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Title: Survival of Early Instars of the Western Spruce Budworm (Choristoneura occidentalis Freeman)

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Survival of early instars of the western spruce budworm was studied on two 1.7 hectare plots in the Okanogan highlands of northcentral Washington. Methods of sampling hibernating larvae were compared for accuracy of estimating population numbers and for practicality. The within-tree distribution of hibernating larvae was studied on boles, limbs, and foliated twigs of 53 Douglas-fir, three ponderosa pine, and two western larch trees. Sampling designs were devised for estimating the density of hibernating larvae on the bole, limbs and foliated twigs of Douglas-fir.

Mean survival rates for the 2 plots were 96% during the egg stage, 58% from eclosion to the establishment of a hibernaculum, 77% during hibernation, and 44% from emergence from hibernation to the establishment of a feeding site in the spring.

dependence of acidifying processes such as nitrification, CO_2 release via plant and microbial respiration, mineralization of organic matter and dissociation of organic acids in soil solution. Calcium release via mineral weathering appeared to have an important effect on soil pH and extractable Ca, particularly in the absence of large inputs of acidifying materials such as NH_4 fertilizers.

The Woodburn sil is an important agricultural soil in the Willamette Valley which is well suited for alfalfa (Medicago sativa L.) production. The growth response of alfalfa to lime was examined on a soil at pH 5.5. Growth was very poor in unlimed soil although soil and plant tissue analysis did not identify elements other than N in critical nutrient deficiency or toxicity ranges. Nitrogen was deficient but only in plants grown in soil below pH 6.0.

Field and greenhouse experiments with pH, Ca, N and Mo variables and evaluation of nodulation were used to characterize the 300-400% increase in dry matter yield when lime applications increased the soil pH to the recommended level of 6.4. Plants grown at pH levels between 5.5 to 6.4 in the field and 5.3 to 6.5 in the greenhouse were all well nodulated. No increase in yield or nodulation was measured in response to the application of $CaSO_4$.

Marked response to N and Mo, especially at the lower pH levels, suggested that the growth response of alfalfa to lime is due primarily to increased nodule efficiency, resulting from greater Mo availability as soil pH is raised. Application of Mo to alfalfa grown in the Woodburn or similar soils may be a feasible alternative

to large lime applications in cases where Mo deficiency, and not poor nodulation, is the major growth limiting factor.

Survival of Early Instars of the Western Spruce Budworm (*Choristoneura occidentalis* Freeman)

by

Thomas H. Egan

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Redacted for Privacy

Head of department of Entomology

Redacted for Privacy

Dean of Graduate School

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Chapter I Introduction

Survival of Early Instars of the Western Spruce Budworm (*Choristoneura occidentalis* Freeman)

The western spruce budworm (*Choristoneura occidentalis* Freeman) is a major defoliator of conifers throughout most of western North America. Major hosts include Douglas-fir (*Pseudostuga menziesii* (Mirb.) Franco) and several true firs (*Abies* spp.).

The distribution and life history of the insect are summarized by Fellin and Dewey (1982).

The western spruce budworm is univoltine. Eggs are deposited on host foliage in masses of about 40 eggs per mass during July and August. The eggs hatch in about 10 days. The first instars (which are about 2-mm long) seek shelter under loose bark, in bark crevices, and among lichens on host trees. There they spin a cylindrical silk tent or hibernaculum which fastens them to the surrounding substrate. Within their hibernacula, the larvae molt to the second instar and hibernate until spring. Hibernating larvae occur throughout the branches and bole of a host tree. During May and June of the following spring, the second instars emerge from their hibernacula and move to host foliage to feed. The second instars mine swelling conifer buds and continue to feed on the new foliage after budburst. If budswelling has not commenced, the larvae mine

older needles but will soon move to swelling buds or expanding foliage where development is completed. Most larvae pupate during July on host foliage.

The pupal stage lasts one to two weeks. Adults mate within hours after emergence from the pupa. The female deposits her eggs within two weeks and dies. The life cycle is illustrated in Figure I.1.

Each stage of the western spruce budworm is subject to numerous mortality factors such as predation, parasitism, disease, starvation, and adverse weather. The specific type and impact of these factors vary with each life stage of the insect. The effect of each factor or combination of factors on annual population trends could vary with the conditions at a given time and place. An understanding of such effects on a population requires extensive field data that are summarized in the form of mathematical models.

Another Choristoneura species closely related to the western spruce budworm is the spruce budworm, C. fumiferana (Clem.). It is a major pest of conifers in eastern Canada and the northeastern United States and has life stages identical to those of its western counterpart. The spruce budworm has been intensively studied in eastern Canada since the 1940's. Life table studies by Morris et al. (1956) of the spruce budworm showed that dramatic reductions in insect

numbers occur during the early instars (first through third instars). In those studies, mortality from the time of egg hatch in August to the commencement of feeding in May ranged from 60% to 93%.

Miller (1958) studied spruce budworm mortality during three age-intervals during the early instars. During the first interval, the newly hatched first instar must move from the egg mass to a sheltered site where it will construct the hibernaculum and overwinter. In their search for a hibernation site, many larvae are dislodged from the host tree by air turbulence. They may actively drop from the branches when disturbed by predators or when they come into contact with other larvae. Upon dislodgement from the tree, the larvae extrude a strand of silk from the spinnerette which provides them with enough bouancy to float several meters through the air. Miller reported 64% larval mortality for that period. He attributed the mortality to "air dispersal to non-host material, predation, failure to spin hibernacula, and to diapause-free development." Without the shelter of a hibernaculum and without entering the dormant physiological state of diapause, a larva is unable to survive the winter. Such mortality probably results from desiccation, starvation, and freezing.

The second interval studied by Miller (1958) was the sedentary hibernaculum stage. Sixteen percent of the larvae died within the hibernaculum. The causes of that mortality were undetermined. Experiments to estimate losses of hibernating larvae from predation and weathering were inconclusive.

The third interval was from emergence from hibernation to the peak of the third instar feeding on foliage. Mortality averaged 40% and was attributed to air dispersal to non-host material, predation, and failure to establish a feeding site.

Mortality during the first and third intervals is due to a combination of factors which are difficult or perhaps impossible to separate in the field. Air dispersal to non-host material was assumed to be the major factor during those intervals. Miller, therefore, used the term "dispersal loss" to represent the combined factors acting during those intervals.

Life table studies of the western spruce budworm were conducted in Colorado by McKnight (1971). Mean mortality from the egg stage through the third instar was 35% for two generations on six plots (this was later corrected to 81% by Srivastava et al. 1982). McKnight suggested that survival over that interval was negatively correlated with the number

of eggs per unit area of host foliage. Separate estimates of mortality were not made for the fall dispersal, hibernaculum, and spring dispersal intervals.

Campbell et al. (1983) estimated that survival of the western spruce budworm in Washington and Idaho ranged from about 5% to 15% from the egg stage to the fourth instar. They concluded that the variation in survival during that interval was due to differences in stand attributes and weather. They did not make separate mortality estimates of losses during fall dispersal, hibernation, or spring dispersal.

To study survival through the various age intervals discussed above, the insect population must be estimated at the time of egg hatch (L_I), at the beginning and end of hibernation (H_I and H_{II}, respectively) and at approximately the third instar after the larvae have emerged from hibernation and commenced feeding in the spring (L_f). L_I and L_f populations can be estimated on a convenient index of foliage area by assuming the foliated portion of a branch approximates a triangle (length of foliated portion x width of foliated portion x 1/2). Density of the hibernating stage cannot be estimated on the same area index since a variable proportion hibernate on the bole and limbs of a tree. Densities of the three stages must, therefore, be

expressed on a common unit of area such as the number of insects per tree or a per unit area of land surface if changes in population numbers are to be estimated separately for each of these early age intervals. Because of this difficulty, there are no published life tables for the western spruce budworm presenting separate survival estimates for L_I, H, and L_f. One of the objectives of this study was to estimate survival during these sub-intervals by estimating whole-tree populations of the budworm. In order to meet this objective, it was necessary to develop practical and accurate sampling methods for estimating the population of hibernating larvae.

In addition to population dynamics studies, estimating the density of hibernating larvae could be useful in management decisions. Estimates of egg density are considered the information most useful in making control decisions on the western spruce budworm. Sampling eggs requires thorough and tedious inspection of foliage. It also means that management decisions are made with data collected 9 to 10 months prior to the commencement of defoliation. The advantages of sampling the hibernating stage are that it is immoble and is available for sampling from September up to March or April. Such estimates have been made for past control projects (Terrell 1959). The

difficulties of collecting samples in areas of heavy snowfall, uncertainty of the accuracy and consistency of the processing method for collecting the larvae from tree samples, and the lack of statistically determined sample sizes have discouraged managers from pursuing such data. In eastern Canada, however, the hibernating stage of the spruce budworm is routinely sampled prior to control operations.

In Chapter II, two methods of sampling hibernating larvae were compared by artificially infesting small limb sections with larvae and then estimating the percent recovery by each method. Two variations of each method were also studied. Since the larvae hibernate on the bole, limbs, and foliated portions of a tree, the percent recovery of larvae from artificially infested samples of those three substrates was also compared. The effect of the duration of exposure to cold temperature on the rate of emergence from hibernation was examined.

In Chapter III, the within-tree distribution of hibernating larvae was studied on the boles, limbs, and foliated portions of trees. The samples were taken from various heights within the trees to determine vertical differences in insect density.

In Chapter IV, the density of hibernating larvae on the boles was compared to density on limbs. The purpose was to

determine if density on limbs can be used to predict density on boles. Sampling designs were developed for estimating the density of hibernating larvae on the boles, limbs, and foliated portions of trees with predetermined precision levels. The variance to mean relationship used in the sampling designs is based on the regression of mean crowding to mean density. Mean crowding is a measure of aggregation and is a function of variance.

In Chapter V, survival of the budworm was estimated through four age intervals: (1) egg stage, (2) egg hatch to the establishment of a hibernation site, (3) during hibernation, and (4) from the end of hibernation to the establishment of a feeding site in the spring. Estimates of survival were made by estimating budworm numbers for each stage on a per tree basis.

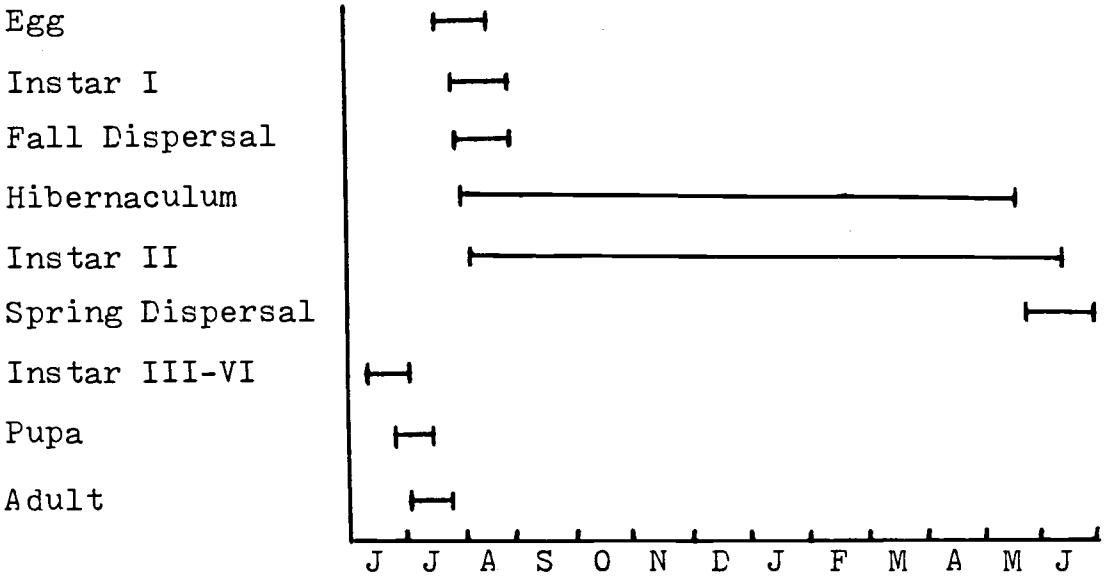


Figure I.1. Life cycle of the western spruce budworm.

Chapter II A Comparison of Methods for Collecting Hibernating Western Spruce Budworm Larvae

Abstract

The second instar of the western spruce budworm overwinters within a silken hibernaculum on the branches and boles of the various tree species within an infested stand. Douglas-fir (Pseudostuga menziesii (Mirb.) (Franco)) is a major component of infested stands and is the most economically important host species. The most common hibernation sites are under loose bark, within bark crevices, and under and within lichens that grow on the host trees. Estimating the population density of the hibernating larvae by visually searching for them is impractical due to their small size (<2-mm) and cryptic locations. In this study, two methods were compared for their accuracy and practicality in recovering hibernating larvae from artificially infested sections of Douglas-fir branches. The first method (washing method), developed by Canadian workers for sampling the spruce budworm, was to soak the infested branch sections in 4% sodium hydroxide (NaOH) to dissolve the hibernacula and then to filter and extract the larvae from the resulting bark debris. Fifty-seven percent of the larvae were recovered by this method when the washing solution was hand-agitated for 30 seconds. Seventy-four percent were recovered if it was mechanically agitated for five minutes.

The second method (rearing box method) was to hold the larvae in cold storage (2°C) until diapause was completed and then place the branch sections in a carton (rearing box) where the larvae were attracted by light to a glass vial inserted in the wall of the carton. Recovery by this method was 87 and 88% for 1-liter and 19-liter cartons, respectively. Presence of lichen on the branch sections had no effect on recovery. The average processing time was 0.96 hours for the washing method and 0.20 for the rearing box method. In another test neither the type of substrate (bole sections, limbs, or foliated twigs) nor its size significantly affected recovery by the rearing box method. With field-collected material, the emergence rate increased as the period of cold storage was increased. Regressions of the number of days to reach 10, 50, and 90% emergence vs. the date of exposure to room temperature are presented.

Introduction

Spruce budworms, Choristoneura spp., are serious pests of coniferous forests in both eastern and western North America. Several of these species overwinter as second instars within a silken hibernaculum on various parts of the host trees. The overwintering stage of the spruce budworm, C. fumiferana (Clemens), is often sampled for research and survey purposes. An advantage of sampling hibernating larvae is their sedentary nature, which provides several months during which the sampling can be completed. A disadvantage is the small size of the larvae (less than 2-mm long). Larvae of the western spruce budworm, C. occidentalis Freeman, hibernate on all parts of the host and on non-host material that provide protective sites, so sampling by visual inspection is impractical.

One commonly used sampling method is to attract emerging larvae to a light source (rearing box method) (Wright et al. 1952, Miller 1958, McKnight 1969). Larvae must have received sufficient cold treatment to complete diapause for this method to be used. Schmidt (1977) compared percent emergence of western spruce budworm larvae

with cold storage time at 2°C. When stored for 14 weeks, only about 10% emerged when transferred to a room temperature of 25°C. Maximum percent emergence occurred following about 22 weeks of cold storage.

Another technique (washing method), developed for the spruce budworm, does not require that diapause be complete (Miller and McDougall 1968, Miller et al. 1971). Samples of host tree branches are placed in a solution of sodium hydroxide (NaOH) for several hours to dissolve the silken hibernacula that hold the larvae to the substrate. The larvae are extracted with benzene or hexane and filtered from the liquid. The methods used in Canada to estimate density of hibernating larvae were summarized by Sanders (1980).

In this study, the washing method and the rearing box method were compared for accuracy and practicality in estimating numbers of hibernating western spruce budworm larvae. This comparison was made by recovering the larvae from artificially infested sections of Douglas-fir limbs. The recovery of larvae from bole sections, limbs, and foliated twigs of Dougas-fir was also compared to determine the effect of hibernation substrate on the accuracy of the rearing method. Regressions are also presented showing the effect of time in cold storage on the emergence rate of larvae from field-collected material.

Methods

Sixty-four basal sections of lower crown branch stems were cut from live Douglas-fir trees and infested in the laboratory with hibernating larvae. Douglas-fir branches were used as the substrate because they are a major hibernation site for the western spruce budworm (McKnight 1969) and provide a practical sample unit for field studies. The sections were about 18-cm long and from 1.2 to 2.5-cm in diameter. All foliage and twigs were removed; the lichen (mostly Hypogymnia sp.) were hand-stripped from 32 of the 64 sections. Each section was infested with a known number of hibernating larvae (laboratory stock) by pinning about three egg masses to the upper side of the section (Fig. II.1). The egg masses had been deposited by adult female moths on Douglas-fir foliage and strips of waxed paper in paper bags which held the moths. The sections of waxed paper were cut out around each egg mass leaving a large enough border for the pin to pass without damaging the eggs. The sections were held above a sheet of waxed paper coated with Tanglefoot® by a support made from two large (No. 3) paper clips for about 3 weeks. The temperature-controlled laboratory

was held at 23°C, with a 9:15 L:D photoperiod. The eggs hatched, and the larvae established hibernacula. The egg masses were mounted on standard microscope slides and the images were projected on a screen with a Leitz Wetzlar Projector® so that the number of hatched eggs could be counted. The number of hatched eggs per section minus the number of larvae that fell on the paper equaled the number that remained on a section.

Washing Method. After 8 weeks of cold storage at 2°C, eight branch sections with lichens and eight without were placed in a hot (54°C) 4% NaOH solution in 2-liter glass jars. The jars were filled and capped with a metal screw-on lid to keep the sections totally submerged. After 24 hours, each jar was agitated by hand for 30 seconds. The solution was then poured through course and fine soil sieves (8 meshes/cm and 24 meshes/cm, respectively). Each jar and section was rinsed with tap water from a rubber hose. The rinse water was drained through the sieves to remove all loose plant debris and larvae. The contents of the fine sieve were rinsed into a jar, which was capped and identified by section number. These contents were then poured into a 2000-ml separatory funnel. About 10-ml of benzene were added and the funnel was agitated by hand. The water fraction was drained off, leaving the larvae in the benzene.

More water was added and the process repeated to dislodge the finer plant debris caught in the benzene. The benzene fraction was drained into a 19-cm-diameter Büchner funnel with white, gridded filter paper, and then vacuum-filtered. Larvae on the filter paper were counted under a dissecting microscope.

After the treated branch sections were dry, they were inspected for larvae under a dissecting microscope by picking off bark scales and plant debris. Because several larvae were found under bark scales, the preceding process was modified for 16 additional branch sections. These sections were placed in individual jars containing the NaOH solution and capped. Each jar was agitated on an Eberback® model #6360 variable-speed utility shaker at about 200 excursions per minute for 5 minutes. Part of the solution was poured out before agitation to allow free flow over the branch sections. The water fraction of the additional sections was re-extracted with benzene and re-filtered to determine larval loss during the extraction process.

The percent efficiency was determined for each section as 100 x number of larvae on filter paper/number of larvae hibernating on the branch. The average number of hours needed to process each sample was also recorded.

Rearing Box Method. For this method, a glass vial inserted into the wall of a carton allows entry of light to attract the larvae and serves as a collection chamber to trap them as they migrate toward the light. The vial must fit very tightly to prevent larvae from escaping between the vial and the carton. To accomplish a tight fit, a 3 x 3-cm hole was cut in each rearing carton (1-liter paper milk carton). A 5 x 5-cm rubber seal (cut from a bicycle inner tube) with a 1.4-cm diameter hole in the center was taped over the hole in the carton. The 3-dram collecting vials had an outer diameter of 1.9-cm and fit very tightly when pressed into the hole in the rubber seal (Fig. II.2A).

After 25 weeks at 2°C, eight branch sections with lichen and eight without were removed from cold storage and placed in individual 1-liter rearing cartons. The flaps were stapled shut and dipped in melted paraffin to prevent larvae from escaping. A 3-dram glass vial was inserted into the rubber seal. The rearing assembly was placed in a paper bag to reduce light transmission into the carton; a hole in the bag allowed the vial to protrude.

The cartons were placed horizontally on shelves with the vials hanging downward over the edge of the shelf (Fig. II.2B). Ceiling lights and a fluorescent desk lamp directed at the cartons were left on continuously. Average room

temperature was 22°C. Larvae that dropped into the vials were counted and removed twice daily until emergence was completed. The cartons were then opened and inspected, and the number of larvae that had moved from the limb section but failed to reach the vial were added to the number that entered the vial. The percent efficiency for each carton was calculated as 100 x number of larvae recovered/number of larvae hibernating on the branch.

After 30 weeks at 2°C, an additional 16 branches (8 with lichen and 8 without) were placed in individual cylindrical 19-liter cartons, each with two collecting vials (2.4-cm in diameter x 5-cm long) per lid. A strip of masking tape wrapped around the outside of the carton lid prevented larvae from escaping. Ceiling lights and a desk lamp were used to attract the larvae. Average room temperature was 24°C. The cartons were treated like the smaller cartons, including calculation of the percentages of emerging larvae.

With the rearing box method, only larvae that survive the hibernaculum stage can be recovered since they must actively emerge from the hibernaculum and migrate toward the vial. This is in contrast to the washing method which is a completely passive method and will recover both live and dead individuals. The purpose of these tests was to compare

the recovery of the two methods based upon the percentage of larvae that could potentially be recovered by each method. Larvae that died within the hibernaculum during cold storage had no potential for being recovered by the rearing box method. At the end of each test, therefore, mortality within the hibernacula was determined by dissecting 20 hibernacula per branch section from the small cartons and 18 per section for the large cartons. The percent recovery for each treatment (large or small cartons) was adjusted by the respective survival rates.

The percent recovery for each replicate was transformed to arcsin percentage (arcsin $\sqrt{\%}$, Steel and Torrie 1960) and the significance of treatments was determined by analysis of variance and the "least significant difference" criterion (Steel and Torrie 1960).

Effect of Substrate on Rearing Box Method Efficiency with 19-Liter Cartons. To determine the effect of substrate type and surface area on the recovery rate of the rearing box method, a known number of larvae were placed in a 19-liter cylindrical carton with one of the following substrates:

SUBSTRATE	SIZE CLASS	AVERAGE SIZE OF SUBSTRATE
Bole Section,	Large	1630 cm^2
30-cm long	Medium	1226 cm^2
	Small	330 cm^2
Limbs	Large	2404 cm^2
	Medium	801 cm^2
	Small	534 cm^2
Foliated twigs	Large	3/4 of carton volume
(loosely packed)	Medium	1/2 of carton volume
	Small	1/4 of carton volume

Larvae hibernating on cotton gauze patches (3 x 3-cm) for 32 weeks at 2°C were counted, and 1 or 2 patches were placed on the substrate before each carton was closed. An average of 67 larvae were placed in each carton, including the empty cartons. The edges of the carton lids were sealed with masking tape. A glass vial was inserted into the lid as described above. Larvae entering the vials were counted and removed daily for 7 days, after which few emerged. Average room temperature was 23°C. About 3 weeks later, the cartons were opened, and the larvae on the masking tape and inside were counted and added to the number that entered the

glass vial. The dead larvae that remained on the gauze patches were also counted and subtracted from the total number on each patch to yield the number of live larvae that could have emerged. The percent recovery was calculated for each carton. Analysis of variance was performed on the transformed values (Steel and Torrie 1960).

Emergence Rate of Larvae from Field-Collected Material. From 1979 to 1981, 53 Douglas-fir trees were sampled on two plots in northcentral Washington. Samples consisted of 30.4-cm (12-in.) long sections from the bole, limbs, and the foliated twigs pruned from the limbs. About 1,849 such samples were taken. The 1979 samples were collected from the field in September but were stored out-of-doors until February 1980 when they were placed in cold storage at 2°C. On March 14, half of the samples were brought to room temperature (26°C) and placed in individual 19-liter rearing units where the emerging larvae were collected and counted. The second half were placed in the rearing units on April 12, 1980. The 1980 samples were placed in cold storage in March. Half were placed in rearing units on April 24, 1980 and the second half on May 5.

The 1981 samples were taken from the field in April and portions were placed in rearing units on April 24, April 26,

May 22, and May 26. Larvae were collected from the vials and tallied every 1 to 5 days.

When no larvae were found in the vials for 5 to 7 days, emergence was assumed to be complete. The cartons were opened and the larvae that died before reaching the vials were tallied.

Results and Discussion

Comparison Between Washing and Rearing Box Methods. Mean larval recovery was 57% for the hand-agitated NaOH washing method and 88% for the rearing box method (Table II.1). Although mechanical agitation for 5 minutes improved recovery, both washing methods were significantly inferior ($P<.05$) to the rearing box method with either size of rearing carton. The low recovery could, in part, have been because of the coarseness of the Douglas-fir bark which would provide many crevices where the larvae could lodge. Size of the rearing container had no significant effect on larval recovery.

The analysis of variance was first calculated as a factorial design with recovery method as one factor (washing method with hand agitation, washing method with five minutes of mechanical agitation, rearing box method with 1-liter cartons, and rearing box method with 19-liter cartons) and the presence or absence of lichen on limb sections as the second factor (Table II.2). This gave eight replicates for each of the eight treatments. Since the presence or absence of lichen had no significant effect on percent recovery of larvae, the analysis of variance was recalculated as a

one-way classificiation with recovery method as the only factor (Table II.3).

These results differ from those of Miller and McDougall (1968) for the spruce budworm in Canada. They recovered 88 and 100% of the larvae after samples were soaked in 5% NaOH for 5 and 10 hours, respectively. They also compared the washing method with the rearing box method using field-collected branches. Their washing method recovered from 2.3 to 10 times the number of larvae on paired samples as did the rearing box method. However, since they used naturally infested branch samples, the number of live larvae in hibernacula at the start of the test was not known, thus making interpretation of their results difficult. The washing method is a destructive technique that recovers both live and dead larvae. The rearing box method depends on live larvae leaving the substrate and going to a vial where they can be counted. If there were large numbers of dead larvae on the sample branches in the Miller and McDougall study, it would help explain their low recovery by the rearing box method compared to the washing method.

Other problems make the washing method inferior for sampling hibernating western spruce budworms. During my test, an average of 0.96 man-hours per branch section were required for the washing method compared to 0.20 per sample

for the rearing box method. These average times only include preparation and inspection. They do not include soaking time for the washing method or total time the branch sections were held in the boxes for the rearing box method. For a large-scale sampling of field material, several branches could be processed at one time in large buckets or drums; however, this would not provide an estimate of between-branch variability required for most studies. The use of larger containers would likely result in lower recovery rates because of the larger surface areas to which the larvae could adhere. Sanders (1980) reported an average of 0.3 hours of preparation and processing per branch for the washing method. My time was probably longer because of the relatively large volume of debris from the loose, scaley bark of Douglas-fir.

Because a large proportion of western spruce budworm larvae hibernate on the tree bole, either method would have to be adapted to accommodate heavy material or the bark would have to be stripped from the wood for processing. A final consideration is that of safety. The NaOH solution is highly corrosive to human tissue (especially the eyes) and benzene liquid and vapors are highly toxic. Canadian workers now use hexane rather than benzene (Sanders 1980). My methods included some major deviations from those

reported by previous authors (Miller et al. 1971, Sanders 1980). I used a higher concentration of NaOH (4% vs. 1%), a longer soaking time (24 hrs. vs. 5 hrs.), and a different method of agitation (5 minutes of mechanical agitation vs. hand stirring for one hour). Because the washing method depends on separating the larvae from the plant material by dissolving the hibernacula and floating them away, I feel that these modifications would provide a higher yield than the previously published methods.

Effect of Substrate on Larval Recovery. Neither the type nor the surface area of the substrate had a significant effect on recovery. The mean larval recovery from various substrates in 19-liter cartons ranged from 64 to 92% (Table II.4). Recovery from empty 19-liter cartons was 87%, nearly identical to that for small branch sections in 19-liter cartons reported in Table II.1.

Note that the percent recovery of larvae from rearing cartons required a count of the larvae on the inner surfaces of the carton. For the 32 cartons used in the second experiment, only 49 ±25% of the larvae that were recovered had entered the vials; the other 51% were found inside the carton and on the masking tape. Analysis of variance based only on the percentages that entered the vials also showed no significant effect of substrate type or size class.

Emergence Rate of Larvae from Field-Collected Material. The number of larvae collected on each day was converted to a percentage of the total that entered the vials. Plotting the percentage of larvae emerged vs. days at 26°C yielded sigmodial curves. The emergence curves were linearized by transforming the percentages to probits and the days to common logarithms (Fig. II.3) (Finney 1952). The log of the number of days to reach 10, 50, and 90% emergence was read from the curves, transformed back to the arithmetic value and regressed against the Julian date on which the samples were placed in the rearing units (Fig. II.4). The number of days to reach a given percentage of emergence varied with the date of exposure to room temperature.

These results indicate that samples taken from the field in May should be placed immediately in rearing units or in cold storage to prevent the escape of larvae from the material. Samples taken in March must remain in rearing units for 2-3 weeks to complete emergence. Schmidt (1977) found that emergence time of C. occidentalis decreased curvilinearly as storage time at 2°C was increased and that the proportion of larvae that ultimately emerged also increased with exposure to cold temperatures. Volney et al.

(1983) showed that the mean time to emergence after 27 weeks at 2°C varied with exposure temperature and among geographic populations.

I assumed that emergence was completed when no larvae emerged for 5 days. The rearing units were then opened and all larvae were counted that had moved from the sample material but died before entering the vial. The percentage of larvae that entered the vials increased with exposure time to cold temperature (Fig. II.5).

These studies indicate that the rearing box method is the most practical and efficient method for sampling overwintering western spruce budworm larvae. The efficiency of the method, however, depends on the duration of exposure to winter temperatures and on the duration of time allowed for emergence. Larval populations overwintering at high elevations and experiencing an extended period of winter weather may emerge more rapidly in the field with a sudden onset of warm spring weather. Holding time in the rearing boxes can be decreased by collecting samples in late winter or by collecting them in early winter and placing them in cold storage. Samples should be collected about the middle of April (Julian date 105). This would allow time for transportation and handling before larvae would begin to emerge.

Beckwith (personal communication) observed larval emergence at Bill Smith's Place in late April of 1980.

All emergence experiments were conducted in a laboratory where light intensity and temperature could be regulated. Any large deviations in environmental conditions would probably affect larval recovery by the rearing box method.

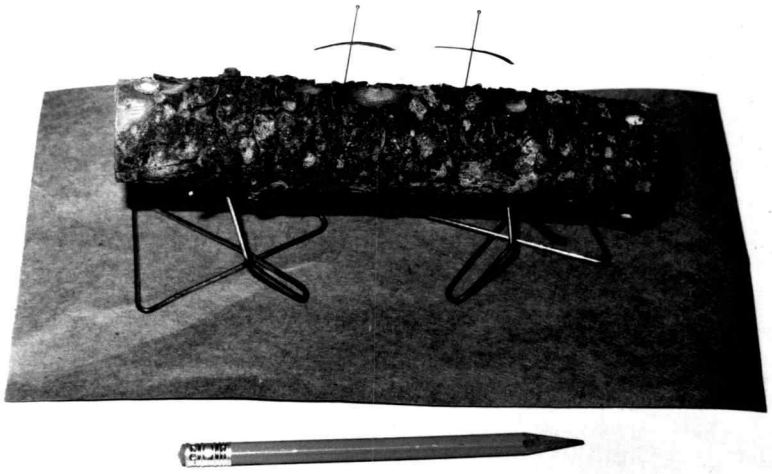
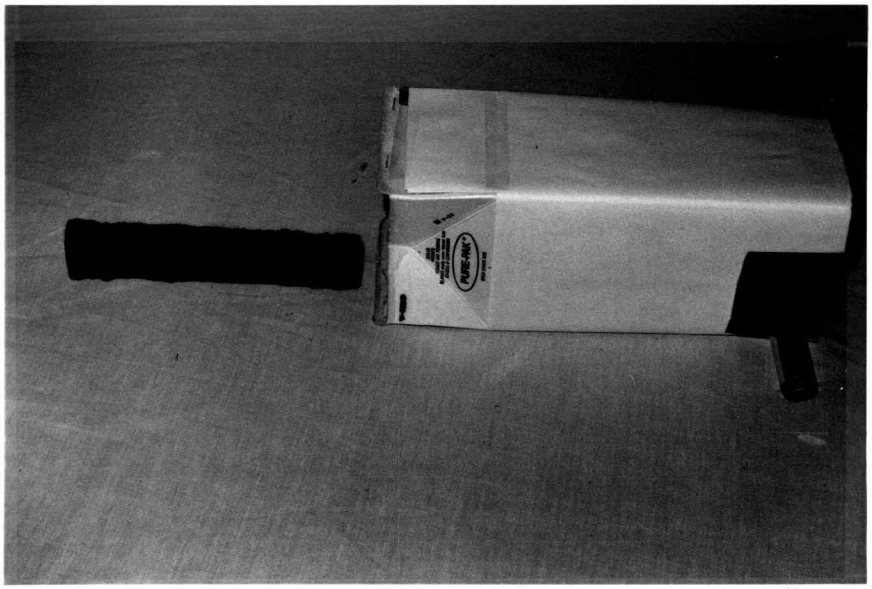


Figure II.1. Egg masses on Douglas-fir needles pinned to a Douglas-fir limb section for artificial infestation with hibernating larvae.

A



B

Figure II.2. Paper milk cartons fitted with glass vials to attract emerging larvae to light: (A) carton and branch section (B) row of illuminated cartons on shelf.

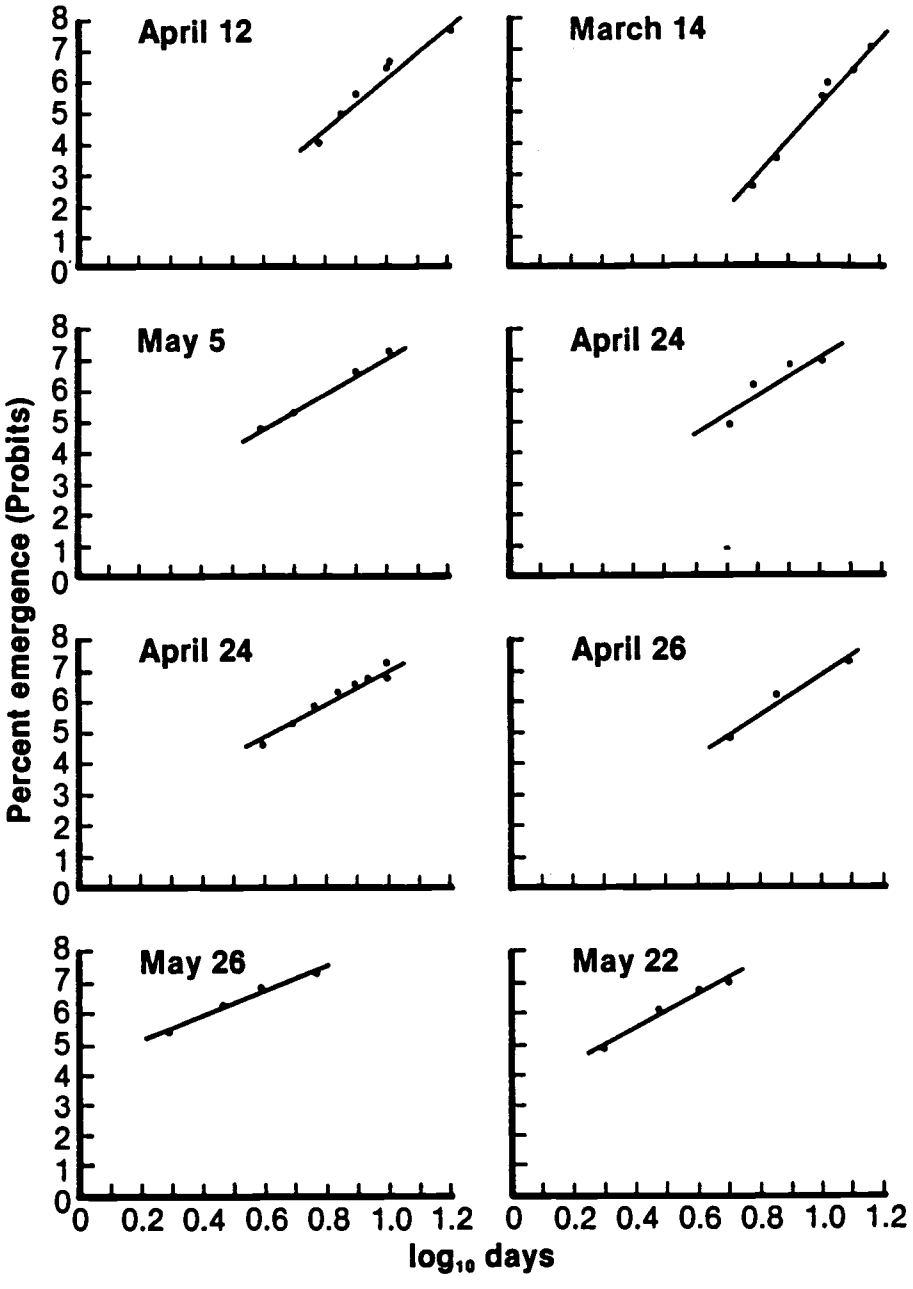


Figure II.3. Percent emergence (in probits) vs. $\log_{10}$ days for samples brought to room temperature (26°) on April 12 (A), March 14 (B), May 5 (C), April 24 (D,E), April 26 (F), May 26 (G), and May 22 (H).

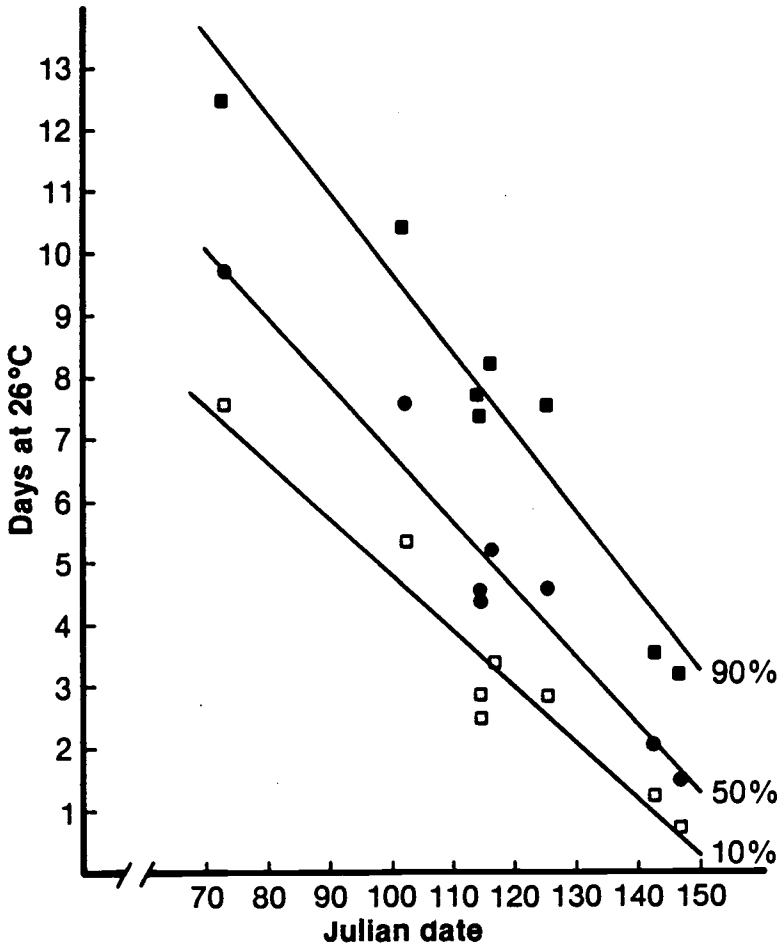


Figure II.4. Days to reach 10 (▫), 50 (•), and 90% (▪) emergence vs. Julian Date.

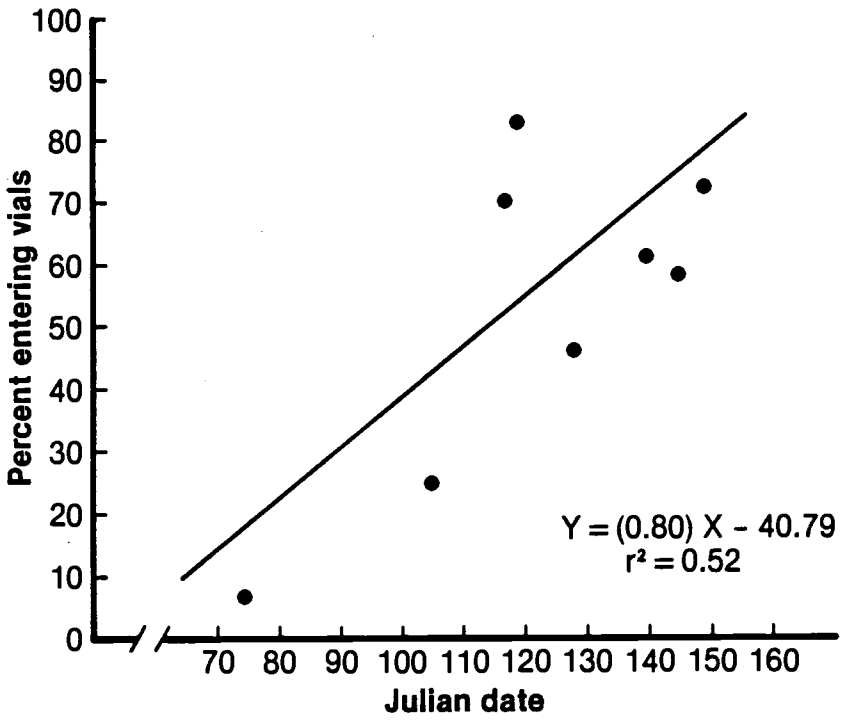


Figure II.5. Percent of larvae that entered lighted vials vs. Julian date.

Table II.1. The mean percentage (±S.D.) of second instars recovered from artificially infested limb sections.[1/]

Washing Method		Rearing Box Method	
30-second hand agitation	5-minute mechanical agitation	1-liter cartons	19-liter cartons
57 ±22.9a[2/]	74 ±17.5b	87 ±12.5c	88 ±6.9c

[1/] Sample size = 16 for each of the four techniques.

[2/] Any two means not having a common letter are significantly different at the 0.05 probability level. Differences were tested by the least significant difference method (Steel and Torrie 1960) on the transformed data (arcsin $\sqrt{\%}$) using the mean square error from Table II.3.

Table II.2. Analysis of variance for recovery of larvae by four techniques with lichen present or absent from limb sections.

Source	Degrees of Freedom	Sum of Squares	Mean Square	F
Treatment	7	(4413)	--	--
Technique	3	4172	1391	9.66*
Lichen	1	81	81	0.56
Technique x lichen	3	160	53	0.37
Error	49	7054	144	--
Total	63	11,467	--	--

*Significant with P<.005.

Table II.3. Analysis of variance for recovery of larvae by four techniques. Presence or absence of lichen on branch section was deleted as a factor.

Source	Degrees of Freedom	Sum of Squares	Mean Square	F
Treatment	3	4,172	1391	11.4*
Error	60	7,295	122	--
Total	63	11,467	--	--

*Significant with P<.005.

Table II.4. Mean percentage (±S.D.) of second instars recovered from 19-liter cartons with various types and sizes of substrates.

Substrate size class	N	Bole	N	Branch stem	N	Foliated twigs
Small	2	70 ± 9	2	73 ± 9	4	79 ±34
Medium	3	92 ± 5	3	69 ±29	6	72 ±20
Large	3	76 ±28	3	84 ±24	6	64 ±19

Chapter III The Within-Tree Distribution of Hibernating Western Spruce Budworm Larvae

Abstract

The within-tree distribution of hibernating larvae of the western spruce budworm, Choristoneura occidentalis Freeman, was studied on 53 Douglas-fir trees, three ponderosa pines, and two western larch trees. The trees were sampled on two plots in northcentral Washington. Each of the three major hibernating substrates (bole, limbs, and twigs) of a tree was divided into four vertical strata. Two 30.5-cm (12-in.) bole sections and two branches were removed from each stratum. The twigs were pruned from each branch. Twigs of Douglas-fir and ponderosa pine were foliated; foliage was not present on the larch twigs. Each sample (bole section, limb, twigs) was placed in an individual rearing unit to collect emerging larvae. Differences in larval density (per m^2 of sample surface) among strata were tested by ANOVA and Tukey's W-procedure. On the bole of Douglas-fir, highest densities occurred in strata associated with the lower crown. Density on the bole below the crown depended upon proximity to the base of the crown. The distribution on the bole of western larch was similar to that on Douglas-fir.

On limbs of Douglas-fir, highest densities occurred in strata of the lower crown. A similar trend occurred on

limbs of western larch. On foliated twigs of Douglas-fir, higher densities occurred in strata of the lower crown in one data set but there were no significant differences among strata. There were no apparent trends on twigs of western larch or on the bole, limbs, or foliated branch tips of ponderosa pine. Of the estimated total number of hibernating larvae on Douglas-fir, about 44% occurred on the bole.

Introduction

The western spruce budworm, Choristoneura occidentalis Freeman, feeds on Douglas-fir, Pseudotsuga menziesii (Mirb.) Franco, and various true firs, Abies spp., throughout the western United States and southwestern Canada. Second instars overwinter within silken hibernacula which are usually located under bark scales and lichens and within bark crevices.

In years past hibernating larvae were sampled prior to several spray programs (e.g. Terrell 1959, etc.). In Canada, hibernating larvae of the spruce budworm, C. fumiferana (Clem.), are routinely sampled for management decisions (Sanders 1980) and were sampled by Miller (1958) in population dynamics studies.

Denton (1951) found a mean of 31 larvae/m^2 of bark on samples from "near the top of the bole in the relatively smooth bark surface area" and 174 larvae/m^2 from "somewhat lower on the bole in the roughed bark surface area." Denton (1952) found highest numbers of larvae at 1.4 meters from the ground, intermediate numbers "immediately below the base of the crown" and lowest numbers at midcrown. He did not determine if the densities were significantly different nor did he report how far below the crown the lowest samples were taken. In neither study did he sample branches.

Buckhorn et al. (1958) and Terrell (1959) sampled limbs and boles of Douglas-fir trees. In both studies, however, only a single bole sample was taken from each tree and the heights of the limb samples were not reported.

On seven trees sampled near Goldendale, Washington, Braidwood (1962) found that larval density on boles increased with height and higher densities occurred on limbs than on boles. The samples, however, were only taken up to 12.2 meters on the bole; and tree heights, crown lengths, and stratum surface areas were not reported.

McKnight (1969) found highest numbers of larvae within bole strata associated with the lower crown and midcrown. Lowest numbers on boles occurred below the live crown and in the upper crown. On branches he found higher numbers within the lower and middle crown. Carolin and Coulter (1972) found higher numbers of larvae on branches of Douglas-fir than on bole samples.

Each of these previous studies increased our knowledge of within-tree distribution of hibernating larvae. Each, however, was deficient in one or more of the following categories: (1) observing vertical differences in density on the bole and/or limbs, (2) comparing densities on boles with densities on limbs and/or foliated twigs, (3) reporting tree height and/or crown length, (4) collecting

samples in the most appropriate season (late winter) or properly storing fall-collected samples to allow for completion of larval diapause, (5) adequate sample sizes or sample design to allow for graphical or statistical analysis of larval distribution. Such data and techniques are required before reliable and practical methods of sampling hibernating larvae can be devised.

My objective was, therefore, to intensively study the within-tree distribution of hibernating larvae. This study contributes information useful in designing practical and statistically sound sampling methods for extensive and intensive sampling programs.

Materials and Methods

The plots used in this study were located in north-central Washington with soils, physiography, and general climate characteristic of the Okanogan Highland Province (Franklin and Dyrness 1973). Plot 1 was in the South Fork Salmon Creek drainage about 11-km south of Conconully, Okanogan County, Washington. The stand consisted of a Douglas-fir overstory with scattered western larch and ponderosa pine. Budworm defoliation was light but readily visible. Plot 2 was in the West Fork Salmon Creek drainage about 8-km northwest of Conconully. The stand consisted of Douglas-fir with an overstory of western larch and ponderosa pine. Defoliation was moderate to severe.

Plot 1 was sampled during the last week of March 1980 and the first week of April 1981. Plot 2 was sampled during September 1979 and the first week of April 1981. In 1979, sample trees in Plot 2 were selected along a 0.1-km section of logging road and within 25 to 150-m of the road. The samples were stored out-of-doors on wooden pallets near Mazama, Okanogan County, Washington, until January 1980.

For the 1980 and 1981 samples, a 1.7-ha plot was staked out at each of the two areas. The plots were divided into 20 equal-sized subplots, and sample trees were selected at

randomly chosen coordinates within the subplots. Sample trees ranged from 9.8 to 19.5-m and 9.4 to 16.8-m in plot 1 for 1980 and 1981, respectively. In plot 2, they ranged from 5.5 to 22.3-m and 15.8 to 23.8-m for 1979 and 1981, respectively. Samples were taken from three hibernation substrates on each tree: (1) the bole, (2) limbs, and (3) foliated twigs (i.e., the lateral twigs and associated needles and buds of a branch). Two 30.5-cm long samples were cut transversly with a chain saw from the center of each of four vertical strata of the bole: (1) B1 - the portion below the lowest living branch, (2) B2 - the portion within the lower third of the crown (i.e., the lower third of the living branches), (3) B3 - the portion within the center third of the crown, and (4) B4 - the portion within the top third of the crown (Fig. III.1).

The trees were felled and the upper and lower ends of the strata were located with a tape measure and marked.

Surface areas of bole strata were calculated from the length and radius at the top and bottom of each stratum (area = π x [$radius_1$ + $radius_2$] x [length]). Length and diameter of each bole sample were recorded for calculation of surface area (area = length x π x diameter).

For limbs and twigs, the crown was divided into four portions of equal length. Starting with the lowest fourth

of the crown, the limb strata were designated as L1, L2, L3, and L4. Twig strata were designated as F1, F2, F3, and F4 (Fig. III.1). Two live branches from the whorl nearest to the center of each stratum were randomly selected and removed for estimation of budworm density on limbs and foliated twigs. Each sample was tagged by tree number and crown position. The basal diameter and total stem length of each limb were recorded. Limbs were assumed to approximate a cone so that the bark surface is the product of π x (basal radius) x (length). With Douglas-fir, an index of the foliated area of a branch was determined by measuring the length (parallel to the branch stem) and greatest width (perpendicular to the stem) of the foliated portion of each branch. The foliated portion was assumed to approximate a triangle so that the area is the product (length) x (width) ÷ 2. Surface area measurements were taken from one branch of each whorl throughout the crown for estimating the total surface area within each stratum. Though foliage is not present on larch trees during the winter, the same method was used to determine the index of twig area for that species. The sample units for the three substrates are shown in Figure III.2.

The samples were transported to the USFS Forestry Sciences Laboratory, Corvallis, Oregon. The 10-hour trip

was made at night to keep the samples cool. Upon arrival in Corvallis, the samples were immediately placed in a refrigerator at 2°C. Half of the samples were loaded into individual 19-liter rearing cartons at room temperature to collect emerging larvae (Chapter II). Foliated twigs were clipped from limbs and placed in separate cartons. The bark was removed from bole sections and placed in the carton if the entire section was too large to fit. Emerging larvae were periodically counted and removed from the collection vials until emergence was completed. Larvae that had moved from the sample material but failed to enter the vial were counted. The second half of the samples were then processed by the same procedure. For Douglas-fir and larch, the number of larvae recovered from each sample was divided by the surface area of the sample to give a measure of larval density. For ponderosa pine, density on twigs was expressed as larvae per foliated branch tip. With these data, estimates could be made of the mean density within strata, mean density for the entire tree, and of the total number of larvae on a tree.

To determine if significant differences in larval density occurred among strata, the data were transformed

($\sqrt{(x + 1)}$) and tested by analysis of variance with a mixed-effects model, complete block design (trees were random, strata were fixed), and Tukey's W-procedure was used to compare means (Neter and Wasserman 1974).

Results

On Douglas-fir trees where the B1 samples were at least 1.5-m below the crown, highest larval density (per m^2) occurred in B2, followed by B3 in all four data sets and when all data sets are combined (Table III.1). Density in B2 and B3 was significantly higher than in B1 and B4 in two data sets (Plot 1, 1980, and Plot 2, 1981) and in the combined data set. Density in B2 was significantly higher than in B3 in only one set (Plot 2, 1979). There were no significant differences in density among strata for Plot 1, 1981, which included the lowest larval densities and only four trees in the data set. Larval density was also significantly higher in B2 and B3 of larch but there were no significant trends on ponderosa pine (Table III.1). When the B1 samples were within 1.5-m below the crown, highest densities occurred in B1 and B2 in all data sets (Table III.1). In no case was the density in B1 significantly different than in B2.

On limbs of Douglas-fir and western larch, highest densities occurred in L1 and L2 in all data sets (Table III.2). For Douglas-fir, density did not differ significantly between L1 and L2 or between L3 and L4. There was no significant trend in density on limbs of ponderosa pine.

On foliated twigs of Douglas-fir, there was a slight trend in density but there were no significant differences in density except that Plot 1, 1981, F3 had a significantly higher density than F4 (Table III.3). There was no significant trend on twigs of larch or foliated branch tips of ponderosa pine.

Figure III.3 shows the average densities in each stratum for the three substrate types on Douglas-fir. The estimated proportions of larvae on the three substrates of Douglas-fir are shown in Table III.4. Data from McKnight (1969) are included for comparison.

Discussion

The vertical distribution of hibernating larvae was consistent over the course of this study. On boles, highest densities occurred in strata associated with the lower portion of the crown. Density in B1 appears to depend on the distance below the lower crown. When the B1 samples are within 1.5-m below the crown, they are essentially part of the lower crown (B2) population.

The bark surface of Douglas-fir trees is roughest at the base of the bole and becomes increasingly smoother toward the top. For the sizes of trees used in this study, the bark became relatively smooth in the region within the midcrown. The distribution of hibernating larvae, therefore, appeared to be determined by two factors. First, the larvae begin their search for a site on the foliage where they hatched from egg masses. Significantly higher egg densities occur in the upper portions of the crown (Campbell et al. 1984). My laboratory observations indicate that a larva will spin its hibernaculum in one of the first few protected sites encountered. Second, since the bark of Douglas-fir becomes increasingly rough toward the base of the tree, there is a greater density of hibernation sites in the lower region of the bole. It is likely that many of the

larvae move from the oviposition sites to the lower crown by off-tree aerial dispersal (Beckwith and Burnell 1982).

Even though the rough bark and greatest density of sheltered sites occur below the crown, the larvae will usually encounter a hibernating site on the bole within the crown.

On branch stems, highest larval densities occur in the lower-crown region because of the high density of sheltered sites in the rough bark and lichens of the oldest branches.

The smooth foliage and twigs of Douglas-fir provide few hibernation sites and there is no apparent difference in foliage texture (with respect to hibernation sites) throughout the crown. This explains the lack of significant differences in larval density among strata.

The bark surface of western larch boles and limbs has the same pattern as Douglas-fir -- roughest in the lower portions and becoming relatively smoother in the midcrown. This would explain the similarity in the distribution of larvae on those two tree species. The ponderosa pine that I sampled had loose, flaky bark throughout the bole and limbs except in the very uppermost portion. This would explain the lack of significant trends in larval density on that species.

The low larval densities on pine and larch compared to Douglas-fir were expected since neither of the two former species are preferred for oviposition by the western spruce budworm in northern Washington. It probably indicates dispersal by first instars which originated from egg masses on nearby Douglas-fir.

Comparisons of the proportions of total larvae occurring on the various substrates indicate that high numbers occur on all parts of Douglas-fir. Variation in the number of branches and in the total surface areas of branch stems and foliated twigs would contribute to variation in the number of larvae occurring on each surface type. Also, limbs of Douglas-fir may vary in roughness among geographic areas and may therefore affect larval density (Carolin and Coulter 1972).

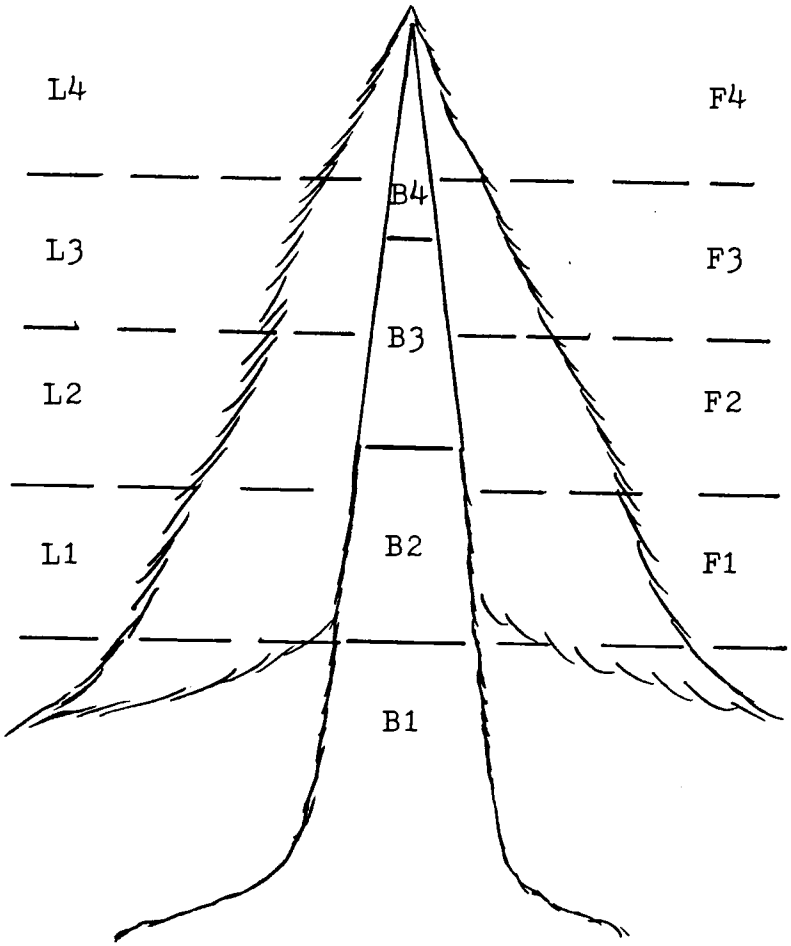


Figure III.1. Vertical strata of the bole (B1-B4), limbs (L1-L4), and foliated twigs (F1-F4).

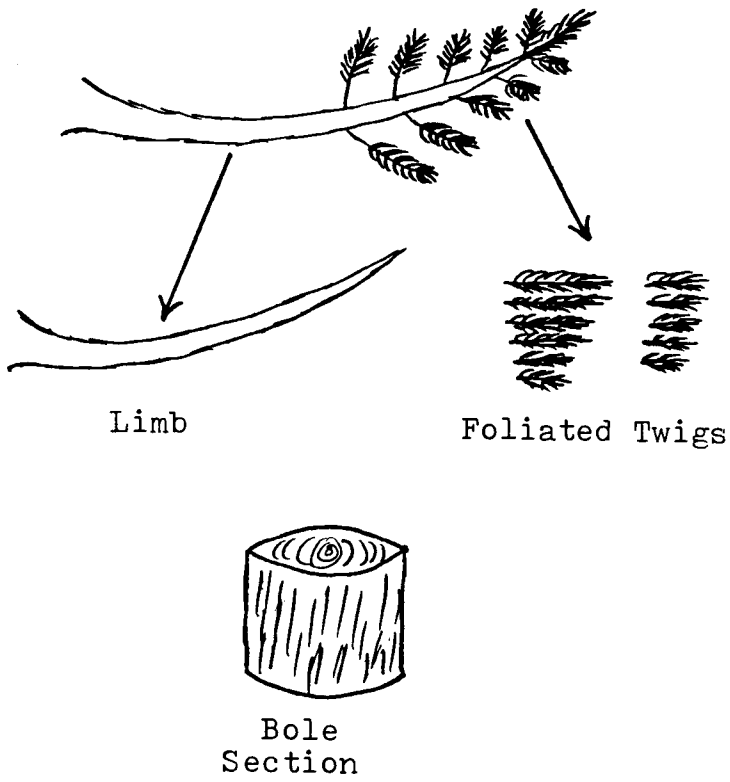


Figure III.2. Within-tree sample units.

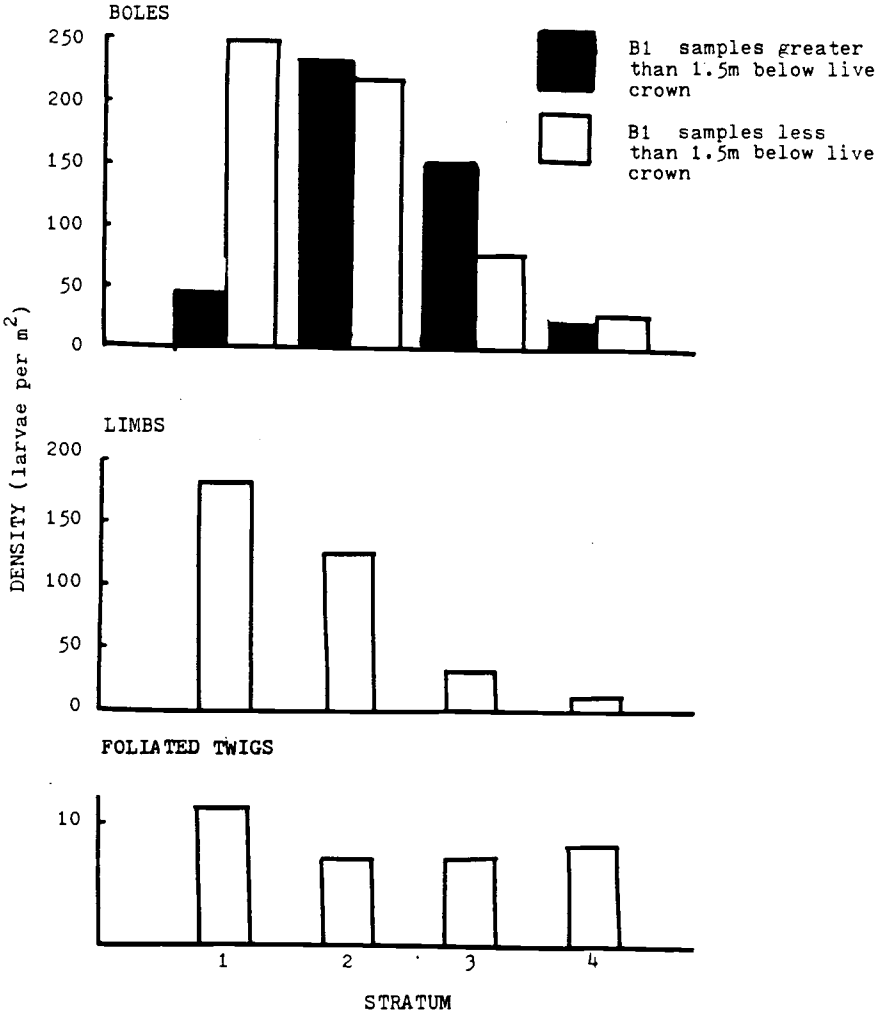


Figure III.3. Mean density of hibernating western spruce budworm larvae in 4 vertical strata on Douglas-fir trees (all years and plots combined).

Table III.1. Density (larvae per m^2) of hibernating larvae on boles[1/].

Tree species	Plot	Year	B1 samples greater than 1.5-m below crown: Number of trees	Stratum B1	B2	B3	B4	B1 samples less than 1.5-m below crown: Number of trees	Stratum B1	B2	B3	B4
D. fir	1	80	7	17a	116b	67b	14a	11	104a,b	128a	61b	44b
		81	4	1a	80a	45a	35a	6	92a	79a	25a,b	4b
	2	79	4	69a	272b	196a	15a	11	500a	314a	114b	15b
		81	8	61a	388b	252b	17a	2	104a,b	516a	104a,b	9b
	1,2	79,80,81	23[2/]	39a	232b	150b	19a	30	247a	213a	76b	23b
W. larch	1	80	2	17a	64b	74b	22a					
P. pine	1	80	2	11a	26a	32a	31a					

[1/]Means followed by the same letter are not significantly different, $P<0.05$ by Tukey's W-procedure. Comparisons are only between columns.

[2/]Combined data from Douglas-fir trees on both plots, all three years.

Table III.2. Density (larvae per m^2) of larvae hibernating on limbs[1/].

Tree species	Plot	Year	Number of trees	Stratum L1	L2	L3	L4
D. fir	1	80	12	87a	68a	21b	8b
		81	9	60a,b	83a	32a,b	18b
	2	81	10	355a	226a	38a	9b
	1,2	80,81	31[2/]	166a	123a	30b	11b
W. larch	1	80	2	146a	42b	28b	41b
P. pine	1	80	3	18a	16a	32a	8a

[1/] Means followed by the same letter are not significantly different, $P<0.05$ by Tukey's W-procedure. Comparisons are only between columns.

[2/] Combined data from Douglas-fir trees on both plots, both years.

Table III.3. Density (larvae per m^2) of larvae hibernating on foliage and twigs[1/].

Tree species	Plot	Year	Number of trees	F1	F2	F3	F4
D. fir	1	80	12	7a	6a	5a	14b
		81	10	4a,b	4a,b	5a	2b
	2	81	10	22a	11a	10a	8a
	1,2	80,81	32[2/]	11a	7a	7a	8a
W. larch	1	80	2	16a	5a	4a	0a
P. pine	1	80	2	3a	3a	3a	1a

[1/] Means followed by the same letter are not significantly different, $P<0.05$ by Tukey's W-procedure. Comparisons are only between columns.

[2/] Combined data from Douglas-fir trees on both plots, both years.

Table III.4. Percentage of larvae hibernating on various substrates of Douglas-fir.

	Bole	Limbs	Foliated twigs
Plot 1, 1980	61	21	18
Plot 1, 1981	26	46	28
Plot 2, 1981	45	13	41
McKnight (1969)	35	36	29

Chapter IV Sampling Designs for Hibernating Western Spruce Budworm Larvae on Douglas-fir

Abstract

Overwintering western spruce budworm larvae occur on three major substrates within a Douglas-fir tree: bole, limbs, and foliated twigs. Sampling the bole destroys the tree and is expensive in time and effort. The possibility of using larval density on limb samples to predict density on boles was studied.

Sampling designs are presented for estimating larval density on each of these substrates over 2-ha plots. The designs are based on regressions of mean crowding on mean density.

Regressing larval density on boles against density on limbs based on samples from individual trees yielded the relationship $y = 63.44 + 0.78X$ with $r^2 = 0.57$. When the regression is based on mean density per plot, the relationship is $y = 44.61 + 0.96X$ with $r^2 = 0.76$. Prediction intervals were wide by both methods. Therefore, even though a positive relationship between the two variables was demonstrated, large errors in such predictions will result.

Required numbers of samples to estimate larval density on boles, limbs, and twigs increase as density decreases. Sample sizes are prohibitive at densities below about 40

larvae per m^2 on boles and limbs and below about 5 per m^2 on foliated twigs. Appropriate within-tree sample units are discussed.

Introduction

Hibernating second instars of the western spruce budworm occur throughout the branches and bole of host trees and probably most non-host trees of an infested stand (Chapter III) from September to about May.

The hibernating stage has been sampled to provide supporting data for spray projects in the western United States (Terrell 1959). This stage of a closely related species, the spruce budworm (C. fumiferana (Clem.)), is routinely monitored prior to control projects in eastern Canada (Sanders 1980).

Since high numbers of hibernating larvae occur on the bole, limbs, and foliated twigs of a host tree, a survey of the larval population requires that either: (1) samples be taken from each of those three substrates, or (2) samples be taken from one substrate that provides an accurate index to densities on the other two. Taking samples from the bole of a tree is destructive and expensive. Some previous studies have, therefore, investigated the possibility of using limbs rather than bole samples in making management decisions. Buckhorn et al. (1958) sampled limbs and boles of 50 trees from ten sites in Oregon. The ratio of larval density on limbs to density on boles was 1 to 1.52. Because

emergence of larvae from bole samples appeared to be erratic, they concluded that limbs would be more reliable sampling units for making control decisions.

Terrell (1959) sampled five Douglas-fir trees and found a 1 to 20 ratio of larvae on limbs to larvae on bole sections, respectively. Carolin and Coulter (1972) found a ratio of 1 to 1.1.

High larval mortality can occur just prior to hibernation when the newly hatched larvae are moving from the oviposition site on the foliage to an overwintering site, and again in the spring when they move from overwintering sites to new foliage. Population estimates prior to hibernation, during hibernation, and following hibernation would provide estimates of fall and spring dispersal mortality.

Whole-tree populations of the spruce budworm were estimated by Miller (1958) for life-table studies. The problem in sampling western spruce budworm larvae for such purposes is that they overwinter on three distinct substrate types within a tree: the bark of the bole, the bark of the limbs, and the small twigs and foliage. In order to relate overwintering population estimates to estimates at other stages, the total population on all three substrates must be estimated and summed to express density on a per-tree basis.

Interest in sampling hibernating western spruce budworm larvae has diminished in recent years partly because of the logistical problems in collecting samples and because no statistically valid sampling design has been developed.

The dispersion of a population refers to the spatial distribution of the individuals. The significance of dispersion was discussed by Southwood (1966). Dispersion determines the relationship between the variance (σ^2) and mean (m) when population estimates are made by counting the number of individuals in a series of randomly placed quadrats. The individuals may be spaced randomly ($\sigma^2 = m$), in clumps ($\sigma^2 > m$), or regularly ($\sigma^2 < m$). Such dispersions result in corresponding mathematical distributions of the frequencies of the quadrat counts (e.g., the Poisson, the negative binomial, and the positive binomial, respectively). The mathematical distribution will affect the required numbers of samples in sampling designs. It also provides behavioral and biological information such as the tendency of individuals to aggregate due to environmental preferences (Mangan and Wutz 1983) or reproduction (Bergman et al. 1983, Reilly and Sterling 1983), and the effectiveness of regulatory factors such as intraspecific competition, predation, parasitism, and disease (Campbell and Srivastava 1982 (unpublished), Campbell et al. 1982 (unpublished), Iwao

1970, McGroarty and Croft 1978, Trumble et al. 1983, and Poston et al. 1983).

In his studies on the importance of spatial distribution in animal ecology, Lloyd (1967) introduced the parameter "mean crowding":

$$\overset{*}{m} = m + \left(\frac{\sigma^2}{m} - 1 \right)$$

where $\overset{*}{m}$ = mean crowding, m = mean density per quadrat, and σ^2 = variance. Iwao (1968) showed that there is often a linear relationship between mean crowding and mean density:

$$\overset{*}{m} = \alpha + \beta m$$

(where α and β are the intercept and slope of the $\overset{*}{m}$ - m regression) and that the variance is related to the mean by:

$$\sigma^2 = (\alpha + 1)m + (\beta - 1)m^2$$

(Iwao and Kuno 1968).

The variance formula can then be substituted into standard equations for estimating required sample sizes in sampling programs. For example, in the case of simple random sampling:

$$n = S^2/(D_o{}^2 \, m^2)$$

becomes:

$$n = \frac{1}{D_o^2} \left(\frac{\alpha + 1}{m} + B - 1\right)$$

(Iwao and Kuno 1971) where S^2 = variance, m = the arithmetic mean, and D_o = the ratio of standard error to the arithmetic mean ($S_{\bar{x}}/m$). The uses of the regression parameters (α and β) and the resulting variance equation have been expanded to more complex applications including multistage and sequential sampling designs (Iwao and Kuno 1971, Kuno 1976).

The $\overset{*}{m}$ - m regression technique has been used to develop sampling designs for agricultural pests (McGroarty and Croft 1978, Poston et al. 1983) and for some forest inhabiting Lepidoptera (Unruh and Luck 1982, Shepherd and Otvos 1984) including sequential designs for the western spruce budworm (Srivastava and Campbell 1983, unpublished). Régnière and Sanders (1983) preferred Taylor's power law over Iwao's $\overset{*}{m}$ - m technique in developing designs for the spruce budworm in eastern Canada. Dobesberger and Lim (1983) based their design for early instars of the spruce budworm on a common k value of the negative binomial distribution.

In addition to their use in sampling designs, the regression parameters α and β also have important ecological interpretations (Iwao and Kuno 1971). α is a measure of the dispersion of individuals. Values of α greater than zero indicate an aggregative tendency among individuals:

> ". . .typically (α + 1) individuals would live together in the same quadrat when the mean density becomes infinitesimal. The positive value of α can be resulted from animal's preference to particularly favorable spots in the habitat, but more generally it seems to be related to the mode of life characteristic of the species, such as collective disposition of eggs (or youngs) and positive interaction between individuals, etc. The slope β of the regression, on the other hand, can be regarded as an index showing the spatial pattern of habitat utilization by individuals or groups of individuals in relation to their population density. Its value is equal to unity when the distributions of individuals or groups of individuals (with a fixed mean size) follow the Poisson series, and larger and smaller than unity when the distributions are overdispersed (such as the negative binomial distributions with a common K). . .the slope β describes the manner in which individuals or groups of individuals distribute themselves in their habitat with changing mean density" (Iwao 1968).

Iwao (1968) termed α the "index of basic contagion" and β as the "density contagiousness coefficient." Some examples of recent ecological studies utilizing the $\overset{*}{m}$ - m statistics were by Steffey and Tollefson (1982), Trumble et al. (1983), Mangan and Wutz (1983), and Campbell and Srivastava (1982, unpublished).

The objectives of this study were to determine if larval density on limbs is a useful predictor of density on boles and to develop sampling designs with acceptable levels of precision for estimating the density of western spruce budworm larvae on the three major hibernation substrates in Douglas-fir trees: bole, limbs, and foliated twigs. The sampling designs are based on regressions of mean crowding on mean density.

Materials and Methods

The data for the current study came from the same samples described in Chapter III; therefore, only a brief description of the sample collection and processing will be given. The samples were collected by a two-stage procedure where individual trees were primary sample units, and bole sections, limbs, and foliated twigs were secondary units. Each sample tree was felled and the bole was divided into four vertical strata. At least two 30-cm long sections were cut from the center of each bole stratum. At least two branches were taken from each of four vertical strata within the live crown. The samples were transported to the laboratory where the surface area of each sample unit was measured. Foliated twigs were excised from each limb. Each sample was placed in an individual rearing carton where the larvae were attracted to a light source and counted. All counts were converted to number of larvae per m^2.

The relationship of larval density on boles to density on limbs was estimated by linear correlation and linear regression (Steel and Torrie 1960). In order to increase the range and number of observations for the bole-limb relationship, the data from Buckhorn et al. (1958), Carolin and Coulter (1972), and Terrell (1959) were also used. In

the study by Buckhorn et al., five trees were sampled on each of ten plots. They removed a 38-cm long bole section and fifteen 38-cm long limb sections from each tree. Their samples were placed in rearing boxes with vials similar to my methods described in Chapter II.

Carolin and Coulter took their samples from 9 trees near Union, Oregon. They took two rectangular bark samples from the midcrown of the bole and every second limb from the two adjacent branch whorls. Terrell (1959) took an unspecified number of limbs and one bole section from each of five trees.

In my study, 20 trees were sampled on one plot in 1980 and ten trees on each of two plots in 1981. Eighteen trees were also sampled in 1979; however, since the limb samples from those trees were not processed, they could not be used in the bole-limb regression. The data from all of my 58 trees were used in the sample design for boles. The data of Buckhorn et al. 1958, Terrell 1959, and Carolin and Coulter (1972) were not used in the sampling designs due to their methods in selecting trees and to the differences in plot sizes compared to my study. Buckhorn et al. purposely selected "nearby trees that showed the heaviest degree of defoliation" and Carolin and Coulter selected trees "that were scattered over a distance of several miles." Terrell

(1959) did not specify plot size or the selection method and data for the individuals trees were not presented. Random selection of trees and a specific plot size are essential in developing sampling designs.

The weighted mean and variance of larval density (per m^2) were calculated for each tree. Weighing coefficients were the relative sizes of the four vertical strata (Jessen 1978). The mean and variance of larval density was calculated for the among-tree distribution of each plot/year combination (Kuno 1976). Means and variances for individual trees were designated as the within-tree statistics and those for among-trees as overall statistics (Kuno 1976). Regression lines of mean crowding on mean density were calculated for the within and the overall distributions (Kuno 1976).

The required number of trees (n) was calculated as:

$$n = \frac{1}{D_o^2}\left[\frac{1}{m}\left(\frac{\alpha'-\alpha+\alpha\beta'+\beta'}{\beta' k} + \frac{\alpha-\alpha'}{\beta'}\right) + \frac{\beta\beta'-\beta}{\beta' k} + \frac{\beta-\beta'}{\beta'}\right]$$

where α' and β' are the intercept and slope of the within-tree distribution, α and β are the slope and intercept of the among-tree (overall) distribution, D_o is the index of precision ($S_{\bar{x}}/m$), m is mean density and k is the number of within-tree samples taken (Iwao and Kuno 1971).

Results and Discussion

Predicting Density on Boles from Density on Limbs. When main stem larval densities on individual trees are regressed against the corresponding branch stem larval densities, the resulting equation is $y = 66.44 + 0.78x$ ($r^2 = 0.57$, $n = 99$) (Fig. IV.1).

The prediction intervals for this regression are too wide to be useful. For example, when limb density (x) is 100 larvae/m^2, the 95% prediction interval on boles is 0 to 481. When x is 500, the interval is 109 to 797, and when $x = 1000$, the interval is 483 to 1203.

The prediction intervals are somewhat reduced if the data are coverted to mean densities per plot. The resulting equation is $y = 44.61 + (0.96)x$ ($r^2 = 0.76$) (Fig. IV.2). The prediction intervals are, however, still very wide. When $x = 100$, the 95% prediction interval is from 0 to 330, and when $x = 500$, the interval is 295 to 750. The results of Terrell (1959) were considered an outlier and were not used in the regression calculations.

Required Sampled Sizes. The regressions of within-tree mean crowding on mean density for boles, limbs, and foliated twigs are shown in Figures IV.3 - IV.5.

Regressions for the overall distributions are shown in Figure IV.6.

The intercepts (α) of the within-tree regressions are low for all three substrates (2.39 for boles, -3.83 for limbs, and -1.16 for foliated twigs). Intercepts of the among tree parameters for boles and limbs, however, increase greatly in the among tree regressions (87.36 and 46.81, respectively). The among tree value for foliated twigs (0.62) is only slightly larger than the within-tree value. As discussed in the introduction of this chapter, $\alpha + 1$ is the average number of individuals in a quadrat when density is infinitesimal or, from the regression, $\alpha = \overset{*}{m}$ at a mean density of zero. $\overset{*}{m}$ is a function of variance:

$$\overset{*}{m} = (m + \sigma^2/m) - 1$$

The mean densities and mean variances for the within and among tree distributions are shown in Table IV.1. In all cases, the mean among tree variance is greater than the mean within-tree variance and the variance to mean ratios for among trees are greater than for within-trees. The within and among tree variance to mean ratios for boles and limbs are considerably greater than those for foliated twigs.

This explains why the $\overset{*}{m}$ - m intercepts of the among tree regressions are so much greater than for the within-tree regressions for boles and limbs but are approximately equal for foliated twigs. Also, values of α may vary with quadrat size (Iwao 1972). The surface area measurements of bole and limb samples approximate the actual area, whereas the measurement of foliage area (length x width ÷ 2) is only a relative measurement. This may also explain the differences in the among tree values of α.

The degree of aggregation may change with the life stage of an organism (Iwao 1968). $\overset{*}{m}$ - m statistics for egg masses and feeding larvae (mostly fourth instar) were estimated by Campbell and Srivastava (1982, unpublished) and are presented in Table IV.2 for comparison with my data for hibernating larvae on foliated twigs. Aggregation of egg masses results from oviposition behavior of the adult female moths. For feeding larvae it will be influenced by the distribution of new foliage on which the larvae feed. Hibernating larvae exhibit the lowest values of α (within and among trees), the lowest among tree β value and an intermediate within tree β value. The lack of vertical trends in density (Chapter III) and the relatively low variance to mean ratios (Table IV.1.) for hibernating larvae on foliated twigs indicates that during hibernation, the

larvae on that substrate are distributed much more uniformly than at other stages. I hypothesize that this is largely due to two factors: (1) the process of aerial dispersal during the fall, and (2) the relatively uniform texture of foliated twigs which in turn provides a more uniform distribution of hibernation substrates.

Required numbers of samples at a range of mean densities and two levels of precision are shown in Figures IV.7 - IV.9. As larval density declines, required numbers of samples increase. This same pattern (rapid increase in required number of samples) was found by Morris (1955) for egg masses, larvae, and pupae of the spruce budworm (C. fumiferana) in eastern Canada.

On boles, the required number of trees is excessive when mean density is less than $40/m^2$ (Fig. IV.7). Substantial savings can be gained by accepting the 0.3 precision level rather than the 0.2.

On limbs, the required number of sample trees is excessive when larval density is less than 30 larvae/m^2 (Fig. IV.8). Sampling effort can be reduced by about one-half if the 0.3 precision level is accepted.

On foliated twigs, fewer than ten trees must be sampled when larval density is greater than 10 larvae/m^2 and there is little gain in accepting the 0.3 precision level beyond

that density (Fig. IV.9). The low numbers of required samples of foliated twigs compared to those for boles and limbs are due to the lower degree of aggregation as indicated by the lower variance to mean ratios and the among tree values of α and β (Table IV.1).

Within-Tree Sample Units.

Vertical trends in larval density were discussed in Chapter III. On boles, density is highest at the base of the crown, is significantly lower in the top third of the crown, and decreases with distance below the crown. This suggests that boles should be divided into three strata: below the live crown, lower two-thirds of the live crown, and the upper third of the crown. One bole section should be cut from the middle of each stratum. A weighted mean density can be calculated if the dimensions of each stratum are recorded (area = π x (radius$_1$ + radius$_2$) x length). A 30-cm long section is about the maximum size bole section that can be conveniently transported and processed. A single secondary sample unit consists, therefore, of three 30-cm sections taken, one from each of the three vertical strata described above. The mean density on boles for a plot is:

$$\bar{x} = \frac{\sum_{i=1}^{n} \left(\sum_{i=1}^{3} \frac{a_i}{a} X_i \right)}{n}$$

where a_i is the area of the i^{th} stratum, a is total area, X_i is the larval density on the section taken from the i^{th} stratum, and n is the number of trees sampled.

On limbs, larval density decreases steadily from the base of the crown to the top. I have arbitrarily suggested three vertical strata (lower, middle, and upper thirds) within the crown. The ratios of average limb size from the lower third to the top are, respectively, 4:4:1. The ratios of total limb surface area are 2:2:1. To obtain a representative sample, the number of limbs that should be taken from a tree are one, one, and two from the lower third, middle third, and top third, respectively. Since this would be a representative sample, the four limbs could be processed in the same rearing unit. The mean larval density for the plot would be:

$$\bar{x} = \frac{\sum_{i=1}^{n} (l/a)}{n}$$

where l is total larvae from the three limbs of a tree, a is the total surface area of the three limbs, and n is the number of trees sampled.

Since there was no significant trend in density on foliated twigs, the foliage and twigs of a single midcrown branch from each tree would be a sufficient secondary sample unit for that substrate.

The correlation of larval density on limbs with the density on boles of individual trees is low ($r^2 = 0.57$) and consequently the prediction interval of an estimate based on regression is large. The correlation is higher ($r^2 = 0.76$) and prediction intervals are narrower when the data are consolidated to a per plot basis. Since pest managers are interested in estimating larval density for a plot and not for an individual tree, estimated density on limbs has potential as an index to density on boles. Prediction intervals will, however, be wide.

The data of the three studies used in the limb-bole regressions were obtained by somewhat different techniques. Further studies using more uniform methods and a larger data base may indicate a higher correlation.

The amount of labor required to estimate density on boles is probably prohibitive when more than 20 trees must be felled. Furthermore, most land managers would be reluctant to allow such routine destruction of timber for insect sampling. Assuming that 20 trees is the maximum number that could be sampled, density estimates on boles

could be made within the 0.3 precision level for densities approximately as low as 55 larvae per m^2.

A major drawback in using predetermined sample sizes as presented here is that prior knowledge of the population mean is necessary to determine the required sample size. Either a preliminary sample must be taken or some index must be used to make the preliminary estimate. Bole larval density (mean per plot) for this study ranged from 50 to 189 per m^2. Defoliation by the preceding generation was light but readily visible to an observer on the ground and was highly visible at the higher density. Since required sample size increases rapidly at densities below 50 per m^2, sampling would not be practical in stands where defoliation is not apparent by ground observation. Similarly for limbs, required sample size increases rapidly below the lowest mean density (43 per m^2) sampled for this study.

On foliated twigs, the lowest mean density sampled was 4.79 per m^2. Required sample size rises rapidly below that density indicating that sampling foliage also is not practical where defoliation is not apparent.

The reliability of these sampling designs depends upon the accuracy in estimation of the $\overset{*}{m}$ - m regressions. That is, the sampling designs that were derived are based on statistics which are themselves subject to sampling error.

Both the overall and within-tree distributions require further verification. The estimates of the overall distributions are based on three or four sampling points, which is a very minimal number for a regression. Also, my data are from populations ranging from low to moderate density. The highest overall mean density that I observed on boles was 189 larvae/m^2. This is low compared to 498/m^2 observed by Buckhorn et al. (1958) and 513/m^2 observed by Carolin and Coulter (1972). Unfortunately, I could not use the data of these two earlier studies in the sampling designs for reasons discussed earlier.

Foliated twigs may be the most useful substrate in sampling hibernating larvae due to the low number of required samples compared to those for boles and limbs. They are also lighter and easier to transport. Future studies should focus on the following aspects: (1) verification of the α and β statistics, (2) accuracy of density on foliated twigs as an index to density on boles and limbs, and (3) accuracy of density on foliated twigs as a predictor of density of subsequent feeding stages.

Conditions that would affect within- or between-tree variation will also affect the $\overset{*}{m}$ - m relationships and in

turn would change the sample curves. Plot size is one factor that could affect the overall distributions. As plot size increases, between-tree variation will increase. These sample designs should therefore be used only on plots of approximately the same size (2-ha) as used in these studies.

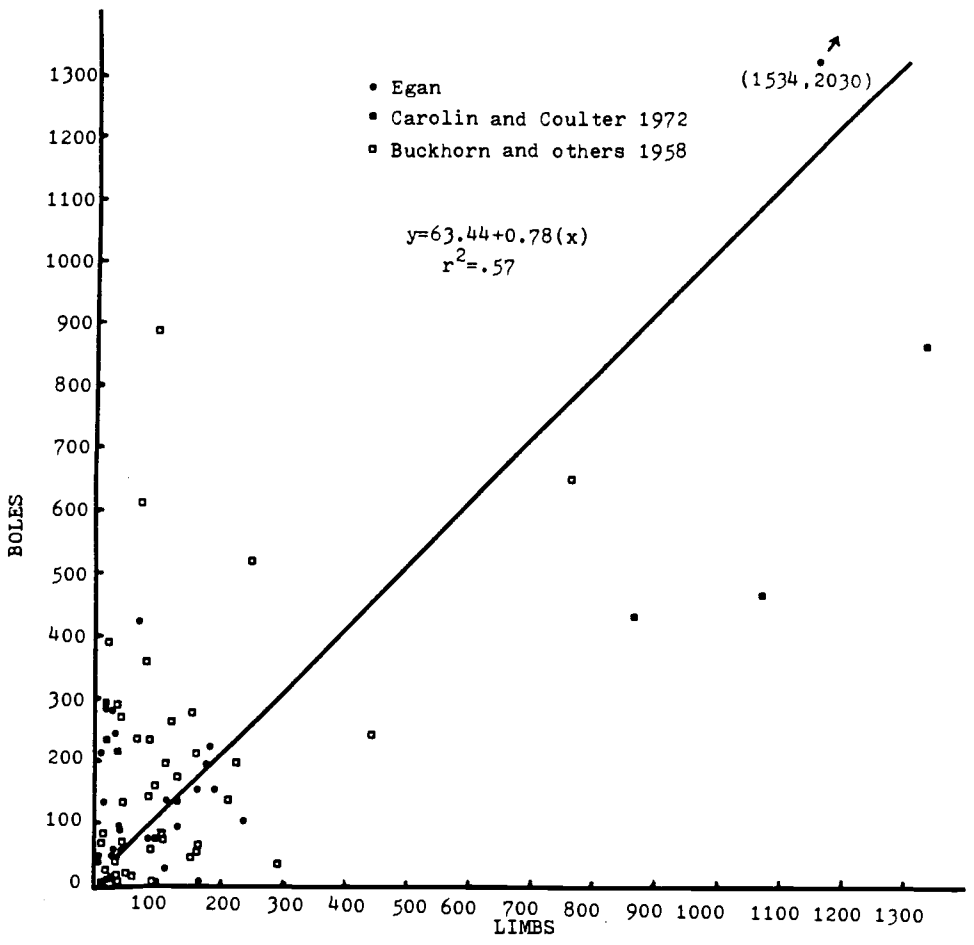


Figure IV.1. Larval density (larvae per m^2) on boles vs. larval density on limbs for individual trees.

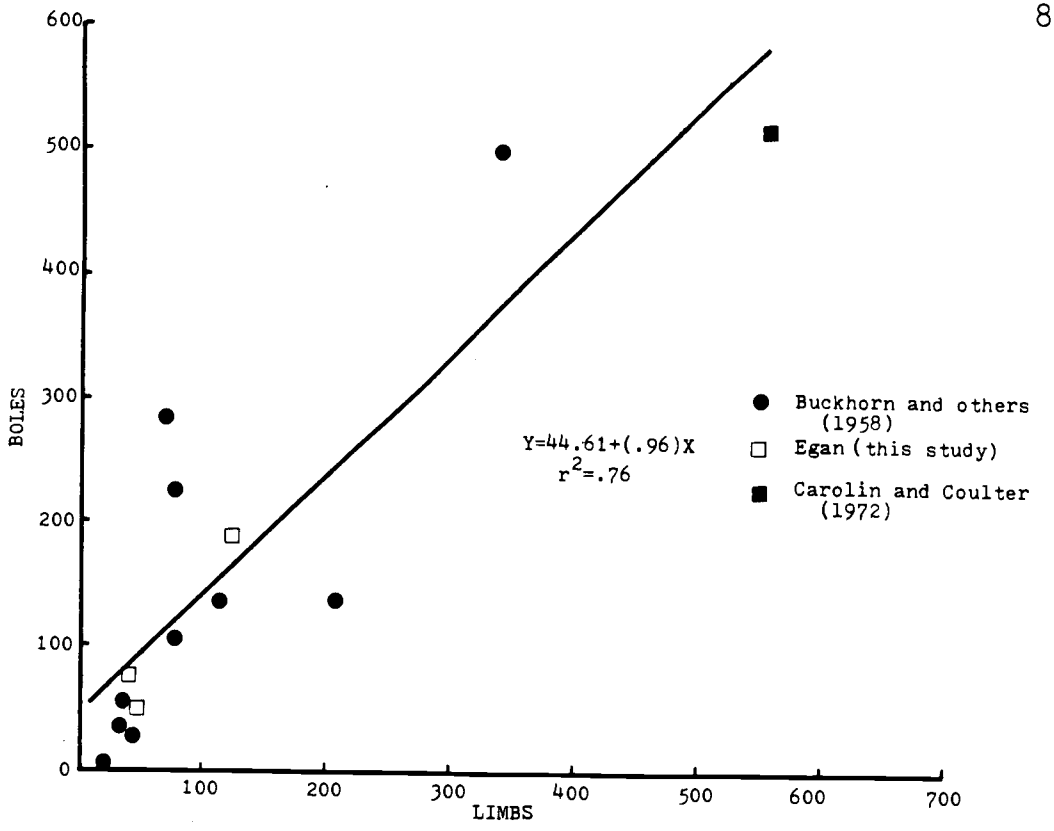


Figure IV.2. Larval density (larvae per m^2) on boles vs. larval density on limbs for overall plot means.

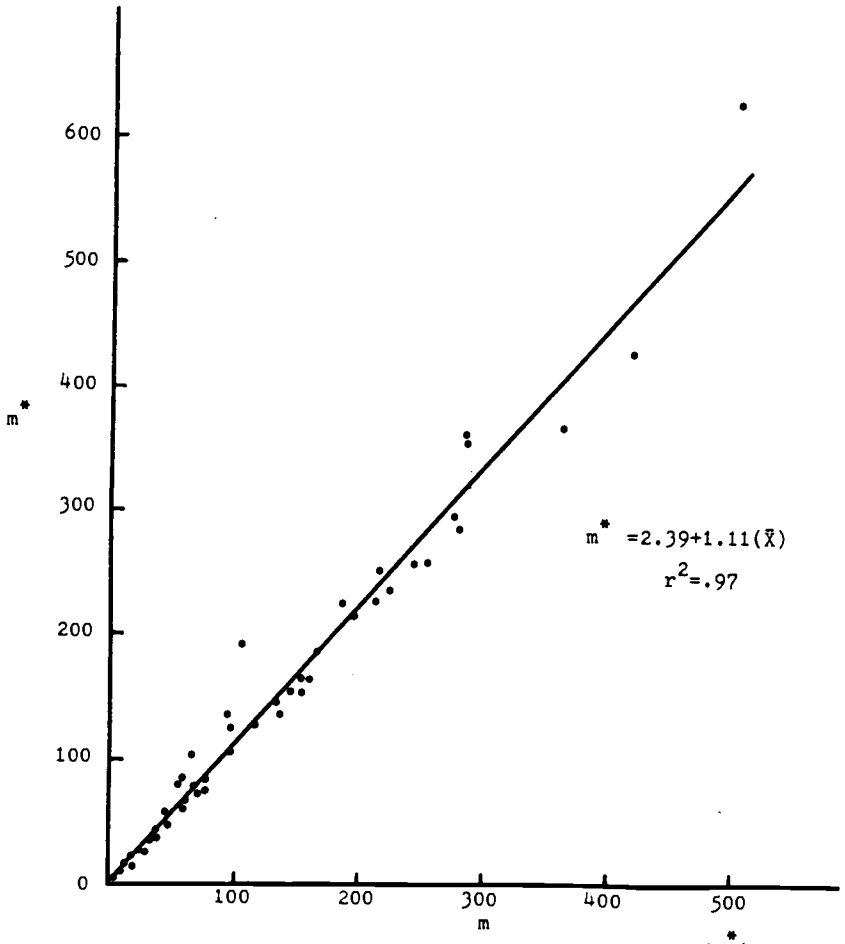


Figure IV.3. Within-tree relationship of mean crowding (m^*) vs. mean density (m) for boles.

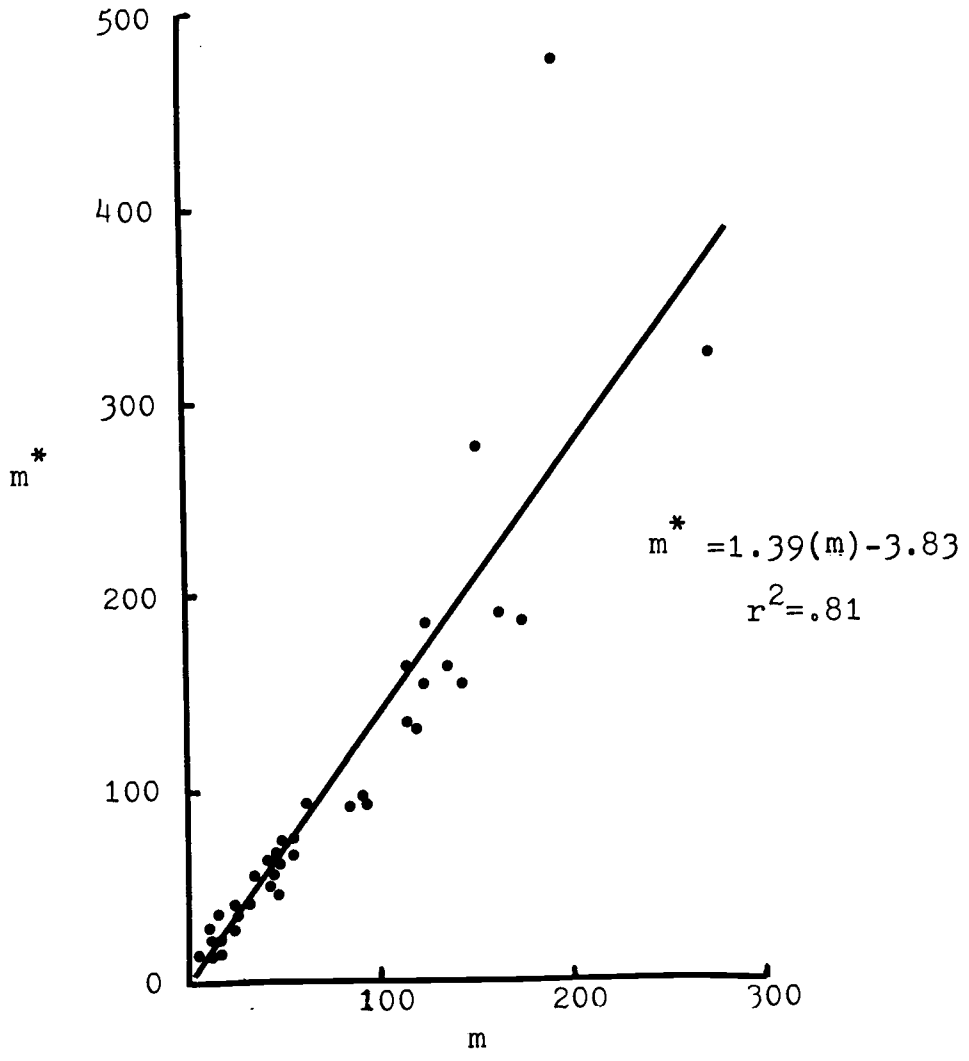


Figure IV.4. Within-tree relationship of mean crowding (m^*) vs. mean density (m) for limbs.

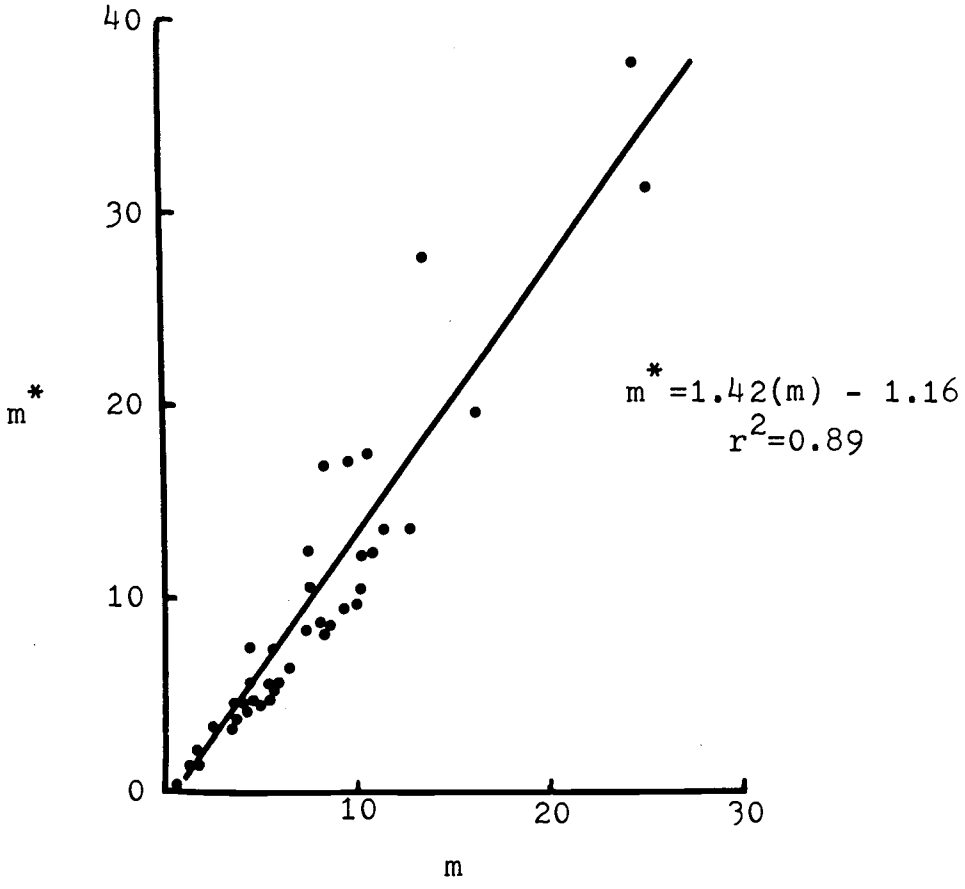


Figure IV.5. Within-tree relationship of mean crowding (m^*) vs. mean density (m) for foliated twigs.

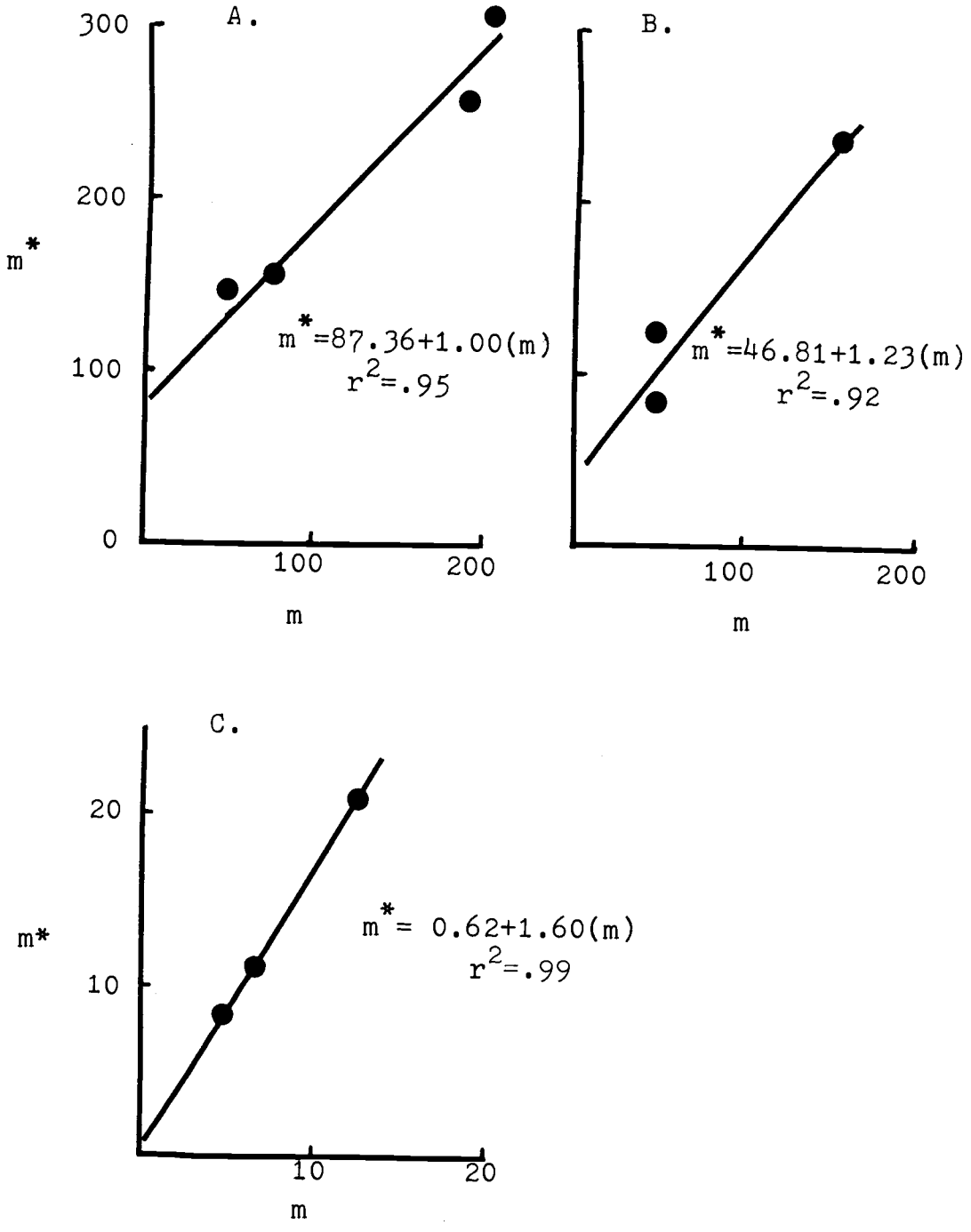


Figure IV.6. Overall relationships of mean crowding (m^*) vs. mean density (m) for (A) boles, (B) limbs and (C) foliated twigs.

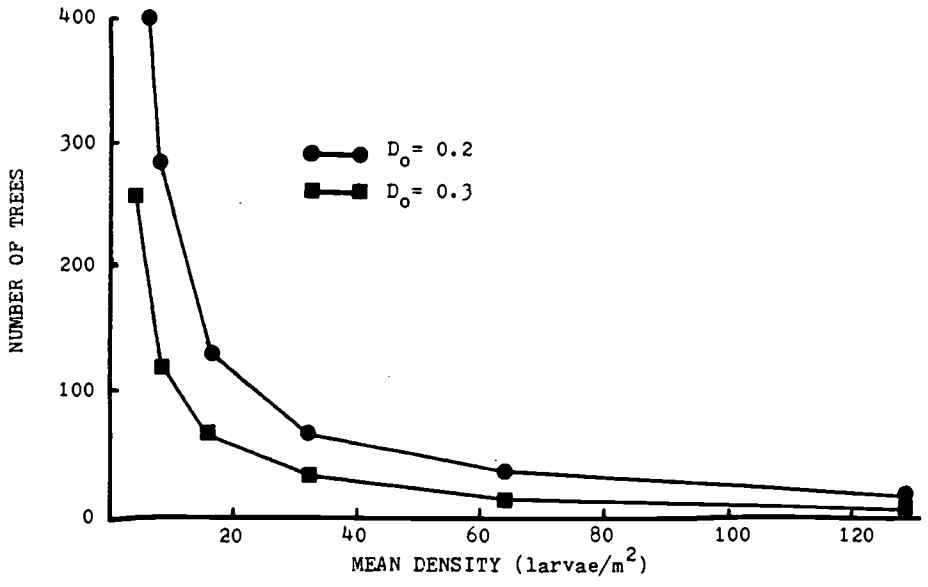


Figure IV.7. Required numbers of trees to estimate mean larval density on boles.

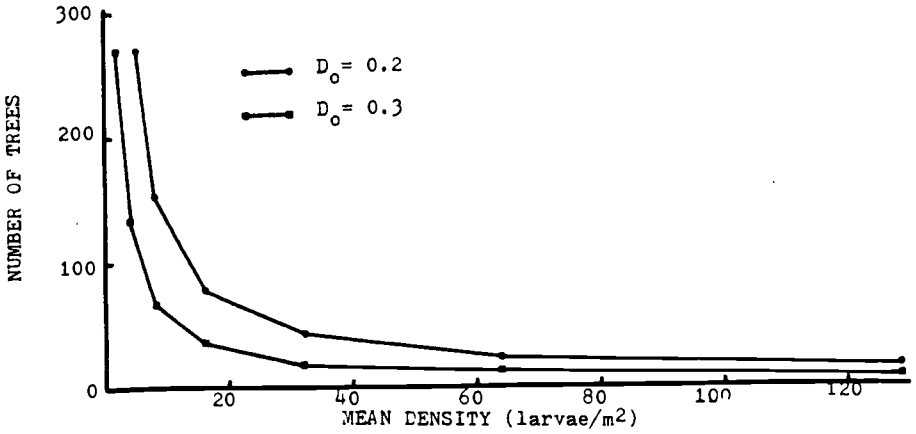


Figure IV.8. Required numbers of trees to estimate mean larval density on limbs.

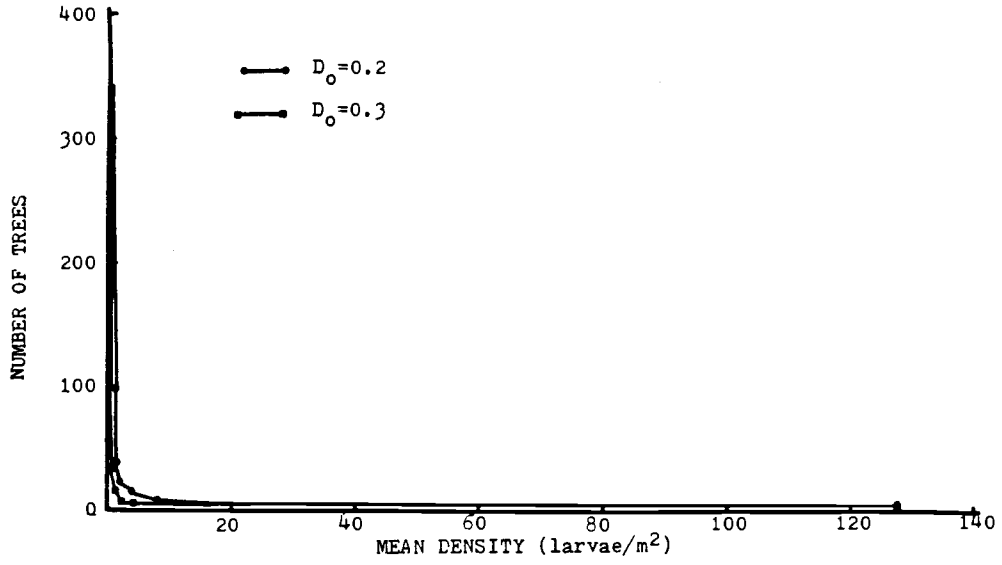


Figure IV.9. Required numbers of trees to estimate mean larval density on foliated twigs.

Table IV.1. Within and among tree means, variances and $\overset{*}{m}$ - m statistics for hibernating larvae[1/].

Substrate	Within or Among Trees	Mean Density	Mean Variance	Ratio of Variance to Mean	α	β
Boles	Within	125.64	3362.64	27	2.39	1.11
	Among	125.64	11496.82	92	87.36	1.00
Limbs	Within	74.18	3414.54	46	-3.83	1.39
	Among	74.18	5050.36	68	46.81	1.23
Foliage	Within	7.59	34.86	5	-1.16	1.42
	Among	7.59	52.52	7	0.62	1.60

[1/]Density expressed as number of larvae per m^2.

Table IV.2. $\overset{*}{m}$ - m regression statistics for egg masses, hibernating larvae, and feeding larvae.

Statistic	Within or Among Tree	Stage			
		Egg Masses[1/]	Larvae Hibernating on Foliage	Feeding Larvae[1/]	Pupae[1/]
α	Within	---	-1.16	4.84	0
	Among	14.62	0.62	26.58	7.68
β	Within	---	1.42	1.23	1.60
	Among	1.55	1.60	1.01	1.34

[1/] from Campbell and Srivastava (1982, unpublished).

Chapter V Mortality Factors of Early Larvae of the Western Spruce Budworm

Abstract

Survival of early instar western spruce budworm eggs and larvae was studied on two plots in northcentral Washington. Results are given in partial life tables which include survival rates for four age intervals: oviposition to eclosion, eclosion to the beginning of hibernation, during hibernation, and from the end of hibernation to the beginning of feeding in the spring. Survival over all four age intervals was 30% and 12% for the South Salmon Creek plot and the Bill Smith's Place plot, respectively. Survival during the egg stage and during hibernation was high in both plots, indicating that most mortality occurred during fall and spring dispersal. Mean survival during hibernation was 77%.

Introduction

Eggs of the western spruce budworm are deposited in July or August. Soon after eclosion, the larvae locate a hibernation site where they spin protective hibernacula, molt to the second instar, and lie dormant until the following spring (Fellin and Dewey 1982). Several factors cause high mortality during this 9 or 10 month period. The eggs, which are deposited on the foliage of host trees, are attacked by a parasitoid (Trichogramma minutum) (Carolin and Coulter 1959) and probably by predators (birds, mites, and insects). In their search for a hibernation site many larvae drop or are blown from the host trees (Beckwith and Burnell 1982). Larvae that drop to the ground may desiccate or overheat if the soil surface is hot and dry. Those that are blown too far from host foliage may successfully hibernate but will starve or desiccate before relocating a suitable host for feeding in the spring (Wellington and Henson 1947). Even larvae that hibernate in close proximity to host foliage are subject to desiccation or may drop or be blown away prior to establishing a feeding site in the spring. They are subject to predation by birds, spiders, and insects while searching for a hibernation site, during hibernation, and while searching for suitable host foliage

in the spring. There are two species of Hymenoptera (Glypta fumiferana (Vier.) and Apanteles fumiferana Vier.) which parasitize the newly hatched larvae (however, the parasitized larvae successfully overwinter and do not succumb until the following summer) (Carolin and Coulter 1959). Mortality that occurs during the search for a hibernation site in the fall and during the search for a feeding site in the spring was termed "dispersal mortality" by Morris et al. (1956). He showed that in eastern Canada, fall and spring dispersal mortality cause the greatest losses during the early instars of the spruce budworm.

Population density of budworm eggs, larvae, and pupae can be expressed on the basis of per unit area of foliage. Since it is not practical to measure the actual surface area of the needles of a conifer, it is expressed as the index $A = l \times w/2$ where l = the length of the foliated portion parallel to the axis of the limb and w = the width of the foliated portion perpendicular to the limb axis. The hibernating stage, however, occurs on all parts of a tree and unit area measurements of bark surface area are not compatible with the foliage area index. If studies of intra-generation survival are to include estimates of hibernating larval density, the density estimates must be

made on a per tree basis rather than per unit area of foliage.

Because of this difficulty in sampling hibernating larvae, population estimates are usually made for the egg stage and then again for larvae the following spring. Mortality occurring during fall dispersal, hibernation, and spring dispersal are, therefore, usually lumped together in population dynamics studies (McKnight 1971, Campbell et al. 1983).

The objective of the current study was to estimate total within-tree budworm populations so that survival could be estimated for the egg stage and for those three age intervals which have formerly been lumped together. The techniques and findings described in the previous chapters for sampling hibernating larvae were employed in order to accomplish this objective.

Materials and Methods

The studies were performed on 2 plots in the Okanogan Highlands of northcentral Washington. The South Salmon Creek plot was on state-owned land about 11 km south of Conconully, Washington, at an elevation of 950 m. Basal area of the standing timber was about 4.3 m^2 per hectare composed of 24% Douglas-fir, 61% ponderosa pine, 14% western larch, and 1% lodgepole pine with mean diameter at breast height of 13.9-cm, 19.1-cm, 18.5-cm, and 8.0-cm, respectively. Larval density during the preceding generation (1979-80) was about 15 larvae/m^2 at the fourth instar, resulting in low but visible defoliation.

The Bill Smith's Place plot was about 8 km northwest of Conconully on Road 365 in the Conconully Ranger District at an elevation of 1,160 m. Basal area of standing timber was about 11.1 m^2 per hectare composed of about 96% Douglas-fir, 4% western larch, and with a minor fraction of ponderosa pine and lodgepole pine. Mean diameter at breast height of the Douglas-fir and western larch were 22.9 cm and 19.1 m, respectively. Both plots are within the Okanogan Highlands Province as characterized by Franklin and Dyrness (1973). Larval density of the preceding generation was about 43

larvae per m^2 (Beckwith, personal communication) and caused heavy defoliation of the new growth.

Estimating Total Hatched Eggs per Tree. Egg mass density was estimated on 10 trees at each plot during August 1980. For this estimate, 2 branches were cut from either 2 or 3 vertical strata of each tree. The area of each branch was recorded [(length x width)/2] and all of the foliage on one side (randomly selected) of the branch was inspected for egg masses. The number of egg masses per m^2 was calculated. These same trees were later felled (see the section on Estimation of Total Hibernating Larvae, this chapter) and total foliage area was estimated so that the total number of egg masses per tree could be calculated.

The average number of hatched and unhatched eggs per egg mass was determined from a subsample of the egg masses from each plot (n = 47 for South Salmon Creek and n = 55 for Bill Smith's Place).

The difference (mean eggs per mass - mean unhatched eggs per mass) is the mean number of successfully hatched larvae per mass. The product (total foliage area x hatched eggs per mass x egg masses per m^2) is the estimated total first instar larvae on a tree. Total foliage area is the mean area for the 10 trees that were felled for the hibernation sample.

Estimating Total Hibernating Larvae per Tree. During the first week of April 1981, the same 20 trees that were sampled for egg masses were sampled for hibernating larvae. The trees were felled and sampled as described in Chapter III, except that 10 sections from the bole and 16 branches were processed from each tree. The larvae were reared from the samples and total larvae per tree was estimated.

A sample of the larvae emerging from hibernation (56 from South Salmon Creek and 69 from Bill Smith's Place) were provided with artificial diet and reared. Parasites (G. fumiferana and A. fumiferana) emerging from the larvae were counted and percent parasitization was calculated.

Only a fraction of the hibernating larvae in a sample are recovered from the rearing boxes (Table II.1). To estimate this proportion, small branch sections were artificially infested with known numbers of hibernating larvae (by the method described in Chapter II) and fastened to plot trees on September 5, 1980. Fifteen of these branch sections were installed at South Salmon Creek and 20 were installed at Bill Smith's Place. These branch sections were retrieved in April 1981, when the trees were being felled for the hibernation sample. They were placed in 1 liter rearing boxes and the number of larvae recovered was tabulated.

A portion of the larvae on the small branch sections died during the winter. Since the dead larvae could not be recovered from the branch sections, including them in the number of larvae that could potentially emerge would cause an error in adjusting for the inefficiency of the rearing boxes. Survival of hibernating larvae was estimated by marking hibernating larvae on a second set of branch sections which were left in place until June 1981, after emergence was completed as described below (Estimation of Survival During Hibernation). The mean total number of live hibernating larvae per tree was therefore estimated by:

$$H_{II} = T \times [r/(n \times s)]$$

where H_{II} is the total number of live hibernating larvae in April, T is the estimated total number of larvae per tree unadjusted for inefficiency of the rearing box method, r is the number of larvae recovered from the small branch sections, n is the number of larvae on the branch sections at the time of installation in the field, and s is the percent survival of marked larvae.

Estimation of Survival During Hibernation. Fourteen small branch sections (17-cm long by about 2.5-cm diameter) were infested with hibernating larvae by the

method described in Chapter II. Individual hibernacula were located using a dissection microscope and marked with a metal pin. On November 8, 1980, 7 of the sections were fastened to trees in Bill Smith's Place and 7 to trees at South Salmon Creek. The sections were left in place until June 1981, when they were retrieved and the hibernacula inspected using a dissection microscope. If a single, circular hole was found in a hibernaculum, the larva was considered to have successfully emerged. If a desiccated larva was found inside, it was counted as dead. If a hibernaculum was damaged with an irregular hole and contained no larva, or if the hibernaculum was missing, the larva was counted as dead. Percent survival and percent mortality due to the various categories were calculated. This part of the experiment was repeated in the winter of 1981-82. Samples for the 1981-82 season were installed on September 1, 1981. Thirteen were installed at South Salmon Creek and 14 at Bill Smith's Place. They were retrieved in June of 1982.

Estimating Total Feeding Larvae per Tree. During June 1981, 20 trees at each plot were sampled to determine the density of larvae that had established feeding sites. The 45-cm terminal was cut from each of 2 midcrown branches of each tree. The area of each terminal was recorded and the

terminals were inspected for larvae. The mean number of larvae per m^2 was calculated and mean whole stand density was estimated from the regression method of Srivastava et al. (1982) where whole stand larval density = (0.238)x mean density on midcrown branch terminals. The product of mean density and mean foliage area of the 20 trees sampled for hibernating larvae equaled the estimated total feeding larvae that would have occurred on the trees sampled for hibernating larvae.

Results and Discussion

The estimated total eggs and total hatched eggs per tree are given in Table V.1. Total hatched eggs equaled the total first instars. Total hibernating larvae (H_{II}) per tree are given in Table V.2, and feeding larvae (L_f) in Table V.3. The distribution of larval instars at the time of sampling was determined from head capsule measurements. For South Salmon Creek, 9% were third instar, 84% were fourth instar and 7% were fifth instar (n = 188). For Bill Smith's Place, 82% were third instar and 18% were fourth instar (n = 151). Survival of the marked hibernating larvae for both plots during both years is shown in Table V.4.

The survival of early instar larvae as calculated from the previous data is summarized in life table format (Table V.5) and Fig. V.1.

Overall survival from eggs to L_f was 30% and 12% for South Salmon Creek and Bill Smith's Place, respectively. Survival in other plots in northcentral Washington ranged from 4% to 24% (Beckwith, personal communication). With the spruce budworm, Mott (1963) presented some evidence that mortality during the early instars was density dependent. Campbell et al. (1983), however, found no relationship between egg density and survival rate of the western spruce

budworm. They concluded that "density-related processes may play a relatively minor role during this age interval."

Survival of eggs was high (96%) in both plots. Trichogramma minutum is a common hymenopterous egg parasite of the western spruce budworm and the spruce budworm. Carolin and Coulter (1959) recorded low mean percent parasitism (<5.5%) of western spruce budworm eggs from several sites in Oregon over a 5-year period. McKnight (1971) found a mean of 1.0% parasitism from the egg through the third instar for two generations on six plots in Colorado. Harris and Dawson (1972) found 17% egg parasitism in British Columbia. Torgersen et al. (1984) found a mean of 1.2% parasitism by Trichogramma over a wide range of western spruce budworm densities (<1 to 70 egg masses per m^2).

Highest mortalities occurred during fall and spring dispersal in both plots. Morris et al. (1956) had similar results with the spruce budworm in New Brunswick. Miller (1958) suggested several "probable" mortality factors to account for these large losses but stated that "wastage of a part of the population on nonhost material. . .is probably the ultimate fate of a major portion of the population as a result of spring and fall dispersal." Beckwith and Burnell (1982) studied larval density in the spring of 1980 adjacent to my "Bill Smith's Place" plot by hanging sticky traps at

various heights within the canopy. The highest traps (10 m) caught the greatest number of larvae and the lowest traps (0.5 m) caught the least. They concluded that this pattern was due to a filtering effect of the forest canopy which would intercept falling larvae, and that only about 25% of all dispersing larvae would perish by falling to the non-host material below the canopy. Régnière and Fletcher (1983) had similar findings on the spruce budworm in Ontario. They observed that most first instar (i.e., fall) dispersal was within the tree crowns. Second instars dispersed more readily between tree crowns. Only about 5% of the population ultimately landed on the ground and about 15% of those proceeded to crawl back up the trunks of trees.

Various studies have shown that dispersal losses are related to forest composition and structure. Morris et al. (1956) observed 60% dispersal mortality of the spruce budworm in dense balsam fir stands and 93% in 5-acre plots surrounded by clearcutting. Jennings et al. (1983) found that strip clearcutting increased dispersal losses of the spruce budworm and that spring dispersal losses were higher than fall losses. They concluded, however, that "such losses may be insignificant in terms of overall generation survival." The observations of these other studies (Beckwith and Burnell 1982, Régnière and Fletcher 1983, and

Jennings et al. 1983) indicate that most of the dispersal mortality observed in my study and by Morris et al. (1956) occurred within the canopy and was not due to wastage by dispersal to non-host material. Predation by birds and arthropods is a likely explanation of these losses.

Survival during hibernation was high and relatively constant on both plots for the two years studied. Overall mean survival was 77%. Most mortality was termed "desiccation" but the actual cause is unknown. It may have been due to excessive solar radiation (Wellington and Henson 1947). The sections were fastened to the south sides of trees below the crown. At times when the sun was shining on a given branch section, about half of the larvae would be on the exposed side. Some of these larvae may also have suffered from some physiological defect. The category of "damaged hibernaculum" is subjective. It was interpreted as predation but could possibly be due to weathering (i.e., ice formation and thawing) or to handling during installation and retrival of the branch sections. Miller (1958) reported 84% survival of spruce budworms during hibernation which included both artificially and naturally infested branches. He found very little variation in such mortality during a nine-year study and found no variation associated with stand type. Lucuik (1984) showed that exposing spruce budworms to

simulated rainfall during emergence was deleterious. Mortality increased from 18% with no rainfall to 85.8% with eight days of rainfall. He believed that larvae within hibernacula were not affected by the rainfall and that the mortality was due to washing of the larvae from the host foliage after they emerged and attempted to feed. He also found that exposure of second, third, and fourth instars to freezing temperatures (-4°C) did not affect survival. Hibernating western spruce budworms are highly resistant to effects of cold temperatures (Terrell 1960). Minimum temperatures for the winter of 1980-81 were -14°C and -19°C for South Salmon Creek and Bill Smith's Place, respectively. Maximum temperatures were 31°C and 23°C, respectively (temperatures were recorded on minimum/maximum thermometers fastened to the south side of a tree bole at about 1.4 m above the ground). Unseasonably cold temperatures in spring could result in starvation of larvae by destroying new host foliage (Fellin and Schmidt 1973).

Percent parasitism by Apanteles and Glypta was low in my study compared to observations of other workers. Those species are often the predominant parasites of the western spruce budworm (Carolin and Coulter 1959, and Harris and Dawson 1979). Torgersen et al. (1984) analyzed the effects of parasites (including Trichogramma, Apanteles, and Glypta) on the population dynamics of the western spruce budworm and

concluded that "for the various host densities we observed over a large portion of the insects range, parasites may have a lesser role in the population dynamics of the western spruce budworm than previously thought."

From my results and this literature review, I conclude that: (1) most mortality during the early instars occurred during the fall and spring dispersal intervals, (2) most of this mortality probably occurred within the canopy rather than from deposition of larvae on non-host material below the crown, and (3) larvae are well protected from predation and severe weather during hibernation. My results are based on very limited data all collected within the same geographic region. I cannot draw conclusions on the differences in survival between the two study plots or between fall and spring dispersal losses.

Silvicultural manipulation of stand structure and composition is the most promising method of reducing western spruce budworm survival during these early instars. Future studies should be initiated to compare larval survival over a range of stand parameters.

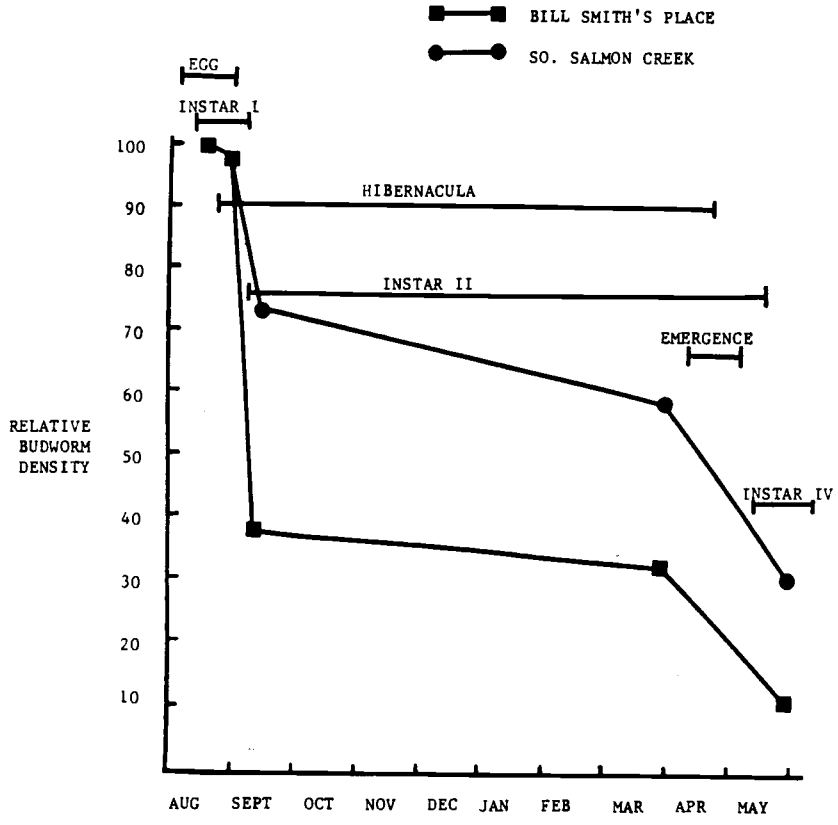


Figure V.1. Survivorship curves for the western spruce budworm through the early instars on two sites in northcentral Washington, 1980-1981.

Table V.1. Egg masses per m^2 and total eggs per tree, August 1980[1/].

Plot	1 Mean egg mass density (m^2)	2 Mean eggs per mass	3 Mean hatched eggs per mass	4 Mean foliage area per tree (m^2)	(1 x 2 x 4) Total eggs per tree	(1 x 3 x 4) Total hatched eggs per tree
South Salmon Creek	1.71	36.44	35.12	56.90	3,546	3,417
Bill Smith's Place	12.46	35.91	34.59	41.40	18,524	17,843

[1/]All surface areas are mean areas of the 10 trees from the hibernation sample.

Table V.2. Hibernating larvae per m^2 and total hibernating larvae per tree, April 1981[1/].

Plot	Bole		Foliage		Limbs		Dead Branches		Total larvae per tree
	Mean density	Total area	Mean density	Total area	Mean density	Total area	Mean density	Total area	
South Salmon Creek	50.03	5.06	4.77	56.90	48.9	8.57	12.78	2.69	977
Bill Smith's Place	189.30	9.25	12.52	41.40	150.7	8.56	89.60	3.56	3,878

Adjustment for inefficiency of collection method:

South Salmon Creek

adjusted larvae per tree = H_{II} = T/[r/(n x s)] = 977/[1123/(3001 x 0.796)] = 2078

Bill Smith's Place

adjusted larvae per tree = H_{II} = T/[r/(n x s)] = 3878/[1867/(3392 x 0.86)] = 6059

Where H_{II} is the total number of live, hibernating larvae in April, T is the unadjusted total, r is the number of larvae recovered from the small branch sections, n is the number of larvae on the branch sections at the time of installation in the field, and s is the percent survival of marked larvae.

[1/]All surface areas are mean areas of the 10 trees from the hibernation sample.

Table V.3. Feeding larvae per m^2 and total feeding larvae per tree, June 1981[1/].

Plot	Mean larval density on midcrown terminals	Larval density over entire stand[2/]	Total foliage area per tree	Total larvae per tree
South Salmon Creek	79.57	18.94	56.90	1,078
Bill Smith's Place	220.00	52.44	41.40	2,171

[1/] All surface areas are mean areas of the 10 trees from the hibernation sample.

[2/] Determined from regression given Srivastava et al. 1982.

Table V.4. Percent survival and mortality (± standard error) of marked larvae during hibernation.

	South Salmon Creek		Bill Smith's Place	
	1980-81	1981-82	1980-81	1981-82
Emerged	79.6 ± 5.7	71.2 ± 7.5	87.0 ± 6.5	76.1 ± 5.5
Desiccated larvae	14.4 ± 3.5	20.7 ± 8.2	5.9 ± 2.8	17.2 ± 3.7
Missing	0	8.1 ± 2.2	5.4 ± 2.6	3.6 ± 1.5
Damaged hibernaculum	6.0 ± 3.2	0	1.6 ± 1.6	3.1 ± 2.0
Number of branch sections	7	13	7	14

Table V.5. Partial life table for early instar larvae, 1980-81 generation[1/,2/].

Age interval	Mortality factor	South Salmon Creek N	South Salmon Creek M	South Salmon Creek 100 M/N	South Salmon Creek S	Bill Smith's Place N	Bill Smith's Place M	Bill Smith's Place 100 M/N	Bill Smith's Place S
Eggs (to eclosion)	Parasites, infertility, etc.	100	4	4	0.96	100	4	4	0.96
Eclosion to H I	Fall dispersal predation, etc.	96	22	23	0.77	96	58	61	0.39
During hibernation	Within hibernaculum	74	10.4	14	--	38	2.2	5.9	--
	Removal by predators, weathering	--	5.2	7	--	--	2.7	7.0	--
	Total	--	15.6	21	0.79	--	4.9	12.9	0.87
H II to L_f	Spring dispersal, predation, etc.	59	29	49	0.52	33	21	64	0.36
L_f	Parasitism	30.2	--	--	--	11.6	--	--	--
	by Apanteles	--	--	7.1	--	--	--	10.1	--
	by Glypta	--	--	3.6	--	--	--	5.8	--

[1/] N = number alive at beginning of age interval, M = number dying, M/N = proportion dying, S = survival.

[2/] H I = number of larvae at the beginning of hibernation in the fall. H II = number of larvae at the end of hibernation in the spring. H I = (1/survival during hibernation) x H II.

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