DISTRIBUTION OF EGGS OF WESTERN BLACKHEADED BUDWORM, ACLERIS GLOVERANA (WALSINGHAM) (LEPIDOPTERA: TORTRICIDAE), AND OF FOLIAGE OVER THE CROWNS OF WESTERN HEMLOCK, TSUGA HETEROPHYLLA (RAF.) SARG.

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Abstract

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Eggs of western blackheaded budworm, *Acleris gloverana* (Walsingham), were found on the underside of needles of western hemlock, *Tsuga heterophylla* (Raf.) Sarg., with higher densities in the mid-crown area toward the outer tips of branches. Fringe and dominant trees were preferred oviposition sites over trees in lower crown classes or shaded positions. Vertical differences in needle density were considerable and led to high variability in insect densities when expressed on a per branch basis. When densities of eggs were based on a fresh branch weight basis there was a significant decrease in sample bias caused by the uneven distribution of foliage over the crowns.

Shepherd, R.F., et T.G. Gray. 1990. Distribution des oeufs de la tordeuse à tête noire de l'ouest, *Acleris gloverana* (Walsingham) (Lepidoptera: Tortricidae) et du feuillage à l'intérieur de la cime de la pruche de l'ouest, *Tsuga heterophylla* (Raf.) Sarg. *Can. Ent.* 122: 547–554.

Résumé

Les oeufs de la tordeuse à tête noire de l'ouest, *Acleris gloverana* (Walsingham), sont placés sur la surface inférieure des aiguilles de la pruche de l'ouest, *Tsuga heterophylla* (Raf.) Sarg. Leur densité est supérieure à mi-cime vers la partie terminale des branches. Les arbres dominants et ceux situés en bordure de forêt sont préférés pour l'oviposition comparativement aux arbres de classes de hauteurs inférieures ou situés à l'ombre. La densité des aiguilles varie considérablement selon la verticale et ceci induit une grande variabilité des densités d'insectes lorsqu'elles sont exprimées par unité de branche. Lorsque les densités des oeufs sont présentées en fonction du poids frais des branches, il y a une diminution significative du biais d'échantillonnage causée par une distribution inégale du feuillage dans la cime.

Introduction

Periodic outbreaks of the blackheaded budworm, *Acleris gloverana* (Walsingham), result in severe defoliation in the temperate rain forests of western North America (Anonymous 1972). Methods of estimating insect density are necessary to predict damage, to measure the effectiveness of control programs, and to establish functional characteristics of key factors regulating populations.

This paper describes the distribution of eggs and foliage over the main host tree, western hemlock, *Tsuga heterophylla* (Raf.) Sarg., and investigates the influence of crown position, crown exposure, and defoliation upon those distributions. The data provide the basis for development of a sequential sample system outlined in the accompanying paper (Shepherd and Gray 1990). Techniques to minimize sampling variation are discussed.

The western blackheaded budworm, *Acleris gloverana*, is a defoliator of western hemlock, *Tsuga heterophylla*, in the western hemlock zones of British Columbia, southern Alaska, and Washington State (Furniss and Carolin 1977). Eggs hatch in late May or early June and larvae begin feeding on the developing shoots. New foliage is consumed first, followed by the older foliage as the larvae mature. Pupation occurs in late July to early August and lasts about 2 weeks. Moths fly in August and September and lay yellow eggs on the lower surface of needles. Eggs remain on the foliage throughout the winter and offer a relatively stable stage to sample.

Methods

The distribution of eggs (Fig. 1) over the foliage of immature and mature tree crowns was determined on branch samples cut from felled trees. Additional branch samples were taken to determine the effects of specific factors such as needle surface, shading, partial defoliation, tree size, crown position, and crown exposure. The study was carried out from 1971 to 1973 on Vancouver Island, B.C., during a major outbreak of this pest.

Distribution of Eggs on Needles. The needle surface selected for egg laying on immature and mature foliage was recorded. Branches were cut from the upper crown of two immature trees where needles tend to lie in a horizontal plane and the location of 200 eggs from each tree was noted. Seven hundred eggs were obtained from branches of a mature tree, where needles have less horizontal orientation, and their positions were similarly noted.

All needles from the top 91 cm of two partially defoliated western hemlock trees were removed and the frequency distribution of eggs per needle was determined. This was compared with a Poisson (random) distribution with a chi-square test. Branches from one tree were clipped into sections of sparse and dense needles before the eggs were counted to determine if the secretive moths lay more eggs in the denser parts of the foliage.



Fig. 1. Blackheaded budworm eggs on the underside of western hemlock needles.

Distribution of Eggs on Branches and Crowns. Branches were taken, two per crown level, from eight levels of 10 immature non-defoliated trees about 9 m tall. Distal and basal 46-cm portions were cut from the branches and double-bagged in plastic for transport to the laboratory. The widest branch width was measured and the branches were weighed and treated with a hot-water technique to remove and count the eggs (Gray *et al.* 1973). Tests were made using an NaOH soak technique to remove eggs (Shepherd and Gray 1972), but this was slower than the hot-water method and also affected foliage weights. Needles and twigs were dried at 100°C for 48 h and the dry weights recorded separately. Repeated weighings to a constant weight were used to establish this drying time. Egg density could then be expressed on the basis of a 46-cm branch, branch surface area, fresh branch weight, dry branch weight, dry needle weight, or dry twig weight.

Ten trees similar in crown structure, height, and position to the above trees but which had suffered about 75% defoliation were selected from the same stand and branch sampled in the same manner. Two branches also were sampled from the upper crown of each of 16 felled mature trees from a different stand and 46-cm portions were removed and processed in a similar way. Branches from other crown levels could not be used as they were damaged during felling and could not be related to crown structure.

Distribution of Eggs among Trees. Observations of defoliated trees indicated a high variability in damage between trees. The influence of exposure was investigated by comparing egg and foliage density on the opposite sides of 10 non-defoliated trees which had one side shaded by adjacent trees and one side open. Branch samples (46 cm) were obtained from eight crown levels and processed as above.

In a similar study, densities of eggs and foliage on 46-cm branches, cut two per tree from the upper crown of 10 fringe trees, were compared with densities of branches from 10 understory trees of the same size in the same stand.

A third study was undertaken in a dense young stand, 6–12 m high, where a sample branch (46-cm tip) was removed from the upper crown of each of 90 trees. These trees were classed as either above, at, or below the average crown level. The branch tips were processed as above and egg and foliage densities were compared between crown levels.

Results and Discussion

Distribution of Eggs on Needles. The lower needle surface is the preferred laying site as only 0.5% of the eggs were found on the upper surface of young trees where needles tend to lie horizontally and 10.3% of the eggs were found on the upper needle surface of mature trees where needles had less horizontal orientation. The distribution of eggs on needles was significantly different ($\chi^2_2 = 159$, p < 0.0005) from Poisson. Fewer needles had one egg, and more had two or more eggs than would be expected if the eggs had been randomly distributed over the needles. No difference in frequency distribution of eggs was detected ($\chi^2_2 = 2$, p = 0.37) between bushy and sparse parts of the foliage (Table 1). Some tendency for laying more than one egg on the same needle was found but the reason does not appear to be related to foliage density.

Distribution of Eggs on Branches. The number of eggs on the basal portions of the branches from immature trees was higher than on the distal parts (t-test, p < 0.0003) (Table 2), but the basal part also had more foliage (p < 0.0003). When expressed on a dry needle weight basis, egg density was greatest on the distal portions (p < 0.0003).

The density of eggs on branches from mature trees was slightly less on the basal samples than on the distal portions (p > 0.05) (Table 2), but the foliage density was again much higher in the basal sections (p < 0.05); thus, egg density on a dry needle weight basis was again higher in the distal portions of the branch (p < 0.05). In contrast, Silver (1959) compared 25-cm, 46-cm, and whole branches of western hemlock and found little difference in density of blackheaded budworm eggs based on branch area, but Régnière et al. (1989) found a high proportion of eggs of spruce budworm, Choristoneura fumifer-

Table 1. Frequency distribution of eggs per needle found within the top 91 cm of two partially defoliated western hemlock trees

Number of eggs per needle	Expected random frequency	Observed frequency			
		Tree #1	Tree #2		
			Sparse foliage	Bushy foliage	
0	0.8861	0.8977	0.9315	0.9321	
1	0.1073	0.0867	0.0581	0.0590	
2	0.0064	0.0133	0.0087	0.0089	
3	0.0002	0.0017	0.0017	0.0000	
4	0.0000	0.0004	0.0000	0.0000	
5	0.0000	0.0002	0,0000	0.0000	
umber of needles		4811	1153	1575	

Combined sample vs. random egg distribution: $\chi_2^2 = 159$, p < 0.0005. Tree #2, egg distribution on sparse vs. bushy branches: $\chi_2^2 = 2.0$, p = 0.37.

Table 2. Distribution of eggs and foliage on 46-cm distal and basal branch portions of non-defoliated branches on immature and mature western hemlock trees. Eggs per gram were calculated on a per branch basis, then averaged

	Numbe	Number of eggs		Weight (g) of dry needles		Eggs per gram dry needles	
	Distal	Basal	Distal	Basal	Distal	Basal	
Immature trees	6.5	10.5**	6.7	19.6**	1.20**	0.60	
Mature trees	25.3	22.3	5.5	9.4*	4.8*	2.6	

Paired t-tests, distal vs. basal across rows, * p < 0.0003, ** p < 0.05; n = 160 for immature trees and 32 for mature trees.

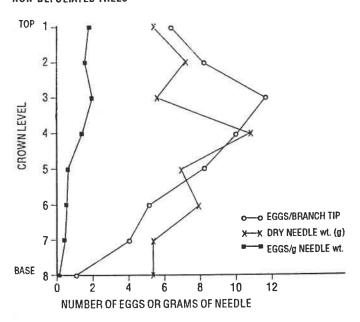
ana (Clemens), on the outer 45 cm of branches of balsam fir, Abies balsamea (L.) Mill., and white spruce, Picea glauca (Moench) Voss.

Distribution of Eggs over Crowns. The vertical distribution of eggs on 46-cm branches over the crown is illustrated in Figure 2 for 9-m non-defoliated trees sampled at eight crown levels. Maximum egg numbers were found in the third level from the top with fairly regular gradients in density above and below that level.

Due to their rapid growth, the upper levels of the tree have fewer needles per branch than in the middle of the crown (Fig. 2). Bud development and numbers of side shoots are reduced in the lower part of the crown, again resulting in less foliage per branch. Egg distribution follows a similar pattern as that of foliage; therefore, when expressed as eggs per needle weight, the vertical gradients are greatly reduced (Fig. 2). Morris (1955), Carolin and Coulter (1972), Harris (1963), Stark (1952), and Mason (1970) reported significant differences in amount of defoliation between crown levels by different pest species. A ratio of 1:2:1 was found by Mason (1970) in the distribution of foliated branch area between three crown levels of *Abies concolor* (Gord.) Engelm., whereas Carolin and Coulter (1972) found a ratio approximating 1:3:5 in the foliated branch area of three crown levels of *Pseudotsuga menziesii* (Mirb.) Franco. The total foliated branch area per crown level measured by those authors is distinct from the density of dry needle weight per branch, as discussed in this paper.

Distribution of Eggs among Trees. Average egg densities between the open and shaded sides of trees were significantly different whether based on eggs per branch (open = 9.7, shaded = 6.0, t-test, p = 0.0002) or eggs per gram of dry needle weight (open = 3.1, shaded = 1.4, p < 0.0001). Similarly, fringe trees supported larger populations when based on either eggs per branch (fringe = 5.4, understory = 3.9, p < 0.01) or eggs per gram of dry needles (fringe = 0.25, understory = 0.12, p < 0.001).

NON-DEFOLIATED TREES



PARTIALLY DEFOLIATED TREES

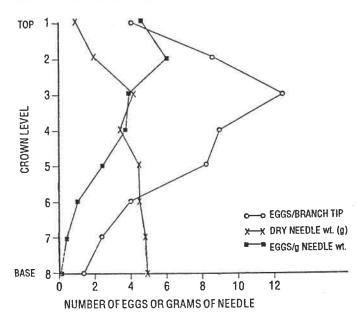


Fig. 2. Numbers of blackheaded budworm eggs, dry weight of needles per 46-cm branch, and number of eggs per dry needle weight calculated on a per branch basis from eight crown levels of non-defoliated and defoliated immature western hemlock.

Table 3. Distribution of eggs and foliage per 46-cm branch sampled from tree crowns above, at, or below the average crown level, n = 30 per level. Eggs per gram were calculated on a per branch basis, then averaged

Tree crown level	Number of eggs per branch	Weight (g) dry needles per branch	Eggs per gram dry needles
Above average	21.1a*	4.9a	5.1a
Average	15.4ab	6.9b	2.5b
Below average	11.5b	5.8ab	2.2b

^{*}Letters followed by the same letter are not significantly different at $p \le 0.05$.

In a dense young stand, egg densities per branch were greatest on crowns that were above average height and were lowest on crowns that were below the average crown level (Table 3). Foliage was most dense at the average crown level. Above this, twig growth rates were greater and needle densities were lower; below average crown level, reduced bud and shoot development again led to lower needle densities. When based on weight of dry needles per branch, egg density above the average crown level was double that of the other two crown levels. These data confirm that moths prefer upper and exposed crowns as oviposition sites. Silver (1959) also noted that defoliation was heaviest in the upper crown section.

Influence of Defoliation. Insect feeding was greatest at the tips of branches and at the tops of the trees resulting in a distributional shift in the remaining foliage toward the base of branches and the lower crowns of the tree (Fig. 2). However, the distribution of eggs over the crowns remains about the same as that of pre-defoliation patterns so if egg densities are based upon needle weight, the density appears higher in upper levels of defoliated trees.

The same effect was found when partially defoliated branches were compared with non-defoliated branches taken from trees within the same stand. Egg densities per branch were similar (6.26 and 6.49, respectively, t-test p = 0.79), but because foliage was reduced on the partially defoliated trees (3.69 and 6.70 g of needles per branch, respectively, p < 0.0001), egg density per gram of dry needle weight was significantly higher on the partially defoliated trees (2.63 and 1.20, respectively, p < 0.0001).

Shepherd et al. (1984) found that distribution of egg masses of Orgyia pseudotsugata (McDunnough) also changed depending on the basic unit selected. However, in contrast to A. gloverana, Condrashoff and Grant (1962) and Mason (1970) found egg mass density of O. pseudotsugata became concentrated in the lower crowns when upper levels were defoliated.

The close relationship between fresh branch weight and dry twig weight (Fig. 3) can be utilized to obtain estimates of defoliation caused by blackheaded budworm. If such a relationship is established for non-defoliated branches from the same crown level of a stand, then the weight loss due to defoliation is the difference between fresh non-defoliated branch weight as estimated from dry twig weight and actual branch weight. It also could be calculated on the basis of dry needle weight. A separate regression must be established for each stand as the relationship varies with growth rate. This method can only be used where the insect, such as blackheaded budworm, does not remove the small twigs during defoliation; other pests such as western hemlock looper, *Lambdina fiscellaria lugubrosa* (Hulst), and western spruce budworm, *C. occidentalis* Freeman, do clip or debark new shoots.

Conclusion

Sampling for insects residing in forest foliage is usually undertaken by cutting partial branches and relating insect density to branch size. If the needle component of the branch is different because of branch or crown position, or some other factor changes as a result

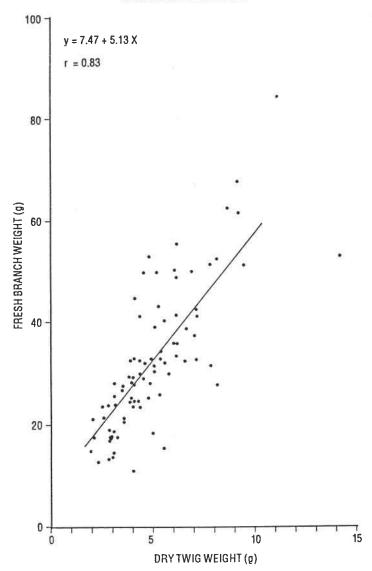


Fig. 3. Relationship between fresh branch weight and dry twig weight for 46-cm non-defoliated branches from all crown levels of immature trees.

of insect feeding, then additional variability and perhaps bias may appear. A knowledge of the distribution of insects and of needles over the surface of the sample trees, as presented here, is important when designing a sample system to keep the samples as consistent and free of bias as possible.

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