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Spruce Budworm Egg Mass Density on Balsam Fir: Low to Extreme Population Levels (Lepidoptera: Tortricidae)

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SPRUCE BUDWORM EGG MASS DENSITY ON BALSAM FIR: LOW TO EXTREME POPULATION LEVELS (LEPIDOPTERA: TORTRICIDAE)[1]

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ABSTRACT

A study was initiated in Michigan's Upper Peninsula to develop improved foliage sampling methods for spruce budworm, *Choristoneura fumiferana* (Clemens), egg masses. Four balsam fir, *Abies balsamea*, trees were chosen from each of four stands in 1979, and four balsam fir trees were chosen from one stand in 1980. The number of new egg masses, foliage surface area, and crown and quadrant classes of each branch were determined for all trees. Egg mass density for each part of the tree was determined by dividing total number of egg masses by total surface area. The 20 trees were divided into five groups with forecasted budworm damage varying from low to extreme. On the average the egg mass density (egg mass/1000 cm²) of the lower-crown was 58% lower than the egg mass density of the entire tree; the mid-crown had 18% higher egg mass density than the entire tree, the upper-crown had 63% higher density than the entire tree, and the tree top had 69% higher density than the entire tree. There was no strong trend to the small absolute differences in density among the four quadrants. Sampling at mid-crown may lead to over- or underestimation of tree egg mass density. The seriousness of such errors would depend on the bias and where the sample is taken vertically in the mid-crown.

The most recent outbreak of the spruce budworm, *Choristoneura fumiferana* (Clemens), has affected the spruce-fir forest type in Michigan since the mid 1970's. Much of the spruce-fir forest in Michigan is over-mature and is highly susceptible to spruce budworm. For specific information on impact see Mog et al. (1982).

The eggs of the insect are laid on balsam fir, *Abies balsamea* (L.) Miller, and white spruce, *Picea glauca* (Meunchhausen) Voss, in late summer. Within a two-week period the larvae hatch from the egg mass and disperse. Since the egg chorion remains on the foliage for a long period of time, in some cases more than a year, it is possible to assess the population density to be expected during the next spring. Branch samples are taken in late August and early September and examined for the number of hatched egg masses contained on them (the samples are taken shortly after the larvae diapause).

A number of sampling schemes have been developed which assist in predicting the population density and the expected damage during the next field season. Atwood (1944) used 18-in. branch samples in insect surveys in Ontario. Dowden and Carolin (1950) used 15-in. samples taken from the terminals of mid-crown branches. Morris (1954) developed a sequential sampling procedure for spruce budworm egg mass surveys in Canada based on either (1) a whole branch taken at the mid-crown of each tree, or (2) one whole branch taken from each of the first two quarters of the crown and one half branch taken from each of the other two quarters. Population density was expressed as the number of egg masses per 100 ft² of foliage surface and was assumed to have a negative binomial distribution. Waters (1955) stated that the number of egg masses of the spruce budworm on 15-in.-twig sampling units from balsam fir trees has approximately a negative binomial distribution. Wilson (1959)

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separated the tips of the shoots from the rest of the branch to reduce the amount of foliage examined for spruce budworm egg masses and increased the number of egg masses on the tips by 16% to obtain the total for the branch.

The Canadian Forestry Service (1975) developed a sequential sampling procedure for spruce budworm egg mass surveys in Newfoundland that assumed that the distribution of egg-masses per branch is approximately described by the negative binomial distribution. Three branches were collected in each sample location, and optimal sample size calculations indicated that 15 sample locations per 500 mi^2 would give suitable accuracy.

Carolin and Coulter (1959) found that either the lower or middle crown thirds could be used for sampling for egg masses of the western budworm, *Choristoneura occidentalis* Freeman, on Douglas-fir, *Pseudotsuga menziesii* (Mirbel) Franco. They examined two longitudinal half-branches from each of five trees in each plot and calculated egg masses per 1000 in.^{2} of foliage by computing branch surface as the product of foliated length and the width at the widest point of the longitudinal half-branches divided by 2. Carolin (1950) found that 15-in. twigs were least useful as a sample of egg mass density. McKnight (1967, 1968) found 24-in. branches from the mid-crown of Douglas-fir trees to be as good as half-branches for estimating numbers of egg masses of western budworm in Colorado. Carolin and Coulter (1972) sampled one whole branch at mid-crown for the egg stage in sampling western spruce budworm on Douglas-fir in eastern Oregon. Carolin and Coulter (1975) used whole branches taken at mid-crown for light infestations and two whole branches in the upper third, two longitudinal half-branches in the middle third, and one whole branch in the lower third of the crown for more severe infestations. They also found that egg mass density varied by tree species and position in the crown.

McKnight et al. (1970) developed a sequential sampling procedure for eastern budworm egg mass surveys in the central and southern Rocky Mountains based on 24-in. branches taken from the mid-crown. The 24-in. branches usually had 250 in.^{2} of foliage, and egg mass densities were converted to per 1000 in.^{2} of foliage which had approximately a negative binomial distribution.

The Canadian Forestry Service (1977) compared longitudinal ½ branch, 18-in. branch tip, and 10-in. branch tip sampling units by sampling two whole branches from each of the upper, middle, and lower crown levels selected from 20 trees from four respective defoliation categories. No significant differences in numbers of egg masses per 1000 in.^{2} were found among the four defoliation classes; however, significant between-tree, between-crown-level, and between-sample-branch size differences were found. Results indicated that 18-in. branches from mid-crown are probably the best sampling units. The number of trees versus the number of branches at a sampling point was examined, and it was found most efficient to take more branches from fewer trees.

One of the purposes of estimating egg mass densities in survey work is to predict the amount of defoliation that will occur in the next season to facilitate the planning of control activities. Webb (1958) predicted defoliation of balsam fir by relating probable percent loss to new growth as a function of egg masses per 100 ft^2 of mid-crown branch area. Terrell (1966) developed a curvilinear relationship between the density of egg masses of the western budworm and subsequent defoliation of Douglas-fir trees. Silver (1960) determined that the relationship between western budworm egg mass density and subsequent defoliation of Douglas-fir was better when data were grouped by age of outbreak. He did not consider egg mass density a reliable index of subsequent defoliation.

A study was initiated in Michigan in 1979 to develop improved foliage sampling techniques for spruce budworm egg masses. The specific objectives were to improve balsam fir and white spruce foliage sampling techniques to include (1) optimal type, size, and number of sampling units per tree for estimating egg mass densities at low to extreme spruce budworm population levels; (2) optimal number of trees per cluster and number of clusters per stand for estimating egg mass densities at low to extreme spruce budworm population densities; (3) optimum sampling schemes for white spruce, balsam fir, and spruce-fir for estimating egg mass densities at low to extreme spruce budworm population densities; and (4) a descriptive and photographic key for differentiating new and old egg masses on both white spruce and balsam fir. This paper is the first of a series of papers related to these objectives. In this paper we provide general descriptive information on methods and general descriptive statistics that have been obtained from our data sets on balsam fir and discuss how this affects

sampling for spruce budworm egg masses. The specific objective of this paper is to examine egg mass density at several different levels: budworm populations, trees, quadrants and crown classes for spruce budworm egg mass data on balsam fir collected in 1979 and 1980.

MATERIALS AND METHODS

This study was conducted in the Ottawa National Forest in Gogebic and Iron counties in Michigan's Upper Peninsula. The spruce-fir type is scattered throughout the region with individual stands ranging from about 30 acres up to about 100 acres in size. Foresters informally recognize two spruce-fir stand types: (1) "upland" spruce-fir and (2) "lowland" spruce-fir. The lowland spruce-fir consists largely of balsam fir, white spruce, and black spruce, *P. mariana* (Miller) Britton, Stearns, and Poggenberg; mixed with eastern larch, *Larix laricina* (Du Roi) K. Koch; and northern white cedar, *Thuja occidentalis* L.. Depending on the specific site conditions, upland spruce-fir is lagely a mixture of balsam fir and white spruce along with white birch, *Betula papyrifera* Marshall; trembling aspen, *Populus tremuloides* Michaux; big tooth aspen, *P. grandidentata* Michaux; red maple, *Acer rubrum* L.; sugar maple, *A. saccharum* Marshall; and yellow birch, *B. alleghaniensis* Britton. Balsam fir and white spruce range in age from about 35 to 80 years old over much of the area, although isolated trees range up to 130 years of age. The land is gently rolling with elevational differences ranging up to about 500 ft. The mean annual temperature is 4.8°C and the mean annual precipitation is 81.5 cm (based on 30 yr. averages). Spruce budworm populations at outbreak levels have been in the area since the early 1970's. In individual stands, budworm population levels have varied from low to extreme.

Nine study areas were established in nine respective stands in 1979 and 1980. A summary of the experimental designs for 1979 and 1980 is presented in Tables 1 and 2. Four spruce-fir

Table 1. Summary of the experimental designs for 1979 on balsam fir trees (moderate to extreme defoliation).

No. of Stands			Clusters per stand	Trees per cluster			Number of trees of each type in each defoliation class			
Defoliation				Defoliation						
Moderate	Extreme	Total		Moderate	Extreme	Total	Feasible[a] Branch	Every[b] Branch	Sampling Scheme	Total
2	2	4	1	5	5	10	3	1	1	5

[a] All feasible branches were also identified and sampled on Every Branch and Sampling Scheme trees.
[b] All whole branches were also sampled for Sampling Scheme trees.

Table 2. Summary of the experimental designs for 1980 on balsam fir and white spruce trees (light defoliation).

No. of Stands	Clusters per stand	Trees per cluster			Number of trees of each type for each species			
		Species						
		Balsam Fir	White Spruce	Total	Feasible[a] Branch	Every[b] Branch	Sampling Scheme	Total
5	1	4	4	8	2	1	1	4
1[c]	1	10	0	10	6	2	2	10

[a] All feasible branches were also identified and sampled on Every Branch and Sampling Scheme trees.
[b] All whole branches were also sampled for Sampling Scheme trees.
[c] This stand is one of the 5 stands containing an 8-tree spruce-fir cluster (4 balsam fir and 4 white spruce). The 4 balsam fir trees served two functions: 1) as a part of the 8-tree spruce-fir cluster and 2) as part of the 10-tree balsam fir cluster.

stands were selected in 1979. Two stands had moderate defoliation while two had extreme defoliation. One 10-tree cluster of balsam fir trees was established in each of the stands. Each cluster included five trees that had moderate defoliation and five trees that had severe defoliation. For three trees in each defoliation class and each cluster, those whole branches which were judged to be "feasible" for clipping with a pole pruner were examined and all egg masses were counted. All whole branches were examined for spruce budworm egg masses for two trees in each defoliation class and each cluster; for one of these trees in each class, each feasible branch examined was divided such that egg masses found respectively on 40, 50, 60, and 70-cm branch tips were tallied. All whole branches judged to be "feasible" for clipping with a pole pruner were identified for later data analysis. This information will be used to determine the optimum branch length to use as a sampling unit in subsequent data analyses.

In 1980, five additional stands were selected, but in this instance, only stands judged to have light defoliation were chosen. One eight-tree cluster (four balsam fir and four white spruce) was chosen from each stand. In one stand, a 10-tree cluster of balsam fir was chosen; four of these trees were the balsam fir trees belonging to the eight-tree cluster established in that stand. All whole branches were examined for egg masses on two trees of each species in each of the eight-tree clusters; for one of those trees each feasible branch was examined such that the number of egg masses on respetive branch lengths of 40, 50, 60, and 70 cm were tallied. Those branches considered "feasible" for clipping with a pole pruner were identified. For the 10-tree balsam fir cluster all whole branches were examined for egg masses on an additional two trees. One of these additional trees was examined such that the number of egg masses on respective branch lengths of 40, 50, 60, 70 cm could be tallied. Those branches considered "feasible" for clipping with a pole pruner were identified as before. Thus, there were four balsam fir trees in the 10-tree cluster that had whole branches examined for egg masses; two of these trees had all feasible branches examined for egg masses for branch lengths of 40, 50, 60, and 70 cm. All whole, feasible branches were examined and the egg masses contained were counted from the remaining trees.

The cluster center of each stand was randomly chosen from 0.5 to 2.5 chains from a section of a secondary truck trail or along a flagged line running through the stand. For each cluster, the 10 (or eight in 1980) closest trees exhibiting the desired characteristics were chosen using the following criteria: trees had to be approximately 30–60 ft tall with no dead tops and with varying live crown lengths. The total height, breast height age, stump height age, and diameter at breast height were determined for each tree. All branches in the mid-crown feasible for sampling with a pole pruner and large enough to yield a 70-cm-long branch from the tip of the branch were identified. Basal area per acre was estimated for the area immediately surrounding each cluster.

As mentioned earlier, for one tree (*every branch tree*) of each defoliation class for each species in each cluster, all branches on the entire tree were examined except for the small branches at the very top of the tree. The total branch length, foliated branch length, maximum foliated branch width, number of branch tips of new foliage, quadrant, and whether the branch was or was not feasible to obtain with a pole pruner was recorded. The distance from the ground to the center of the foliated portion of the branch was measured prior to clipping the branch from the tree. Then the branch surface area was estimated by placing small, cut twigs of the branch on a grid with a 2 cm mesh. Following this measurement, the number of new spruce budworm egg masses on new, old, and dead foliage was determined. The tree top where branches were less than 70 cm long was considered separately. The length of the foliated top, maximum foliage circumference, maximum stem diameter, number of new branch tips, foliated surface area, and number of new egg masses on new, old and dead foliage were determined.

For a second tree (*sampling scheme tree*) from each defoliation class for each species in each cluster, all branches were sampled the same way as was done for the *every branch trees*. In addition, for all branches which were considered feasible to sample with a pole pruner, the number of branch tips of a new foliage, maximum branch width, foliated branch surface area, and number of new egg masses on new, old and dead foliage were determined for the first 40, 50, 60, and 70 cm of branch from the branch tip. There are two *every branch*

trees, with one of these trees also being a *sampling scheme tree,* for each defoliation class (10 balsam fir trees) or species class (four balsam fir and four white spruce trees) of each cluster.

For the remaining trees (*feasible branch trees*) of each defoliation class for each species in each cluster, only the branches considered to be feasible to sample with a pole pruner were sampled, with the same data being recorded as for the *every branch trees.*

The live crown of each tree was divided into four directional quadrants: (1) north—N45°W to N45°E, (2) east—N45°E to S45°E, (3) south—S45°E to S45°W, and (4) west—S45°W to N45°W. All whole branches were classified as to quadrant when cut from the tree. The live crown of each tree was also divided vertically into three equal crown classes: (1) lower-crown, (2) mid-crown, and (3) upper-crown. The upper-crown included the branches in the upper third of the tree plus the tree top. All whole branches were classified to crown class. Branches were assigned to crown classes depending upon where the center of the foliated portion of the branch was located.

The accuracy of determining the number of new egg masses per branch was checked occasionally for each sampler without her or his knowledge at different times of the day. All new egg masses found were stored in vials by stand, cluster, tree, and branch number.

RESULTS

The 20 *every branch trees,* four from each of five stands, were divided into the following five groups by egg mass density (number of egg masses per 1000 cm²): Group 1, four trees, range 0.011–0.066; Group 2, three trees, range 2.20–3.07; Group 3, four trees, range 4.15–7.06; Group 4, six trees, range 10.55–12.91; Group 5, three trees, range 15.39–34.94. With reference to the damage expected at these densities (Dorais 1978), Group 1 would be classified as very light, Group 2 as between moderate and high, Group 3 as very high, and Groups 4 and 5 as extreme where the current year will not produce buds.

The average number of egg masses, foliage surface area, and egg mass densities for the trees in each of the five groups are shown in Table 3. Individual tree information is available from the authors.

In the results to follow, the means for number of egg masses and foliage surface area are arithmetic means, while the mean for egg mass density is a weighted mean (weighted by surface area). Unless otherwise stated, the upper-crown class includes the tree top.

Group 1—low. The average number of egg masses, foliage surface area (1000 cm²), and egg mass density (number of egg masses per 1000 cm² of foliage surface area) for four trees are shown in Table 3 for various parts of the tree.

The average number of egg masses per tree was 23.5 (range, 7–46). On the average, 11.7, 59.6, and 28.7% of the egg masses were found in the lower, middle, and upper thirds of the crown, respectively. The percentages of egg masses found in the north, east, south, and west quadrants were 18.4, 31.0, 19.6, and 31.0, respectively. The percentage of egg masses found in the tree top was 4.3.

The surface area per tree averaged 680.29 (range, 395.95–998.38). The surface areas in the lower, middle, and upper thirds of the crown were, on the average, 37.8, 50.3, and 11.9%, respectively. On the average, 21.1, 23.9, 25.2, and 30.8% of the surface area were in the north, east, south, and west quadrants, respectively. Less than 2% of the surface area was in the tree top.

The egg mass density per tree averaged 0.035 (range, 0.011–0.066). On the average, the lower-crown had 68.6% lower density than the entire tree; the mid-crown had 17.1% higher density than the entire tree; the upper-crown had 140.0% higher density than the entire tree; and the tree top had 134.3% higher density than the entire tree. The east quadrant had an egg mass density 23.5% higher than the entire tree; the south quadrant had 26.5% lower density than the entire tree; the west quadrant had 2.9% lower density than the entire tree; and the north quadrant had 11.8% lower density than the entire tree.

Group 2—moderate to high. The average number of egg masses, foliage surface area, and egg mass density for three trees are shown in Table 3 for various parts of the tree.

Table 3. Average number of egg masses, foliage surface area ($\times$ 1000 cm²), and egg mass density (no. egg masses per 1000 cm²).

Parameter	Tree WT[a]	Tree Top	Tree WOT[b]	Low	Mid	Upper (WOT)	Upper (WT)	N	E	S	W
						Crown Class				Quadrant	
Group 1—Low (4 trees)											
Mean Number of Egg Masses	23.50	1.00	22.50[c]	2.75	14.00	5.75	6.75	4.00	6.75	4.25	6.75
Mean Surface Area (x 1000)	680.29	12.19	668.10	257.39	342.16	68.55	80.74	134.04	158.87	167.90	204.93
Mean Egg Mass Density	0.04	0.08	0.03	0.01	0.04	0.08	0.08	0.03	0.04	0.03	0.03
Group 2—Moderate (3 trees)											
Mean Number[d] of Egg Masses	385.67	96.67	289.00	52.67	209.33	27.00	123.67	73.00	104.33	73.33	38.33
Mean Surface[d] Area (x 1000)	143.89	21.63	122.25	36.01	77.50	8.74	30.38	32.89	45.99	26.39	16.97
Mean Egg Mass[d] Density	2.68	4.47	2.36	1.46	2.70	3.09	4.07	2.22	2.27	2.78	2.26
Group 3—High (4 trees)											
Mean Number of Egg Masses	2146.50	82.25	2064.25	420.00	1337.50	306.75	389.00	675.75	439.25	348.50	600.75
Mean Surface Area (x 1000)	373.52	19.19	354.32	123.64	181.29	49.38	68.58	110.02	80.12	61.51	102.67
Mean Egg Mass Density	5.75	4.29	5.83	3.40	7.38	6.21	5.67	6.14	5.48	5.67	5.85
Group 4—Very High (6 trees)											
Mean Number of Egg Masses	1754.17	239.33	1514.83	253.83	925.83	335.17	574.50	323.83	272.00	436.33	482.67
Mean Surface Area (x 1000)	153.55	10.92	142.64	50.35	71.85	20.43	31.34	27.87	24.52	41.67	48.57
Mean Egg Mass Density	11.42	21.92	10.62	5.04	12.88	16.41	18.33	11.62	11.09	10.47	9.94
Group 5—Extreme (3 trees)											
Mean Number[e] of Egg Masses	4410.33	237.00	4173.33	490.00	2742.33	941.00	1178.00	1156.67	1290.00	1164.33	562.33
Mean Surface[e] Area (x 1000)	163.00	5.30	157.70	46.10	91.92	19.68	24.98	43.43	49.12	45.21	19.94
Mean Egg Mass[e] Density	27.06	44.72	26.46	10.63	29.83	47.82	47.16	26.63	26.26	25.75	28.20
All 20 Trees											
Mean Number of Egg Masses	1679.65	138.50	1541.15	242.10	990.80	308.25	446.75	417.55	379.95	387.10	356.40
Mean Surface Area (x 1000)	302.86	13.59	289.27	103.63	151.66	33.98	47.57	68.62	69.42	69.12	81.63
Mean Egg Mass Density	5.55	10.19	5.33	2.34	6.53	9.07	9.39	6.08	5.47	5.60	4.37

[a] With top

[b] Without top

[c] One branch from one tree was included in tree WOT but was not classified as to quadrant. Thus, the sum of the number of egg masses and foliage surface area across quadrants is less than the tree WOT values.

[d] There were no branches in (WOT) for one tree. This tree was assumed to have zero egg masses, surface area, and egg mass density for (WOT). All averages include these zero values.

[e] The high crown of one tree was completely dead. This tree was assumed to have zero egg masses, surface area, and egg mass density for tree top, (WOT) and (WT). All averages include these zero values.

The average number of egg masses per tree was 385.7 (range, 371–409). On the average, 13.6, 54.3, and 32.1% of the egg masses were found in the lower, middle, and upper thirds of the crown, respectively. The percentages of egg masses found in the north, east, south, and west quadrants were 25.3, 36.0, 25.4, and 13.3, respectively. The percentage of the egg masses found in the tree top was 25.1.

The surface area per tree averaged 143.89 (range 120.83–185.70). The surface areas in the lower, middle, and upper thirds of the crown were, on the average, 25.0, 53.9, and 21.1% respectively. On the average, 26.9, 37.6, 21.6, and 13.9% of the surface area were in the north, east, south, and west quadrants, respectively. Fifteen percent of the surface area was in the tree top.

The egg mass density per tree averaged 2.68 (range, 2.20–3.07). On the average, the lower-crown had 45.5% lower density than the entire tree; the mid-crown had 0.7% higher density than the entire tree; the upper-crown had 51.9% higher density than the entire tree; and the tree top had 66.8% higher density than the entire tree. The east quadrant had an egg mass density 3.8% lower than the entire tree; the south quadrant had 17.8% higher density than the entire tree; the west quadrant had 4.2% lower density than the entire tree; and the north quadrant had 5.9% lower density than the entire tree.

Group 3—high. The average number of egg masses, foliage surface area, and egg mass density for four trees are shown in Table 3 for various parts of the tree.

The average number of egg masses per tree was 2146.5 (range, 943–3527). On the average, 19.6, 62.3, and 18.1% of the egg masses were found in the lower, middle, and upper thirds of the crown, respectively. The percentages of egg masses found in the north, east, south, and west quadrants were 32.7, 21.3, 16.9, and 29.1, respectively. The percentage of egg masses found in the tree top was 3.8.

The surface area per tree averaged 373.52 (range, 227.08–499.86). The surface areas in the lower, middle, and upper thirds of the crown were, on the average, 33.1, 48.5, and 18.4%, respectively. On the average, 31.0, 22.6, 17.4, and 29.0% of the surface area were in the north, east, south, and west quadrants, respectively. Less than 6% of the surface area was in the tree top.

The egg mass density averaged 5.75 (range, 4.15–7.06). On the average, the lower-crown had 40.9% lower density than the entire tree; the mid-crown had 28.3% higher density than the entire tree; the upper-crown had 1.4% lower density than the entire tree; and the tree top had 25.4% lower density than the entire tree. The east quadrant had an egg mass density 6.0% lower than the entire tree; the south quadrant had 2.7% lower density than the entire tree; the west quadrant had 0.3% higher density than the entire tree; and the north quadrant had 5.3% higher density than the entire tree.

Group 4—very high. The average number of egg masses, foliage surface area, and egg mass density for six trees are shown in Table 3 for various parts of the tree.

The average number of egg masses per tree was 1754.2 (range, 1065–3239). On the average, 14.5, 52.7, and 32.8% of the egg masses were found in the lower, middle, and upper thirds of the crown, respectively. The percentages of egg masses found in the north, east, south, and west quadrants were 21.4, 18.0, 28.8, and 31.8, respectively. The percentage of the egg masses found in the tree top was 13.6.

The surface area per tree averaged 153.55 (range, 98.38–285.54). The surface areas in the lower, middle, and upper thirds of the crown were on the average, 32.8, 46.8, and 20.4%, respectively. On the average, 19.5, 17.2, 29.2, and 34.1% of the surface area were in the north, east, south, and west quadrants, respectively. Less than 8% of the surface area was in the tree top.

The egg mass density per tree averaged 11.42 (range, 10.55–12.91). On the average, the lower-crown had 55.9% lower density than the entire tree; the mid-crown had 12.8% higher density than the entire tree; the upper-crown had 60.5% higher density than the entire tree; and the tree top had 91.9% higher density than the entire tree. The east quadrant had an egg mass density 4.4% higher than the entire tree; the south quadrant had 1.4% lower density than the entire tree; the west quadrant had 6.4% lower density than the entire tree; and the north quadrant had 9.4% higher density than the entire tree.

Group 5—extreme. The average number of egg masses, foliage surface area, and egg mass density for three trees are shown in Table 3 for various parts of the tree.

The average number of egg masses per tree was 4410.3 (range 1139–9206). On the average, 11.1, 62.2, and 26.7% of the egg masses were found in the lower, middle, and upper thirds of the crown, respectively. The percentages of egg masses found in the north, east, south, and west quadrants were 27.7, 30.9, 27.9, and 13.5, respectively. The percentage of egg masses found in the tree top was 5.4.

The surface area per tree averaged 163.0 (range, 37.97–263.51). The surface areas in the lower, middle, and upper thirds of the crown were, on the average, 28.3, 56.4, and 15.3%, respectively. On the average, 27.5, 31.2, 28.7, and 12.6% of the surface area were in the north, east, south, and west quadrants, respectively. Less than 4% of the surface area was in the tree top.

The egg mass density per tree averaged 27.06 (range, 15.39–34.94). On the average, the lower-crown had 60.7% lower density than the entire tree; the mid-crown had 10.2% higher density than the entire tree; the upper-crown had 74.3% higher density than the entire tree; and the tree top had 65.3% higher density than the entire tree. The east quadrant had an egg mass density 0.8% lower than the entire tree; the south quadrant had 2.7% lower density than the entire tree; the west quadrant had 6.6% higher density than the entire tree; and the north quadrant had 0.6% higher density than the entire tree.

All Trees Pooled. The average number of egg masses, foliage surface area, and egg mass density for all 20 trees are shown in Table 3 for various parts of the tree.

The average number of egg masses was 1679.7 (range, 7–9206). On the average, 14.4, 59.0, and 26.6% of the egg masses were found in the lower, middle, and upper thirds of the crown, respectively. The percentages of egg masses found in the north, east, south and west quadrants were 27.1, 24.7, 25.1 and 23.1, respectively. The percentage of egg masses found in the tree top was 8.2.

The average foliage surface area was 302.86 (range, 37.97–998.38). On the average, 34.2, 50.1, and 15.7% of the surface area were in the lower, middle, and upper thirds of the crown, respectively. The surface areas in the north, east, south, and west quadrants were 23.8, 24.0, 23.9, and 28.3%, respectively. Less than 5% of the surface area was in the tree top.

The average egg mass density of the entire tree was 5.55 (range, 0.011–34.94). On the average, the lower-crown had 57.8% lower density than the entire tree; the mid-crown had 17.7% higher density than the entire tree; the upper crown had 69.2% higher density than the entire tree; and the tree top had 83.6% higher density than the entire tree. The east quadrant had an egg mass density 2.6% higher than the entire tree; the south quadrant had 5.1% higher density than the entire tree; the west quadrant had 18.0% lower density than the entire tree; and the north quadrant had 14.1% higher density than the entire tree.

DISCUSSION

The majority of egg masses was found in the mid-crown for each of the five groups of trees. With one exception (Group 3), the upper crown had more than twice the egg masses of the lower crown. On the average, 14.4, 59.0, and 26.6% of the egg masses were found in the lower, middle, and upper crown, respectively. On the other hand, approximately half of the foliage surface area was found in the mid-crown for each of the five groups of trees. The lower crown always had considerably more surface area than the upper crown. On the average, 34.2, 50.1, and 15.7% of the surface area were in the lower, middle, and upper crowns, respectively.

There was considerable variability but no discernible trends to either number of egg masses or foliage surface area related to the five groups with respect to quadrant. Approximately 25% of both the number of egg masses and surface area were in each of the quadrants.

Egg mass density of the mid-crown was considerably higher than that of the lower crown for all five groups. On the average, density at mid-crown was 179.1% higher than that of the lower crown with the groups ranging from 84.9 to 272.7%. With one exception (Group 3), density of the upper crown was higher than that of the mid-crown. On the average, density of the upper crown was 43.8% higher than that at mid-crown with the groups ranging from −23.2 to 104.9%. The density of the tree top was less than that of the branches in the upper

crown for three groups with the reverse being true for two groups. On the average, the density of the tree top was 12.3% higher than the density of the upper crown branches with the groups ranging from −41.8 to 44.7%.

Density at mid-crown was higher than that of the entire tree for all groups. On the average, density at mid-crown was 17.7% higher than that of the entire tree with the groups ranging from 0.7 to 28.3%. There was considerable variation of egg mass density with respect to the four quadrants among the groups but no consistent trends. On the average, the densities of the east, south, and west quadrants were 10.0% lower, 7.9% lower, and 28.1% lower, respectively, than that of the north quadrants. On the average, the densities of the north, east, south, and west quadrants were 6.08, 5.47, 5.60, and 4.37, respectively. These differences are not large on an absolute scale, and since the average pattern was not found for any of the groups, it is probably an artifact of the 20 trees, and their respective surface areas, chosen for enumeration.

The implications of this study for sampling to estimate egg mass density on balsam fir are (1) There is considerable tree-to-tree variation; (2) There is considerable variation among the various population density groups examined; (3) It does not matter what quadrant is sampled; (4) Sampling from mid-crown leads to over- or underestimation of egg mass density— the seriousness of such errors depends on the bias, where the sample is taken vertically in the mid-crown, the egg mass density, and possibly other factors; (5) The results apply, on the average, to all densities as no discernible trends were found for the five density groups examined.

These implications suggest that there is a high degree of variability from population to population, from tree to tree, and from crown to crown when sampling to estimate egg mass density. Estimation bias caused by sampling from mid-crown can be large and extremely variable. More detailed information on development of an optimum sampling scheme for estimating egg mass density will be reported in subsequent papers in this series.

ACKNOWLEDGMENTS

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