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

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

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ABSTRACT

As part of a study to develop improved foliage sampling methods for spruce budworm, *Choristoneura fumiferana* (Clemens), egg masses, two balsam fir (four in one stand), *Abies balsamea*, and two white spruce, *Picea glauca*, trees were chosen from each of five spruce-fir stands in Michigan's Upper Peninsula in 1980. All stands had very low to low population densities. Each tree was completely enumerated so that the number of new egg masses, foliage surface area, and egg mass density could be determined for the entire tree, three crown classes, four quadrants, and the tree top. Results indicated (1) considerable tree-to-tree and stand-to-stand variation; (2) no meaningful or consistent differences among quadrants within or between species; (3) the average density in white spruce trees was 3.2 times larger than that in balsam fir trees; (4) the tree-to-tree variation of density in white spruce trees was 8.4 times larger than that in balsam fir trees; (5) densities in the mid-crown, upper-crown, and tree top are considerably higher than that in the lower-crown for both species; the relative differences for balsam fir are about twice that of white spruce; and (6) on the average, density at mid-crown was close to that of the entire tree for balsam fir, but density at mid-crown was 17.9% lower than that of the entire tree for white spruce. These results have important implications to the development of sampling plans for estimating egg mass density in spruce-fir stands.

This is the second paper in a series where we explore ways to improve the sampling of balsam fir foliage, *Abies balsamea* (L.). Miller, and white spruce foliage, *Picea glauca* (Meunchhausen) Voss, for estimating egg mass densities of the spruce budworm, *Choristoneura fumiferana* (Clemens). In this paper we report general descriptive statistics that were obtained from our data sets on balsam fir and white spruce. In this instance we report results from studies conducted at very low to low egg mass densities.

MATERIALS AND METHODS

This study was conducted in the Upper Peninsula of Michigan. For a general description of the study, see Fowler and Simmons (1982). In 1980 five study areas were established. Balsam fir and white spruce trees were selected in such a way to provide very low to low egg mass population densities. This required searching stands containing largely mature hardwood species such as white birch, *Betula papyrifera* Marshall, trembling aspen, *Populus tremuloides* Michaux, red maple, *Acer rubrum* L., sugar maple, *A. saccharum* Marshall, and yellow birch, *B. alleghaniensis* Britton. Such stands could not be classed as spruce-fir stands, but they contained some spruce and fir, usually less than 20% of the basal area.

Study areas were centered in small pockets of spruce and fir either along a ridge or at the edge of a bog. Four balsam fir and four white spruce trees were selected for study in each of

four areas. In a fifth area 10 balsam fir trees and four white spruce trees were chosen. This was done to add a replicate balsam fir stand to the 1979 study reported in Fowler and Simmons (1982). Four of the 10 balsam fir trees were utilized in the two species study reported here.

The following criteria, in order of priority, were used to select trees: (a) overtopped by hardwoods (least attractive for oviposition by budworm moths), (b) least defoliation and healthiest tops, (c) proximity to spruce-fir pocket, (d) from 30 to 60 ft tall with no dead tops, and (e) desirable crown structure. For each tree, 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. The basal area per acre and species contribution to basal area figures were estimated from the center of each sample tree. For a detailed description of study areas consult Montgomery (1981).

This study was based on *every branch trees* where every branch and the tree top were examined for egg masses. Two balsam fir and two white spruce trees were examined for each of four stands, and four balsam fir and two white spruce trees were examined for a fifth stand. For details of the experimental design and methodology, see Fowler and Simmons (1982).

The specific objective of this paper is to examine egg mass density by stand, tree, quadrant, crown class, and species.

RESULTS

Each of the five stands consists of four every branch trees, two each of balsam fir and white spruce except for Stand 1 which has four balsam fir and two white spruce trees. Average values for the balsam fir and spruce trees for each stand and all stands pooled for diameter at breast height (DBH) in centimeters, total tree height in meters, length of live crown in meters (LLC), age of tree at stump height in years, and basal area per hectare (BA) using the tree as point center are given in Table 1.

All stands would be classified as having very light to light population levels of the spruce budworm with reference to the damage forecasted classification system used in New Brunswick and Maine (Dorias 1978) and the infestation classification system of Morris (1954).

In this paper, 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). The average number of egg masses, foliage surface area, and egg mass density for the trees in each stand are shown in Table 2. Individual tree information is available from the authors. Unless otherwise stated, the upper-crown class includes the tree top (WT).

Table 1. Average values for balsam fir and white spruce trees for each stand and all stands pooled for diameter at breast height (DBH) (cm), total tree height (T HT) (m), length of live crown (LLC) (m), age of tree at stump height (years), and basal area (BA) (m²/ha).

	Balsam fir					White spruce				
STAND	DBH (cm)	T HT (m)	LLC (m)	AGE (yrs)	BA (m²)	DBH (cm)	T HT (m)	LLC (m)	AGE (yrs)	BA (m²)
1	20.9	16.2	14.1	47.8	21.5	24.8	14.0	12.4	65.0	20.9
2	18.3	13.9	12.4	38.5	22.0	19.9	12.6	11.7	41.5	22.0
3	17.0	13.2	11.5	63.0	17.6	17.1	13.2	9.8	72.5	17.6
4	15.7	13.9	12.4	43.0	19.8	20.2	14.8	13.1	43.5	20.9
5	12.9	11.0	8.8	28.0	11.0	11.9	9.4	8.4	40.0	12.1
POOLED	17.6	14.1	12.2	40.7	18.9	18.8	12.8	11.1	46.1	18.7

Table 2. Average number of egg masses, foliage surface area ($\times$ 1000 cm^2), and egg mass density (no. egg masses per 1000 cm^2).

Parameter	Tree Species	Tree WT[a]	Tree Top	Tree WOT[b]	Low	Mid	Upper (WOT)	Upper (WT)	N	E	S	W
					Crown Class				Quadrant			
Stand 1: 4 BF, 2 WS												
No. Egg	BF	23.50	1.00	22.50[c]	2.75	14.00	5.75	6.75	4.00	6.75	4.25	6.75
Masses	WS	79.50	10.00	69.50	10.00	33.50	26.00	36.00	12.00	16.00	27.00	14.50
Surface	BF	680.30	12.20	668.10[c]	257.40	342.20	68.60	80.70	134.00	158.90	167.90	204.90
Area	WS	848.80	14.60	834.20	249.90	411.70	172.60	187.20	150.00	254.10	263.90	166.10
Egg Mass	BF	0.04	0.08	0.03	0.01	0.04	0.08	0.08	0.03	0.04	0.03	0.03
Density	WS	0.09	0.69	0.08	0.04	0.08	0.15	0.19	0.08	0.06	0.10	0.09
Stand 2: 2 BF, 2 WS												
No. Egg	BF	34.50	6.50	28.00	2.00	11.00	15.00	21.50	5.50	6.00	7.50	9.00
Masses	WS	113.00	2.00	111.00	19.00	45.50	46.50	48.50	31.50	21.00	33.00	25.50
Surface	BF	584.80	12.10	572.80[d]	163.40	269.50	139.80	151.80	101.00	182.90	139.00	138.20
Area	WS	537.60	5.00	532.50	197.80	244.50	90.30	95.30	138.20	124.90	145.30	124.10
Egg Mass	BF	0.06	0.54	0.05	0.01	0.04	0.11	0.14	0.05	0.03	0.05	0.07
Density	WS	0.21	0.40	0.21	0.10	0.19	0.52	0.51	0.23	0.17	0.23	0.21
Stand 3: 2 BF, 2 WS												
No. Egg	BF	30.50	0.00	30.50	1.00	11.50	18.00	18.00	3.00	7.50	12.50	7.50
Masses	WS	52.00	2.50	49.50	8.00	21.00	20.50	23.00	9.50	13.00	14.00	13.00
Surface	BF	496.20	4.60	491.70	75.30	227.60	188.80	193.40	118.20	110.40	127.90	135.10
Area	WS	411.90	8.80	403.00	128.10	159.80	115.20	124.00	83.00	90.00	145.30	84.80
Egg Mass	BF	0.06	0.00	0.06	0.01	0.05	0.10	0.09	0.03	0.07	0.10	0.06
Density	WS	0.13	0.28	0.12	0.06	0.13	0.18	0.19	0.12	0.14	0.10	0.15
Stand 4: 2 BF, 2 WS												
No. Egg	BF	100.50	10.00	90.50	3.50	37.00	50.00	60.00	17.50	20.50	27.50	25.00
Masses	WS	500.00	13.50	486.50[c]	27.50	147.50	311.50	325.00	64.50	106.00	225.00	86.00
Surface	BF	530.40	11.70	518.70	171.70	254.00	93.00	104.70	94.50	120.60	132.70	170.90
Area	WS	575.00	10.70	564.30[c]	134.30	214.60	215.40	226.10	80.80	94.50	293.00	94.70
Egg Mass	BF	0.19	0.86	0.17	0.02	0.15	0.54	0.57	0.19	0.17	0.21	0.15
Density	WS	0.87	1.26	0.86	0.21	0.69	1.45	1.44	0.80	1.12	0.77	0.91
Stand 5: 2 BF, 2 WS												
No. Egg	BF	61.50	7.50	54.00	5.50	44.00	4.50	12.00	18.00	16.50	11.00	8.50
Masses	WS	92.50	3.00	89.50	15.50	55.00	19.00	22.00	16.50	31.00	37.00	5.00
Surface	BF	256.40	8.80	247.60[d]	106.30	133.80	7.40	16.20	67.40	67.10	52.70	59.50
Area	WS	230.50	5.20	225.30	69.80	114.70	40.70	46.00	32.50	69.70	97.00	26.10
Egg Mass	BF	0.24	0.85	0.22	0.05	0.33	0.61	0.74	0.27	0.25	0.21	0.14
Density	WS	0.40	0.57	0.40	0.22	0.48	0.47	0.48	0.51	0.45	0.38	0.19
Total: 12 BF, 10 WS												
No. Egg	BF	45.70	4.30	41.30	2.90	21.90	16.50	20.80	8.70	10.70	11.20	10.60
Masses	WS	139.50	5.20	134.30	13.30	50.40	70.60	75.80	22.30	31.20	56.00	24.00
Surface	BF	538.07	10.25	527.82	171.94	261.53	94.35	104.60	109.54	133.12	131.35	152.26
Area	WS	520.74	8.88	511.86	155.96	229.05	126.84	135.72	96.88	126.66	188.91	99.15
Egg Mass	BF	0.09	0.42	0.08	0.02	0.08	0.18	0.20	0.08	0.08	0.09	0.07
Density	WS	0.27	0.59	0.26	0.09	0.22	0.56	0.56	0.23	0.25	0.30	0.24

[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] One branch from one balsam fir tree was included in Tree WOT but was not classified as to quadrant. There were no egg masses on this branch. Thus, the sum of the foliage surface area across quadrants is less than the Tree WOT value.

STAND 1

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 six trees are shown in Table 2 for various parts of the tree.

Balsam Fir. 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 (WT) 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. Approximately 4% of the egg masses was found in the tree top.

The average surface area per tree was 680.29 (range, 395.95–998.38). On the average, 37.8, 50.3, and 11.9% of the surface area were in the lower, middle, and upper thirds of the crown, respectively. The percentages of the surface area in the north, east, south, and west quadrants were 20.1, 23.9, 25.2, and 30.8, respectively. Approximately 2% of the surface area was in the tree top.

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

White Spruce. The average number of egg masses per tree was 79.5 (range, 68–91). On the average, 12.6, 42.1, and 45.3% 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 17.3, 23.0, 38.8, and 20.9, respectively. Approximately 13% of the egg masses was found in the tree top.

The average surface area per tree was 848.76 (range, 486.93–1210.60). On the average, 29.4, 48.5, and 22.1% of the surface area were in the lower, middle, and upper thirds of the crown, respectively. The percentages of the surface area in the north, east, south, and west quadrants were 18.0, 30.5, 31.6, and 19.9, respectively. Approximately 2% of the surface area was in the tree top.

The average egg mass density per tree was 0.094 (range, 0.056–0.187). On the average, the lower-crown had 57.4% lower, the mid-crown had 13.8% lower, the upper-crown had 104.3% higher, and the tree top had 628.7% higher densities than the entire tree. The north, east, south, and west quadrants had 3.6% lower, 24.1% lower, 22.9% higher, and 4.8% higher densities than the entire tree, respectively.

Comparison. On the average, the two white spruce trees were larger in DBH, smaller in total height and LLC, were older, and had approximately the same BA's compared to the four balsam fir trees (Table 1). The white spruce trees had considerably more foliage surface and egg masses than the balsam fir trees. The egg mass density of the white spruce trees was 2.7 times larger than that of the balsam fir trees.

The white spruce trees had proportionately more egg masses in the upper-crown and the tree top, more surface area in the upper-crown, approximately the same surface area in the tree top, lower egg mass density in the upper-crown, and higher egg mass density in the tree top than the balsam fir trees. The egg mass density was 17.1% higher and 13.8% lower in the mid-crown compared to the entire tree for balsam fir and white spruce, respectively. There were no meaningful quadrant differences.

STAND 2

The average number of egg masses, foliage surface area, and egg mass density for four trees are shown in Table 2 for various parts of the tree.

Balsam Fir. The average number of egg masses per tree was 34.5 (range, 29–40). On the average, 5.8, 31.9, and 62.3% 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 19.6, 21.4, 26.8, and 32.2, respectively. Approximately 19% of the egg masses was found in the tree top.

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The average surface area per tree was 584.82 (range, 509.25–660.40). On the average, 27.9, 46.1, and 26.0% of the surface area were in the lower, middle, and upper thirds of the crown, respectively. The percentages of the surface area in the north, east, south, and west quadrants were 19.2, 32.1, 24.4, and 24.3, respectively. Approximately 2% of the surface area was in the tree top.

The average egg mass density per tree was 0.059 (range, 0.057–0.061). On the average, the lower-crown had 79.7% lower, the mid-crown had 30.5% lower, the upper-crown had 140.7% higher, and the tree top had 811.9% higher densities than the entire tree. The north, east, south, and west quadrants had 2.0% higher, 67.3% lower, 10.2% higher, and 32.7% higher densities than the entire tree, respectively.

White Spruce. The average number of egg masses per tree was 113.0 (range, 49–177). On the average, 16.8, 40.3, and 42.9% 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 28.4, 18.9, 29.7, and 23.0, respectively. Approximately 2% of the egg masses was found in the tree top.

The average surface area per tree was 537.58 (range, 405.58–669.58). On the average, 36.8, 45.5, and 17.7% of the surface area were in the lower, middle, and upper thirds of the crown, respectively. The percentages of the surface area in the north, east, south, and west quadrants were 25.9, 23.5, 27.3, and 23.3, respectively. Approximately 1% of the surface area was in the tree top.

The average egg mass density per tree was 0.210 (range, 0.121–0.264). On the average, the lower-crown had 54.3% lower, the mid-crown had 11.4% lower, the upper-crown had 142.4% higher, and the tree top had 88.6% higher densities than the entire tree. The north, east, south, and west quadrants had 9.6% higher, 19.2% lower, 9.1% higher, and 1.4% lower densities than the entire tree, respectively.

Comparison. On the average, the two white spruce trees were slightly larger in DBH, smaller in total height and LLC, slightly older, and had the same BA's compared to the two balsam fir trees (Table 1). The white spruce trees had somewhat less foliage surface area and considerably more egg masses than the balsam fir trees. The egg mass density of the white spruce trees was 3.6 times larger than that of the balsam fir trees.

The white spruce trees had proportionately less egg masses in the upper-crown and the tree top, less surface area in the upper-crown, somewhat less surface area in the tree top, approximately the same egg mass density in the upper-crown, and lower egg mass density in the tree top than the balsam fir trees. The egg mass density was 30.5% and 19.2% lower in the mid-crown compared to the entire tree for balsam fir and white spruce, respectively. There were no meaningful quadrant differences.

STAND 3

The average number of egg masses, foliage surface area, and egg mass density for four trees are shown in Table 2 for various parts of the tree.

Balsam Fir. The average number of egg masses per tree was 30.5 (range, 28–33). On the average, 3.3, 37.7, and 59.0% 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 9.8, 24.6, 41.0, and 24.6, respectively. No egg masses were found in the tree top.

The average surface area per tree was 496.24 (range, 461.63–530.85). On the average, 15.2, 45.8, and 39.0% of the surface area were in the lower, middle, and upper thirds of the crown, respectively. The percentages of the surface area in the north, east, south, and west quadrants were 24.0, 22.5, 26.0, and 27.5, respectively. Approximately 1% of the surface area was in the tree top.

The average egg mass density per tree was 0.061 (range 0.061–0.062). On the average, the lower-crown had 78.7% lower, the mid-crown had 16.4% lower, the upper-crown had 52.5% higher, and the tree top had 100.0% lower densities than the entire tree. The north, east, south, and west quadrants had 59.7% lower, 9.7% higher, 58.1% higher, and 11.3% lower densities than the entire tree, respectively.

White Spruce. The average number of egg masses per tree was 52.0 (range, 40–64). On the average, 15.4, 40.4, and 44.2% 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 19.2, 26.3, 28.2, and 26.3, respectively. Approximately 5% of the egg masses was found in the tree top.

The average surface area per tree was 411.88 (range, 409.35–414.40). On the average, 31.1, 38.8, and 30.1% of the surface area were in the lower, middle, and upper thirds of the crown, respectively. The percentages of the surface area in the north, east, south, and west quadrants were 20.6, 22.3, 36.1, and 21.0, respectively. Approximately 2% of the surface area was in the tree top.

The average egg mass density per tree was 0.126 (range, 0.096–0.156). On the average, the lower-crown had 50.8% lower, the mid-crown had 4.0% higher, the upper-crown had 46.8% higher, and the tree top had 124.6% higher densities than the entire tree. The north, east, south, and west quadrants had 6.5% lower, 17.1% higher, 22.0% lower, and 24.4% higher densities than the entire tree, respectively.

Comparison. On the average, the two white spruce trees had approximately the same DBH and total height, were somewhat smaller in LLC, were older, and had the same BA's compared to the two balsam fir trees (Table 1). The white spruce trees had less foliage surface area and considerably more egg masses than the balsam fir trees. The egg mass density of the white spruce trees was 2.1 times larger than that of the balsam fir trees.

The white spruce trees had proportionately less egg masses in the upper-crown, more egg masses in the tree top, less surface area in the upper-crown, more surface area in the tree top, somewhat lower egg mass density in the upper-crown and considerably higher egg mass density in the tree top than the balsam fir trees. The density was 16.4% lower and 4.0% higher in the mid-crown compared to the entire tree for balsam fir and white spruce, respectively. There were no meaningful quadrant differences.

STAND 4

The average number of egg masses, foliage surface area, and egg mass density for four trees are shown in Table 2 for various parts of the tree.

Balsam Fir. The average number of egg masses per tree was 100.5 (range, 85–116). On the average, 3.5, 36.8, and 59.7% 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 19.3, 22.7, 30.4, and 27.6, respectively. Approximately 10% of the egg masses was found in the tree top.

The average surface area per tree was 530.40 (range, 329.10–731.69). On the average, 32.4, 47.9, and 19.7% of the surface area were in the lower, middle, and upper thirds of the crown, respectively. The percentages of surface area in the north, east, south, and west quadrants were 18.2, 23.2, 25.6, and 33.0, respectively. Approximately 2% of the surface area was in the tree top.

The average egg mass density per tree was 0.189 (range, 0.158–0.258). On the average, the lower-crown had 89.4% lower, the mid-crown had 22.8% lower, the upper-crown had 203.2% higher, and the tree top had 352.4% higher densities than the entire tree. The north, east, south, and west quadrants had 6.3% higher, 2.3% lower, 19.0% higher, and 16.1% lower densities than the entire tree, respectively.

White Spruce. The average number of egg masses per tree was 500.0 (range, 413–587). On the average, 5.5, 29.5, and 65.0% 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 13.4, 22.0, 46.7, and 17.9, respectively. Approximately 3% of the egg masses was found in the tree top.

The average surface area per tree was 574.96 (range, 477.06–672.85). On the average, 23.4, 37.3, and 39.3% of the surface area were in the lower, middle, and upper thirds of the crown, respectively. The percentages of the surface area in the north, east, south, and west quadrants were 14.3, 16.8, 52.1, and 16.8, respectively. Approximately 2% of the surface area was in the tree top.

The average egg mass density per tree was 0.870 (range, 0.866–0.872). On the average, the lower-crown had 76.4% lower, the mid-crown had 21.0% lower, the upper-crown had 65.2% higher, and the tree top had 45.1% higher densities than the entire tree. The north, east, south, and west quadrants had 7.3% lower, 30.0% higher, 10.1% lower, and 5.5% higher densities than the entire tree, respectively.

Comparison. On the average, the two white spruce trees had considerably larger DBH's, somewhat larger total heights and LLC's, were approximately the same age, and had somewhat higher BA's compared to the two balsam fir trees (Table 1). The white spruce trees had more foliage surface area and considerably more egg masses than the balsam fir trees. The egg mass density of the white spruce trees was 4.6 times larger than that of the balsam fir trees.

The white spruce trees had proportionately more egg masses in the upper-crown, less egg masses in the tree top, more surface area in the upper-crown, somewhat less surface area in the tree top, and considerably lower egg mass density in the upper-crown and the tree top than the balsam fir trees. The density was 22.8% and 21.0% lower in the mid-crown compared to the entire tree for balsam fir and white spruce, respectively. There were no meaningful quadrant differences.

STAND 5

The average number of egg masses, foliage surface area, and egg mass density for four trees are shown in Table 2 for various parts of the tree.

Balsam Fir. The average number of egg masses per tree was 61.5 (range, 53–70). On the average, 8.9, 71.6, and 19.5% 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 33.3, 30.6, 20.4, and 15.7, respectively. Approximately 12% of the egg masses was found in the tree top.

The average surface area per tree was 256.38 (range, 149.70–363.05). On the average, 41.5, 52.2, and 6.3% of the surface area were in the lower, middle, and upper thirds of the crown, respectively. The percentages of the surface area in the north, east, south, and west quadrants were 27.3, 27.2, 21.4, and 24.1, respectively. Approximately 3% of the surface area was in the tree top.

The average egg mass density per tree was 0.240 (range, 0.193–0.354). On the average, the lower-crown had 78.3% lower, the mid-crown had 37.1% higher, the upper-crown had 208.8% higher, and the tree top had 255.0% higher densities than the entire tree. The north, east, south, and west quadrants had 22.5% higher, 12.8% higher, 4.1% lower, and 34.6% lower densities than the entire tree, respectively.

White Spruce. The average number of egg masses per tree was 92.5 (range, 53–132). On the average, 16.8, 59.4, and 23.8% 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 18.4, 34.6, 41.4, and 5.6, respectively. Approximately 3% of the egg masses was found in the tree top.

The average surface area of the tree was 230.54 (range, 220.41–240.68). On the average, 30.3, 49.8, and 19.9% of the surface area were in the lower, middle, and upper thirds of the crown, respectively. The percentages of the surface area in the north, east, south, and west quadrants were 14.4, 30.9, 43.1, and 11.6, respectively. Approximately 2% of the surface area was in the tree top.

The average egg mass density per tree was 0.401 (range, 0.240–0.548). On the average, the lower-crown had 44.6% lower, the mid-crown had 19.5% higher, the upper-crown had 19.2% higher, and the tree top had 42.4% higher densities than the entire tree. The north, east, south, and west quadrants had 28.0% higher, 12.1% higher, 4.0% lower, and 51.6% lower densities than the entire tree, respectively.

Comparison. On the average, the two white spruce trees had somewhat smaller DBH's, total heights, and LLC's, were considerably older, and had somewhat higher BA's compared to the two balsam fir trees (Table 1). The white spruce trees had less foliage surface

area and considerably more egg masses than the balsam fir trees. The egg mass density of the white spruce trees was 1.7 times larger than that of the balsam fir trees.

The white spruce trees had proportionately somewhat more egg masses in the upper-crown, considerably less egg masses in the tree top, considerably more surface area in the upper-crown, somewhat less surface area in the tree top, and considerably lower egg mass density in the upper-crown and the tree top than the balsam fir trees. The density was 37.1% and 19.5% higher in the mid-crown compared to the entire tree for balsam fir and white spruce, respectively. There were no meaningful quadrant differences.

ALL TREES POOLED

The average number of egg masses, foliage surface area, and egg mass density for the 12 balsam fir trees and 10 white spruce trees are shown in Table 2 for various parts of the tree.

Balsam Fir. The average number of egg masses per tree was 45.7 (range, 7–116). On the average, 6.4, 48.0, and 45.6% 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 21.1, 26.0, 27.2, and 25.7, respectively. Approximately 9% of the egg masses was found in the tree top.

The average surface area per tree was 538.07 (range, 149.70–998.38). On the average, 32.0, 48.6, and 19.4% of the surface area were in the lower, middle, and upper thirds of the crown, respectively. The percentages of the surface area in the north, east, south, and west quadrants were 20.8, 25.3, 25.0, and 28.9, respectively. Approximately 2% of the surface area was in the tree top.

The average egg mass density per tree was 0.085 (range, 0.011–0.354). On the average, the lower-crown had 80.0% lower, the mid-crown had 1.2% lower, the upper-crown had 134.1% higher, and the tree top had 394.1% higher densities than the entire tree. The north, east, south, and west quadrants had 1.3% higher, 2.6% higher, 9.0% higher, and 10.3% lower densities than the entire tree, respectively.

White Spruce. The average number of egg masses per tree was 139.5 (range, 40–587). On the average, 9.5, 36.1, and 54.4% 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 16.7, 23.4, 41.9, and 18.0, respectively. Approximately 4% of the egg masses was found in the tree top.

The average surface area of the tree was 520.74 (range, 220.41–1210.60). On the average, 29.9, 44.0, and 26.1% of the surface area were in the lower, middle, and upper thirds of the crown, respectively. The percentages of the surface area in the north, east, south, and west quadrants were 18.9, 24.8, 36.9, and 19.4, respectively. Approximately 2% of the surface area was in the tree top.

The average egg mass density per tree was 0.268 (range, 0.056–0.872). On the average, the lower-crown had 68.3% lower, the mid-crown had 17.9% lower, the upper-crown had 108.6% higher, and the tree top had 118.7% higher densities than the entire tree. The north, east, south, and west quadrants had 12.2% lower, 6.1% lower, 13.0% higher, and 7.6% lower densities than the entire tree, respectively.

Comparison. On the average, the 10 white spruce trees were somewhat larger in DBH, smaller in total height and LLC, approximately five years older, and approximately the same in BA compared to the 12 balsam fir trees (Table 1). The white spruce trees had 3.1 and 0.97 times as many egg masses and as much foliage surface area, respectively, than the balsam fir trees. The egg mass density of the white spruce trees was 3.2 times larger than that of the balsam fir trees. The arithmetic average of this ratio on a stand basis is 2.92 and significantly larger than 1.00 (upper one-sided t-test, $p < 0.025$, $n = 5$).

The white spruce trees had proportionately (1) more egg masses in the lower- (9.5 to 6.4%) and upper- (54.4 to 45.6%) crowns and less egg masses in the middle-crown (36.1 to 48.0%) than the balsam fir trees and (2) less surface area in the lower- (29.9 to 32.0%) and middle- (44.0 to 48.6%) crowns and more surface area in the upper crown (26.1 to 19.4%) than the balsam fir trees. The egg mass density for the lower-crown for the white spruce trees was 68.3% lower than that of the entire tree while it was 80.0% lower for the balsam fir trees. The

density for the mid-crown of the white spruce trees was 17.9% lower than that of the entire tree while it was 1.2% lower for the balsam fir trees. Six balsam fir trees had mid-crown densities lower than the entire tree while the other six trees had mid-crown densities higher than the entire tree. Seven white spruce trees had mid-crown densities lower than the entire tree while the other three trees had mid-crown densities higher than the entire tree. The density for the upper-crown of the white spruce trees was 108.6% higher than that of the entire tree while it was 134.1% higher for the balsam fir trees.

The differences between quadrants in terms of number of egg masses, foliage surface area, and egg mass density showed considerable tree-to-tree variation and no meaningful patterns based on averages for each tree species. The density for the south quadrant was higher than that of the entire tree for both white spruce (13.0% higher) and balsam fir (9.0% higher). The densities for the north, east, and west quadrants were (1) 12.2, 6.1, and 7.6% lower, respectively, than that of the entire tree for the white spruce trees and (2) 1.3% higher, 2.6% higher, and 10.3% lower, respectively, than that of the entire tree for the balsam fir trees. These differences are not large and well within expected micro-site variation. There are no meaningful differences between the two tree species.

The white spruce trees had proportionately fewer egg masses (3.7 to 9.4%) and less foliage surface area (1.7 to 1.9%) in the tree top than the balsam fir trees. The egg mass density of the tree top was 118.7 and 394.1% higher than that of the entire tree for the white spruce and balsam fir, respectively. Even though the egg mass density in the top of the tree was 4.9 times higher than that of the entire tree for the balsam fir trees compared to 2.2 times higher for the white spruce trees, the egg mass density of the tree top for the white spruce trees was 1.4 times larger than that for the balsam fir trees.

DISCUSSION

As expected, considerable tree-to-tree variation was found in terms of number of egg masses, foliage surface area, and egg mass density for both tree species.

On the average, white spruce trees had 3.1 times as many egg masses, 0.97 times as much foliage surface area, and 3.2 times larger egg mass densities than balsam fir trees.

The majority of egg masses was found in the mid- or upper-crowns for all stands and both tree species. For the balsam fir trees, on the average, 6.4, 48.0, and 45.6% of the egg masses were found in the lower-, middle-, and upper-crowns, respectively; the same percentages for white spruce trees were 9.5, 36.1, and 54.4%, respectively. The percentages of egg masses found in the tree top were 3.7 and 9.4 for white spruce and balsam fir trees, respectively.

Close to half of the foliage surface area was found in the mid-crown for both tree species. For balsam fir trees, on the average, 32.0, 48.6, and 19.4% of the foliage surface area were in the lower-, middle-, and upper-crowns, respectively; the same percentages for white spruce trees were 29.9, 44.0, and 26.1, respectively. The percentages of the foliage surface area found in the tree top were 1.9 and 1.7 for white spruce and balsam fir trees, respectively.

On the average, egg mass densities of the mid-crown were 2.59 and 4.94 times that of the lower-crown for white spruce and balsam fir trees, respectively. On the average, densities of the upper-crown were 6.58 and 11.71 times that of the lower-crown for white spruce and balsam fir trees, respectively. On the average, densities of the tree top were 1.05 and 2.4 times that of the upper-crown branches for white spruce and balsam fir, respectively. On the average, densities at mid-crown were 17.9 and 1.2% lower than that of the entire tree for white spruce and balsam fir trees, respectively.

The tree-to-tree variability of egg mass density for white spruce trees ($s^2 = 0.0960$) is significantly larger (F-test, $p < 0.001$, $n_1 = 9$, $n_2 = 11$) than that for balsam fir trees ($s_2^2 = 0.0114$).

No explainable or meaningful trends were observed in the tree-to-tree, stand-to-stand, and white spruce versus balsam fir quadrant differences for number of egg masses, foliage surface area, and egg mass density. The differences are not large on an absolute scale and are well within real-world sampling variation.

The implications of this study for sampling to estimate egg mass density in mixed spruce-fir stands of low populations are (1) Considerable tree-to-tree and stand-to-stand variation;

(2) It does not seem to matter what quadrant is sampled; (3) The average egg mass density in spruce trees may be considerably higher than that in balsam fir trees; (4) The tree-to-tree variation of density may be considerably larger for white spruce trees than for balsam fir trees; (5) Densities in the mid-crown, upper-crown, and tree top are considerably higher than that in the lower-crown for both species, but the relative differences may be approximately twice as large for balsam fir trees compared to white spruce trees; (6) Densities at mid-crown may over- or underestimate the density of the entire tree, depending on the tree and the stand, and densities at mid-crown may be closer to the density of the entire tree for balsam fir trees compared to white spruce trees; and (7) Sampling at mid-crown may be adequate for balsam fir trees, but sampling for white spruce trees possibly should be in the upper part of the mid-crown.

These implications suggest that there is a high degree of stand-to-stand and tree-to-tree variability when sampling to estimate egg mass density. Estimation bias caused by sampling at mid-crown can be large and extremely variable. Any sampling scheme to estimate egg mass density in spruce-fir stands must take into account the difference in density mean and variance between spruce and fir trees. More detailed information on development of an optimum sampling scheme for estimating egg mass density at low population levels will be reported in subsequent papers in this series.

ACKNOWLEDGMENTS

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