alaska. Canadian Journal of Forest Research. 16:660-664.

Ramaswamy, S. B. and R. T. Cardé. 1982. Nonsaturating traps and long-life attractant lures for monitoring spruce budworm males. Journal of Economic Entomology. 75:126-129.

Ramaswamy, S. B., R. T. Cardé and J. A. Witter. 1983. Relationships between catch in pheromone-baited traps and larval density of the spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). The Canadian Entomologist. 115:1437-1443.

Régnière, J and R. M. Fletcher. 1983. Direct measurement of spruce budworm (*Lepidoptera : Tortricidae*) larval dispersal in forest stands. Environmental Entomology. 12: 1532-1538.

Régnière, J., T. J. Lysyk and M. Auger. 1989. Population

density estimation of spruce budworm, *Choristoneura fumiferana* (Clem.) (*Lepidoptera*: *Tortricidae*) on balsam fir and white spruce from 45-cm mid-crown branch tips. The Canadian Entomologist. 121:267-281.

Régnière, J and C. J. Sanders. 1983. Optimal sample size for the estimation of spruce budworm (*Lepidoptera*: *Tortricidae*) population on balsam fir and white spruce. The Canadian Entomologist. 115:1621-1626.

Retnakaran, A. 1983. Spectrophotometric determination of larval ingestion rates in the spruce budworm (*Lepidoptera: Tortricidae*). The Canadian Entomologist. 115:31-40.

Sanders, C. J. 1969. Extrusion of the female sex pheromone gland in the eastern spruce budworm *Choristoneura fumiferana* (Lepidoptera: Tortricidae). The Canadian Entomologist. 101: 760-762.

Sanders, C. J. 1978. Evaluation of sex attractant traps for monitoring spruce budworm populations (*Lepidoptera*: *Tortricidae*). The Canadian Entomologist. 110:43-50.

Sanders, C. J. 1980. A Summary of Current Techniques Used for Sampling Spruce Budworm Populations and Estimating Defoliation in Eastern Canada. Canadian Forestry Service. Report: O-X-306. 33 pp.

Sanders, C. J. 1981. Release rates and attraction of PVC lures containing synthetic attractant of the spruce budworm, *Choristoneura fumiferana*. The Canadian

Entomologist. 113:103-111.

Sanders, C. J. 1986a. Evaluation of high-capacity, nonsaturating sex pheromone traps for monitoring population densities of spruce budworm (*Lepidoptera: Tortricidae*). The Canadian Entomologist. 118:611-619.

Sanders, C. J. 1986b. Accumulated dead insects and killing agents reduce catches of spruce budworm (*Lepidoptera: Tortricidae*) male moths in sex pheromone traps. Journal of Economic Entomology. 79:1351-1353.

Sanders, C. J. 1988. Monitoring spruce budworm population density with sex pheromone traps. The Canadian Entomologist. 120:175-183.

Sanders, C. J. 1991. Biology of North American spruce budworm. pp.579-620 *in* van der Geest, L. P. S., and H. H. Evenhuis, Tortricid Pests, Their Biology, Natural Enemies and Control. Elsevier Science Publishers. Amsterdam.

Sanders, C. J. and G. S. Lucuik. 1975. Effects of photoperiod and size on flight activity and oviposition in the eastern spruce budworm. The Canadian Entomologist. 107:1289-1299.

Sanders, C. J. and E. A. Meighen. 1987. Controlled-release sex pheromone lures for monitoring spruce budworm populations. The Canadian Entomologist. 119:305-313.

Sanders, C. J. and J. Weatherston. 1976. Sex pheromone of the eastern spruce budworm: Optimum blend of trans- and cis- 11 - tetradecenal. The Canadian Entomologist.

108:1285-1290.

Shaw, G. G. and C. H. A. Little. 1973. Dispersal of second instar spruce budworm. Canadian Forestry Service Bi-monthly Research Notes. 29:30-31.

Silk, P. J., S. H. Tan, C. J. Wiesner, R. J. Ross and G. C. Lonergan. 1980. Sex pheromone chemistry of the eastern spruce budworm, *Choristoneura fumiferana*. Environmental Entomology. 9:640-644.

Smyth, J. H. and K. L. Campbell. 1987. Selected Forestry Statistics, Ontario: 1987. Environment Canada, Canadian Forestry Service, Sault Ste. Marie, Ontario. Information Report O-X-387. 106 pp.

Swaine, J. M., F. C. Craighead and I. W. Baily. 1924. Studies on the spruce budworm (*Cacoecia fumiferana* Clem.). Dominion of Canada, Department of Agriculture, Technical Bulletin No.37. Ottawa, Canada.

Sweeney, J. D., J. A. McLean and R. F. Shepherd. 1990. Factors affecting catch in pheromone traps for monitoring the western spruce budworm, *Choristoneura occidentalis* Freeman. The Canadian Entomologist. 122:1119-1130.

Weatherston, J., W. Roelofs, A. Comeau and C. J. Sanders. 1971. Studies of physiologically active arthropod secretions. X. Sex pheromone of the eastern spruce budworm, *Choristoneura fumiferana* (*Lepidoptera; Tortricidae*). The Canadian Entomologist. 103:1741-1747.

Wellington, W. G. 1948. The light reaction of the spruce

budworm, *Choristoneura fumiferana* Clemens *(Lepidoptera: Tortricidae)*. The Canadian Entomologist. 80:56-82.

Wellington, W. G. 1954. Atmospheric circulation processes and insect ecology. The Canadian Entomologist. 86:312-333.

Wellington, W. G. and W. R. Henson. 1947. Notes on the effects of physical factors on the spruce budworm, *Choristoneura fumiferana* (Clem.). The Canadian Entomologist. 79:168-170.

Wurtz, T. L. and J. C. Zasada. 1986. An exceptional case of natural regeneration of white spruce in interio Alaska. *In* Current Topics in Forest Resaerch: Emphasis on Contribution by Woman Scientists. Proceedings of a National Symposium, November 4-6, 1986. Gainesville, Florida. USDA Forest Service, General technical Report SE-46.

Zoladeski, C. A., and P. F. Maycock. 1990. Dynamics of the boreal forest in Northwestern Ontario. The American Midland Naturalist. 142:289-300.

APPENDICES

Appendix 1. All 2-tailed significance levels of *t*-tests about egg mass densities (egg masses per 150-g branch tip) in the uncut treatment and two partial cuts of plots B1 and 4 near Black Sturgeon Lake in 1994 and 1995.

Paired host tree groups in different cut treatments	2-tailed significance	
	1994	1995
Uncut BF/SW	0.002	0.002
Uncut BF/SB	0.676	0.923
Uncut SW/SB	0.000	0.002
Uncut SW/partial cut B1 SW	0.008	0.307
Uncut SB/partial cut B1 SB	0.894	0.981
Uncut SW/partial cut 4 SW	0.026	0.004
Partial cut B1 SW/4 SW	0.703	0.001
Partial cut B1 SW/SB	0.017	0.000

BF = balsam fir, SB = black spruce and SW = white spruce.

Appendix 2. All 2-tailed significance levels of *t*-tests about second-instar larval densities (larvae per 150-g branch tip) in the uncut treatment and two partial cuts of plots B1 and 4 near Black Sturgeon Lake in 1995.

Paired host tree groups in different cut treatments	significance
	1995
Uncut BF/SW	0.001
Uncut BF/SB	0.452
Uncut SW/SB	0.004
Partial-cut B1 SW/SB	0.052
Uncut SB/partial cut B1 SB	0.023
Uncut SW/partial cut B1 SW	0.771
Uncut SW/partial cut 4 SW	0.075
Partial cut B1 SW/4 SW	0.010

BF = balsam fir, SB = black spruce and SW = white spruce.

Appendix 3. All 2-tailed significance levels of *t*-tests about the large larval densities (larvae per 150-g branch tip) in the uncut treatment and two partial cuts of plots B1 and 4 near Black Sturgeon Lake in 1994 and 1995.

Paired host tree groups in different cut treatments	2-tailed significance	
	1994	1995
Uncut BF/SW	0.164	0.020
Uncut BF/SB	0.007	0.116
Uncut SW/SB	0.000	0.000
Partial cut B1 SW/SB	0.000	0.000
Uncut SB/partial cut B1 SB	0.751	0.917
Uncut SW/partial cut B1 SW	0.099	0.682
Uncut SW/partial cut 4 SW	0.675	0.607
Partial cut B1 SW/4 SW	0.055	0.392

BF = balsam fir, SB = black spruce and SW = white spruce.

Appendix 4. All 2-tailed significance levels of *t*-tests about comparing second-instar and large larval densities (larvae per 150-g branch tip) in the uncut treatment and two partial cuts of plots B1 and 4 near Black Sturgeon Lake in 1995.

Paired larval densties in different cut treatments	2-tailed significance
Uncut BF L2/LL	0.012
Uncut SB L2/LL	0.397
Uncut SW L2/LL	0.089
Partial cut B1 SB L2/LL	0.162
Partial cut B1 SW L2/LL	0.055
Partial cut 4 SW L2/LL	0.021

BF = balsam fir, SB = black spruce, SW = white spruce, L2 = second instar and LL = large larvae.

Appendix 5. All 2-tailed significance levels of *t*-tests about overstory defoliation determined by Fettes' method in the uncut treatment and two partial cuts of plots B1 and 4 near Black Sturgeon Lake in 1994 and 1995.

Paired host tree groups in different cut treatments	2-tailed significance	
	1994	1995
Uncut BF/SW	0.067	0.000
Uncut BF/SB	0.003	0.792
Uncut SW/SB	0.000	0.000
Partial cut B1 SW/SB	0.000	0.000
Uncut SB/partial cut B1 SB	0.800	0.633
Uncut SW/partial cut B1 SW	0.392	0.009
Uncut SW/partial cut 4 SW	0.256	0.008
Partial cut B1 SW/4 SW	0.069	0.661

BF = balsam fir, SB = black spruce and SW = white spruce.

Appendix 6. All 2-tailed significance levels of *t*-tests about sticky trap catches (larvae per trap during the entire season) in all treatments of plots B1 and 4 near Black Sturgeon Lake in 1994 and 1995.

Paired sticky trap catches in different cut treatments	2-tailed significance		
	1994 L1	1995 L1	1995 L2
Uncut BF/SB	0.179	1.000	0.836
Uncut BF/SWN	0.253	0.107	0.604
Uncut BF/SWS	0.168	0.121	0.583
Uncut BF/OP	0.920	0.609	0.392
Uncut SB/SWN	0.858	0.098	0.223
Uncut SB/SWS	0.853	0.109	0.307
Uncut SB/OP	0.124	0.583	0.126
Uncut SWN/SWS	0.752	0.838	0.896
Uncut SWN/OP	0.189	0.213	0.564
Uncut SWS/OP	0.119	0.256	0.729
Partial B1 SB/SWN	0.039	0.626	0.846
Partial B1 SB/SWS	0.061	0.122	0.318
Partial B1 SB/OP	0.045	0.276	0.045
Partial B1 SWN/SWS	0.784	0.295	0.285
Partial B1 SWN/OP	0.769	0.101	0.099
Partial B1 SWS/OP	1.000	0.003	0.002
Partial cut 4 SWN/SWS	0.792	0.644	0.046
Partial cut 4 SWN/OP	0.617	0.210	0.951
Partial cut 4 SWS/OP	0.761	0.544	0.022
Uncut OP/partial cut B1 OP	0.048	0.731	0.000
Uncut SB/partial cut B1 SB	0.059	0.093	0.000
Uncut SWN/partial cut B1 SWN	0.001	0.630	0.001
Uncut SWS/partial cut B1 SWS	0.003	0.064	0.001
Clear cut/uncut OP	0.000	0.257	0.000
Clear cut/partial cut B1 OP	0.012	0.095	0.468

Clear cut/partial cut 4 OP	0.002	0.409	0.222
Uncut OP/partial cut 4 OP	0.377	0.737	0.002
Uncut SWN/partial cut 4 SWN	0.022	0.475	0.003
Uncut SWS/partial cut 4 SWS	0.004	0.402	0.067
Partial cut B1 OP/4 OP	0.250	0.466	0.054
Partial cut B1 SWN/4 SWN	0.720	0.192	0.817
Partial cut B1 SWS/4 SWS	0.375	0.006	0.045

BF = sticky traps under balsam fir, OP = sticky traps in the open or under non-host trees, SB = sticky traps under black spruce, SWN = sticky traps under the north sides of white spruce and SWS = sticky traps under the south sides of white spruce.

Appendix 7. All 2-tailed significance levels of *t*-tests about water trap catches (larvae per trap during the entire season) in the uncut treatment and two partial cuts of plots B1 and 4 near Black Sturgeon Lake in 1994 and 1995.

Paired water trap catches in different cut treatments	2-tailed significance	
	1994	1995
Ucut BF/SB	0.298	0.563
Ucut BF/SWN	0.153	0.005
Ucut BF/SWS	0.012	0.030
Ucut BF/OP	0.060	0.063
Uncut SB/SWN	0.014	0.003
Uncut SB/SWS	0.002	0.021
Uncut SB/OP	0.218	0.158
Uncut SWN/SWS	0.110	0.655
Uncut SWN/OP	0.002	0.001
Uncut SWS/OP	0.001	0.009
Partial B1 SB/SWN	0.005	0.026
Partial B1 SB/SWS	0.009	0.007
Partial B1 SB/OP	0.022	0.002
Partial B1 SWN/SWS	0.896	0.530
Partial B1 SWN/OP	0.000	0.001
Partial B1 SWS/OP	0.001	0.000
Partial cut 4 SWN/SWS	0.850	0.486
Partial cut 4 SWN/OP	0.002	0.000
Partial cut 4 SWS/OP	0.004	0.000
Uncut OP/partial cut B1 OP	0.161	0.709
Uncut SB/partial cut B1 SB	0.643	0.308
Uncut SWN/partial cut B1 SWN	0.148	0.424
Uncut SWS/partial cut B1 SWS	0.752	0.551
Uncut OP/partial cut 4 OP	1.000	0.347
Uncut SWN/partial cut 4 SWN	0.772	0.062

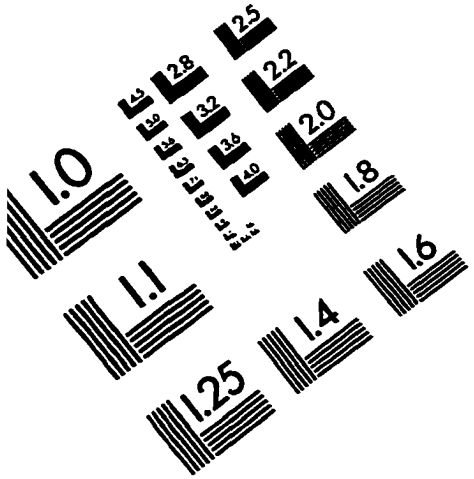
Uncut SWS/partial cut 4 SWS	0.131	0.182
Partial cut B1 OP/4 OP	0.352	0.147
Partial cut B1 SWN/4 SWN	0.226	0.241
Partial cut B1 SWS/4 SWS	0.239	0.199

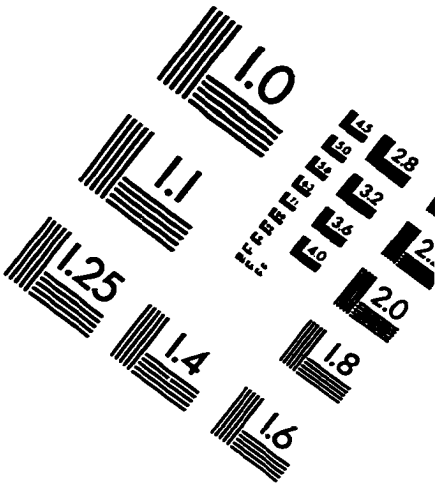
BF = water traps under balsam fir, OP = water traps in the open or under non-host trees, SB = water traps under black spruce, SWN = water traps under the north sides of white spruce, SWS = water traps under the south sides of white spruce.

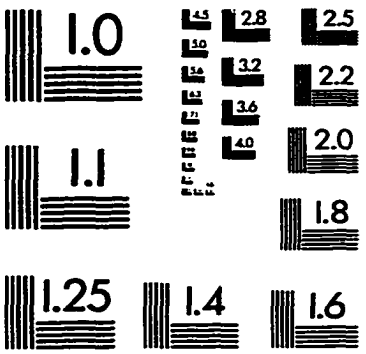
Appendix 8. All 2-tailed significance levels of *t*-tests about moth catches (moths per trap during the entire season) in all treatments of plots B1 and 4 near Black Sturgeon Lake in 1994 and 1995.

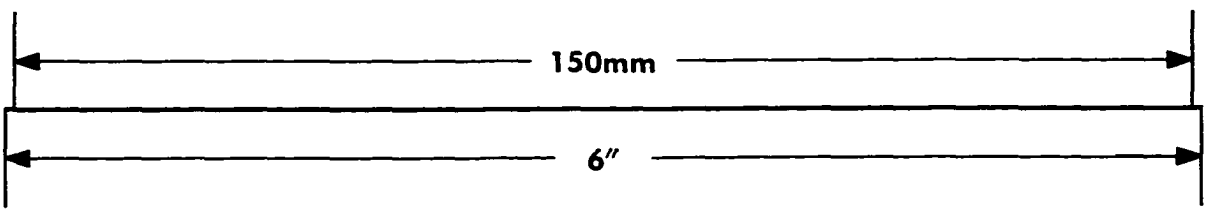
Paired trap catches in different cut treatments	2-tailed significance	
	1994	1995
Uncut/partial cut B1	0.114	0.013
Uncut/clearcut	0.073	0.001
Uncut/partial cut 4	0.026	0.056
Partial cut B1/4	0.106	0.413
Clearcut/partial cut B1	0.005	0.000
Clearcut/partial cut 4	0.004	0.001

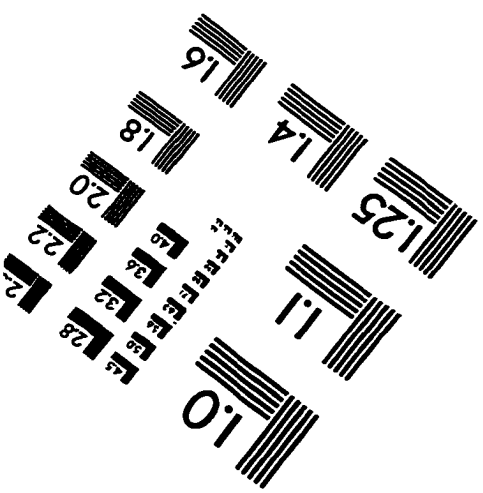
IMAGE EVALUATION TEST TARGET (QA-3)

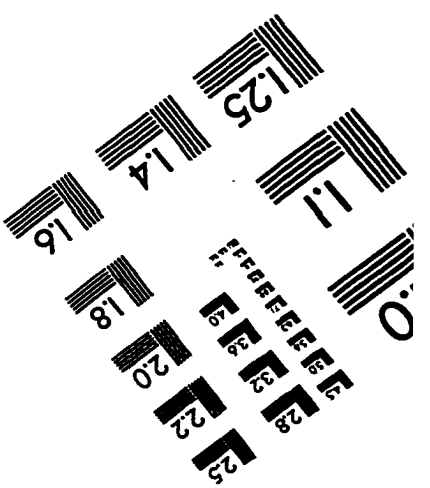












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