

Self-regulation in Populations of the Elongate Hemlock Scale, *Fiorinia externa* (Homoptera: Diaspididae)

Mark S. McClure

Department of Entomology, The Connecticut Agricultural Experiment Station
P.O. Box 1106, New Haven 06504 Ct, USA

Summary. The presence of numerical self-restraints in populations of the elongate hemlock scale, *Fiorinia externa* Ferris (Homoptera: Diaspididae), was investigated by determining the effects of scale density on development rate, fecundity, mortality, and dispersal. Evidence indicates that populations are, to some extent, numerically self-regulated on eastern hemlock, *Tsuga canadensis* (L) Carr. Development rate, fecundity and survival for two consecutive years were all negatively correlated with scale density on 10 hemlocks in a Ridgefield, CT, USA forest. On hemlocks which had supported the higher densities, the summer, 1977 generation developed more slowly, produced significantly fewer eggs, and suffered up to four times greater mortality than it did on less heavily infested trees.

Percent parasitism by *Aspidiotiphagus citrinus* (Craw.) (Hymenoptera: Aphelinidae) was positively correlated with scale density for two years, reconfirming the density-dependent nature of this parasite-host interaction.

First instar nymphs (crawlers) readily dispersed on the wind during both the spring and autumn hatching periods. However, the proportion of crawlers which dispersed from trees supporting the higher densities was no greater than from trees supporting lower densities, indicating that dispersal is density-independent.

Self-restraints on *F. externa* populations imposed at high densities are related to changes in the quality and availability of essential resources for feeding nymphs.

Introduction

Evidence of numerical self-regulation in populations of phytophagous insects mainly has been provided through studies of defoliating Lepidoptera. Leonard (1970a, b) presented evidence indicating that the gypsy moth, *Porthetria dispar*

(L) is numerically self-regulating through a shift in the quality of individuals induced by changes in nutrition. Dispersal, behavior, development rate, and fecundity were qualities so affected. Similarly, Wellington and Maelzer (1967) showed that nutrition was responsible for qualitative changes in populations of the western tent caterpillar, *Malacosoma phiviale* (Dyar). Variations in the nutritional quality of balsam fir and white spruce also have been offered to explain outbreaks of the spruce budworm, *Choristoneura fumiferana* (Clem.) in Canada (Kimmins, 1971).

Studies on the effects of nutrition on populations of sucking, phytophagous insects (Homoptera) were pioneered by A.F.G. Dixon in Scotland and T.R.C. White in Australia. Dixon (1966, 1970) found that the nutritive quality of sycamore affected the reproductive rate, dispersal, and numbers of the aphid, *Drepanosiphum platanooides* (Schr.). White (1969) postulated that physiological stress on host plants increased the amount of nitrogenous food available to psyllids, in particular *Cardiaspina densitexta* Taylor, thus greatly increasing their chances for survival and reproduction.

More recent evidence of self-regulation in the Homoptera was provided from studies on scale insects. High densities of the red pine scale, *Matsucoccus resinosa* B and G, were found to impose severe self-restraints on population growth (McClure, 1977a). Scale-induced reduction in the nutritional quality of red pine, indicated by resinosis from feeding wounds, was likely responsible for corresponding reductions in development rate, fecundity, and survival of feeding nymphs. Similarly, overpopulation may be a factor controlling populations of the elongate hemlock scale, *Fiorinia externa* Ferris (Homoptera: Diaspididae) (Johnson and Lyon, 1976). Populations of this scale were influenced by changes in the nutritional quality of hemlock related to edaphic conditions of the growing site (McClure, 1977b) and to changes in the intensity of scale feeding following application of an insecticide (McClure, 1977c). Reported increases in development rate, fecundity, and survival among scales on hemlocks where densities were reduced by insecticide do suggest some degree of population self-regulation.

The purpose of this study was to examine the presence of numerical self-regulation in natural populations of *F. externa* by determining the effect of scale density on development rate, fecundity, survival, and dispersal.

Life History

Several aspects of the bionomics of *F. externa* have been investigated by Wallner (1965), Garrett (1965), and McClure (1978). The following summary is provided to facilitate an understanding of the methods used in this study.

The elongate hemlock scale is a serious pest of Eastern hemlock, *Tsuga canadensis* (L) Carr., in parts of the northeastern U.S. Its distribution is currently well into the natural range of hemlock. Readily dispersed by the wind (McClure, 1977b), *F. externa* is also able to mature and reproduce on many other native and exotic evergreens including at least 57 species from several genera (McClure and Fergione, 1977).

In Connecticut there is usually a single generation per year on hemlock, but mild spring and autumn weather conditions permit a partial second generation. All stages overwinter, though the majority of individuals overwinter as gravid adult females (McClure, 1978).

Eggs which overwinter within the female cover hatch in the spring while those of the partial second generation hatch in autumn and overwinter as first and second instar nymphs. Hatching first instar nymphs (crawlers) preferentially settle on the lower surface of young needles of the lower crown (McClure, 1977b, d). The first instar is the only stage, other than the adult male, which is mobile. Using long, thin stylets, the nymphs suck contents from the internal cells of the needles causing their discoloration and premature drop and often tree death where infestations are high.

Males have five stages: first instar nymph, second instar nymph, pre-pupa, pupa, and two-winged adult. Only the first two stages feed. Females have three developmental stages: first instar nymph, second instar nymph, and adult, all of which feed. Females of *F. externa* are pupillarial: following insemination the female shrinks to the anterior portion of the cast nymphal exuviae within which she deposits her eggs.

Materials and Methods

A study was conducted during 1977 in a forest located at the intersection of Conn. route 102 and Minuteman Road in Ridgefield, Fairfield County, Connecticut, USA. The forest comprised approximately 1 km² of conifers and mixed hardwoods wherein *T. canadensis* was predominant in both the overstory and understory. This forest was reported to be heavily infested by *F. externa* in a winter 1976–77 survey (McClure and Fergione, 1977).

Twenty mature hemlocks approximately 15–20 m tall were sampled in April to determine scale density. Of these, 10 trees supporting a range of densities from high to low were chosen. These trees, separated from one another by a minimum distance of 50 m, were of approximately equal size, age and crown development and were growing under similar soil and moisture conditions.

Weekly from April through Sept and biweekly from Oct through Nov, 5 branches were sampled from the lower crown of each tree. The number of scales on 100 youngest needles for each branch was counted which provides an accurate determination of *F. externa* densities on hemlock (McClure, 1977d). Stage of development was recorded for the first 20 individuals encountered on each branch.

Overwinter mortality in 1976–77 was determined in May for each tree by counting the number of dead scales (all stages) on 500 youngest needles (100 per branch). On Aug 2, mortality of settled first and second instar nymphs (crawlers which had hatched during May and June) was determined by counting living and dead scales on 100 young (1977) needles per branch for the 10 trees. The shriveled, dark brown appearance of dead scales was used to distinguish them from the plump, yellowish-green, living scales. Dead scales remain firmly attached to the needle providing a means for accurate determination of mortality.

A small parasitic wasp, *Aspidiotiphagus citrinus* (Craw.) (Hymenoptera: Aphelinidae), is potentially valuable for biological control of *F. externa* (McClure, 1977d). Parasitism by this wasp was determined for the 1976 generations on May 18, 1977 and for the 1977 generations on Sept 21, 1977. Since there is very little adult parasite activity between Sept and May (McClure, 1978) determinations of percent parasitism made on the above two dates were comparable. Using a technique involving subillumination microscopy (Wallner, 1965; McClure, 1977d) the presence of parasite eggs, larvae, pupae, and adults within second instar females was determined for the first 100 individuals encountered on young needles of each of 5 branches. On several dates throughout the season young foliage from the lower crown of each tree was placed in emergence cages (see

McClure, 1977d) and examined after 2 weeks so that adult parasites could be collected and identified. On May 18 mortality of parasites on each tree was determined by counting those which had ceased development or had failed to eclose, indicated by their shriveled, discolored appearance.

Living and dead scales occurring on each of the past 4 years needles were counted on November 7 to determine the effect of needle age on the survival of settled nymphs. For each tree 20 needles of each age class were examined per branch (100 needles per tree). None of the branches had foliage older than 4 years.

In May and Sept the first 100 adult females observed (20 per branch) for each tree were assessed for the proportion with eggs. The percentage of adult females with eggs can be used to compare development times of *F. externa* among trees (McClure, 1977b). Since there is virtually no development during the overwintering period (Nov to April) (McClure, unpublished) females with eggs in May, 1977 are those which also had eggs in Nov, 1976. The May determination, therefore, can be used to indicate development time for the 1976 generations. Development for the 1977 generations was indicated from determinations made on Sept. 21.

The number of eggs that females produced by Nov provides a valid fecundity estimate for *F. externa* as egg production by females which initiated oviposition in autumn was likely completed by this time (McClure, 1977c). Accordingly, on May 18 and November 7 the number of eggs produced per female for 25 gravid females on each tree was counted so that density effects on fecundity could be evaluated. The first 25 gravid females occurring alone on a young hemlock needle were used for fecundity estimates. Egg counts included eggs developing within the female, eggs deposited within the nymphal exuviae, and chorions left by hatched crawlers.

On a tree supporting a moderate density (75 scales per 100 needles) in April, 20 females, each occurring alone on a young needle, with 2 other individuals, and with 4 other individuals, were examined in May and their fecundity determined. This provided a means for evaluating effects of density on fecundity within the sample unit (needle).

Dispersal from the 10 trees was monitored by catching falling crawlers on slides beneath each tree. Eight glass slides (5×7.5 cm) coated with silicone grease were placed atop 0.4 m wooden stakes. Stakes were placed at each of the 4 cardinal directions at distances of 1 and 3 m from the trunk. Collections were made between May 31 and July 13 for the spring hatch and between September 14 and October 25 for the fall hatch. Slides were replaced biweekly and the number of crawlers caught on a 5×5 cm area of each slide (total of 200 cm^2 per tree) was counted.

Data were subjected to linear regression analysis and analysis of variance using Duncan's (1955) test for comparing means.

Results

Densities of *F. externa* in April differed significantly among the 10 hemlocks at Ridgefield. The mean number of scales (all stages) which entered the 1976–77 overwintering period ranged from 24.8 ± 2.9 to 163.6 ± 14.9 per 100 needles. For the following 1977–78 overwintering period mean density ranged from 66.2 ± 4.8 to 211.2 ± 10.3 scales per 100 needles. However, trees which had supported the highest densities in 1976 did not necessarily support the highest densities in 1977. There was a highly significant negative correlation ($p < 0.01$) between scale density in 1976 and the percent increase or reduction in density determined in Nov 1977 (Fig. 1). For the 6 hemlocks supporting densities < 75 scales per 100 needles in 1976 scale numbers increased by 75% to 299% ($\bar{x} = +165.4$). Changes in density on the 4 trees with initial densities > 100 scales per 100 needles ranged from an increase of 23% to a decrease of 291% ($\bar{x} = -107.8$).

Development of the 1976 generations, measured as the percent of females which were gravid by May 1, and of the 1977 generations, measured on September 21, was significantly faster on hemlocks which had supported the lower

Fig. 1. Relationship between the mean number of *Fiorinia externa* per 100 needles which entered the 1976-77 overwintering period and the percent increase or reduction in scale density determined from the number which entered the following 1977-78 overwintering period for 10 hemlocks ($p < 0.01$)

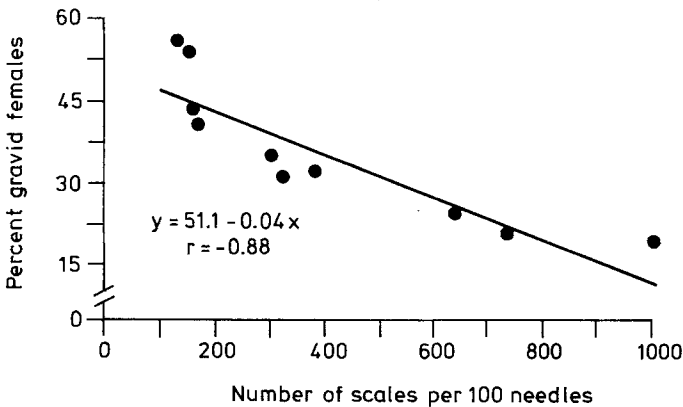
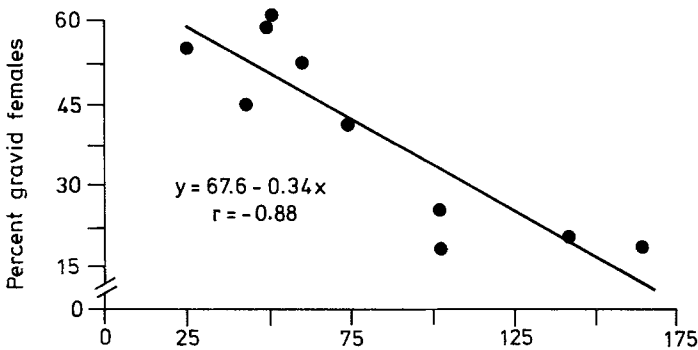
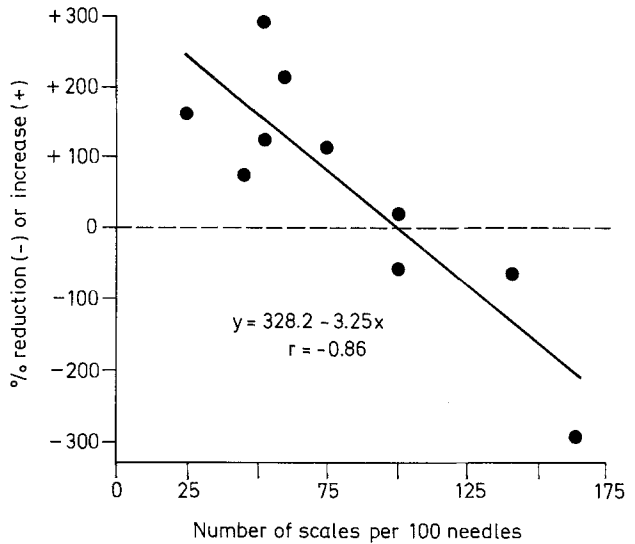


Fig. 2. Relationship between (1) the mean number of *Fiorinia externa* per 100 needles which entered the 1976-77 overwintering period and mean percent of females which were gravid in May (indicative of development time during 1976) ($p < 0.001$; above), and (2) the mean number of *F. externa* per 100 needles on August 2 and mean percent of females which were gravid in September (indicative of development time during 1977) ($p < 0.001$; below)

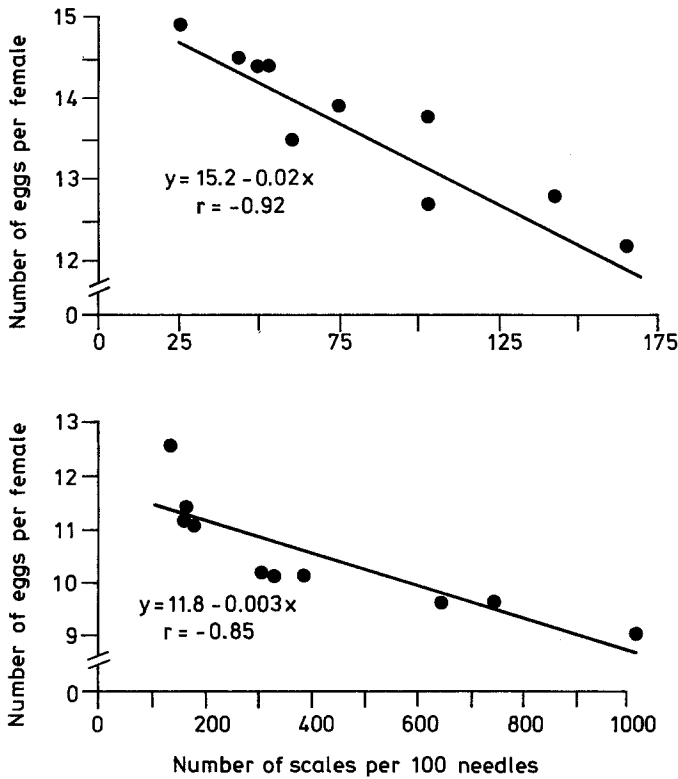


Fig. 3. Relationship between density of *Fiorinia externa* on 10 hemlocks and the mean number of eggs produced by females of the 1976 generation ($p < 0.001$; above) and by females of the 1977 generation ($p < 0.01$; below). Densities are as in Fig. 2

scale densities during each period. For both years highly significant negative correlations were obtained between percent of adult females gravid and scale density (p 's < 0.001) (Fig. 2).

Number of eggs produced by females for both the 1976 and 1977 generations was also significantly influenced by scale density. Highly significant negative correlations were obtained between the density of scales overwintering during 1976-77 and settling in Aug 1977 and fecundity of females which subsequently developed on the 10 hemlocks (p 's < 0.01) (Fig. 3). Significantly fewer eggs were produced by females which had developed on trees supporting the greatest number of feeding nymphs. On the hemlock which had supported the lowest scale density ($\bar{x} = 24.4 \pm 2.9$ per 100 needles) females produced on average 14.8 ± 1.1 eggs while on the highest density tree ($\bar{x} = 1011.1 \pm 79.2$) females produced on average only 9.2 ± 1.0 eggs.

Differences in the number of eggs produced by females which had developed on needles supporting different numbers of individuals were not significant (p 's < 0.05). However, there was a trend toward reduced egg production as numbers of scales per needle increased. For 20 females occurring alone on

Table 1. Number of eggs and settled crawlers on 100 youngest hemlock needles and number of dispersing crawlers caught on sticky slides for the spring and autumn hatchings of *Fiorinia externa* on the 10 trees at Ridgefield, Ct. Numbers are means based on 5 branches per tree for eggs and settled crawlers and on 24 slides per tree per hatch for dispersing crawlers. Data for the 2 hatch periods as presented are not paired by tree

Spring			Autumn		
Eggs	Crawlers settling	Crawlers dispersing	Eggs	Crawlers settling	Crawlers dispersing
171.6	134.0	54.0	71.6	24.4	41.1
194.4	158.2	81.5	127.0	21.6	45.9
256.4	173.4	60.1	138.2	21.6	49.8
257.6	383.6	75.1	148.0	17.2	38.0
288.0	164.0	66.5	170.0	20.6	50.0
380.8	305.0	98.4	220.8	27.8	58.3
422.6	325.0	148.3	299.8	28.2	77.3
561.4	649.2	110.3	325.2	36.6	90.4
660.4	738.0	168.3	338.0	37.3	88.6
878.4	1011.0	216.2	441.6	39.4	114.9

a needle mean fecundity was 13.3 ± 2.6 , for females occurring with two other individuals mean fecundity was 12.7 ± 2.3 , and for those occurring with 4 other individuals mean fecundity was 12.1 ± 2.2 .

Density did not significantly influence the behavior of crawlers relative to their dispersal or to their choice of colonization sites on branches of the lower crown (p 's > 0.05). The greatest numbers of crawlers were caught on sticky slides beneath the more heavily infested trees during both the spring and autumn hatching periods (Table 1). However, comparison of egg densities initially present with densities of crawlers which subsequently settled or dispersed indicated that dispersal was not density-dependent. During the spring hatching period the greater portion of the crawlers settled on the young (1977) needles. On several hemlocks densities of settled crawlers even exceeded densities of eggs initially present (Table 1). The greater than expected numbers of settled crawlers likely resulted from crawlers in the upper levels of the crown falling and settling on young needles of the lower crown where samples were taken.

Only a small portion of the eggs present in autumn on the 10 trees hatched; most of the eggs overwintered as such within the female cover. Therefore, the numbers of crawlers which settled in autumn were considerably lower than those in the spring. However, numbers of crawlers caught on sticky slides were comparable for the two trapping periods (Table 1), indicating that a greater portion of the crawlers which hatched in autumn dispersed.

On all trees crawlers which hatched during the spring and fall hatching periods preferentially colonized the youngest hemlock needles. For the 10 trees a mean percent of 75.2 ± 4.8 settled on 1977 needles, 23.2 ± 4.2 on 1976 needles, 1.6 ± 1.5 on 1975 needles, and none on 1974 needles. Since these crawlers hatched from eggs occurring predominantly on 1976 foliage, their preponderance on 1977 needles indicates a strong preferential response by crawlers to youngest growth.

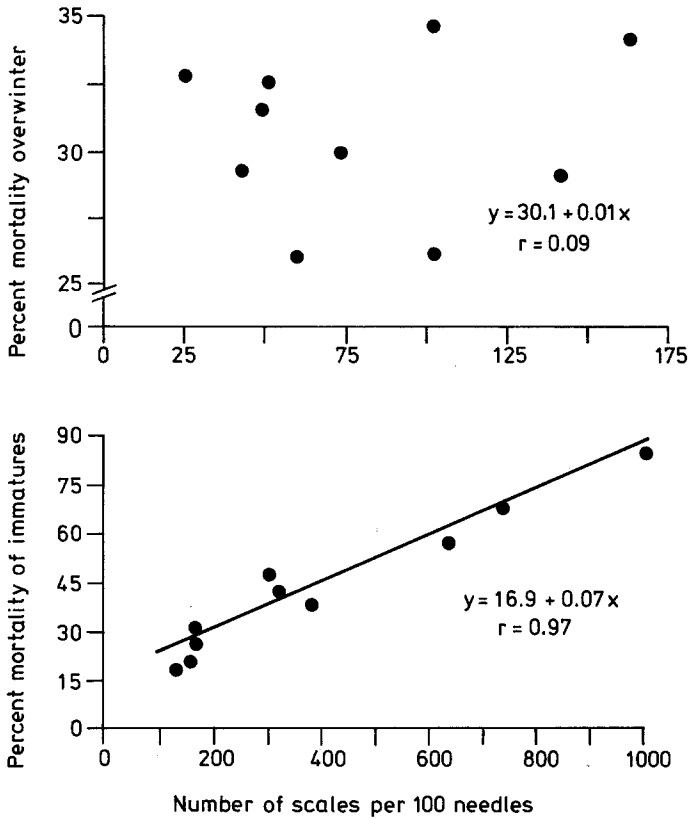


Fig. 4. Relationship between density of *Fiorinia externa* on 10 hemlocks and the mean percent mortality suffered by overwintering scales ($p > 0.05$; above), and by first and second instar nymphs from hatch to August 2 ($p < 0.001$; below). Densities are as in Fig. 2

The predominant overwintering stage on all 10 trees was the third instar (adult) female. Due to the partial second generation which hatched in autumn and the resulting overlap of developmental stages a small percentage of the population overwintered as first instar nymphs ($\bar{x} = 3.2 \pm 2.0$) and as second instar nymphs ($\bar{x} = 16.3 \pm 5.6$).

Percent mortality suffered by all stages during the 1976–77 overwintering period ranged from 26.2 ± 5.2 to 34.8 ± 7.6 ($\bar{x} = 30.7 \pm 3.0$) for the 10 hemlocks. There were no significant differences between overwintering mortality on trees supporting different scale densities ($p > 0.05$) and the correlation coefficient obtained for the data was insignificant ($p > 0.05$) (Fig. 4). In contrast mortality among immatures of the summer 1977 generation was significantly correlated with the density of crawlers which settled on young (1977) needles following the spring hatch ($p < 0.001$) (Fig. 4). Nymphs on the hemlock supporting the highest scale density suffered on average $84.6 \pm 9.3\%$ mortality while those on the least heavily infested tree suffered only $18.6 \pm 5.1\%$ mortality.

The percent of settled nymphs (spring and autumn hatching nymphs combined) which survived from August 2 to November 7 on 1977 needles ($\bar{x} =$

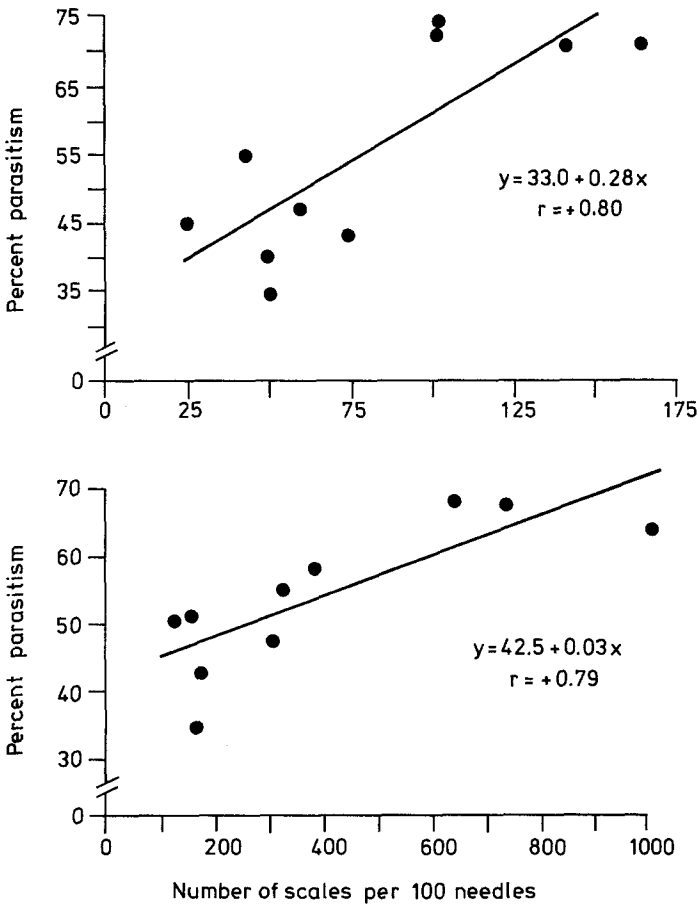


Fig. 5. Relationship between density of *Fiorinia externa* on 10 hemlocks and the mean percent parasitism by *Aspidiotiphagus citrinus* during 1976 ($p < 0.01$; above) and during 1977 ($p < 0.01$; below). Densities are as in Fig. 2

77.2 ± 7.0) and on 1976 needles ($\bar{x} = 77.0 \pm 8.4$) did not differ significantly ($p > 0.05$). Nymphs on older needles were too few for meaningful determination of percent survivorship.

The only parasite of *F. externa* collected from emergence cages during 1977 was *A. citrinus*. All stages of this parasite were observed, but only within second instar females. Parasitized females had neither matured nor oviposited. Percent parasitism during 1976 ranged from 34.6 ± 4.6 to 74.4 ± 6.8 ($\bar{x} = 55.5$) and during 1977 ranged from 34.6 ± 4.2 to 68.4 ± 3.2 ($\bar{x} = 54.2$) for the 10 trees. For both years significant positive correlations were obtained between percent parasitism and scale density (p 's > 0.01) (Fig. 5). On the more heavily infested trees parasitism was approximately double that on the less heavily infested trees.

Percent mortality suffered by *A. citrinus* overwintering within its host during 1976–77 did not vary significantly among trees and ranged from 58.0 ± 7.3 to 64.8 ± 5.3 ($\bar{x} = 62.4 \pm 2.5$) ($p > 0.05$).

Discussion

Evidence is presented to indicate that populations of *F. externa* on hemlock are, to some extent, numerically self-regulated. The highly significant negative correlation between scale density and population increase after one year (Fig. 1) suggests an inverse density-dependent relationship. Eberhardt (1970) cautioned against inferring density-dependent population regulation on the basis of correlation analyses alone. However, the biological evidence reported herein substantiates the presence of self-restraints on elongate hemlock scale populations. Development time, fecundity, and survival were all significantly influenced by scale density for two consecutive years. On hemlocks supporting the higher scale densities the summer, 1977 generation developed more slowly, produced fewer eggs, and suffered four times greater mortality than on the less heavily infested trees.

In a previous study (McClure, 1977c) development of *F. externa* was accelerated and fecundity increased on hemlocks where density had been reduced by insecticide. Where densities in August were between 100 and 150 scales per 100 needles, mean percent of adult females gravid in late September (a measure of development time) was 55.2 ± 5.3 and mean fecundity was 12.8 ± 0.4 . These previous results support the presence of a mechanism of self-regulation and are remarkably consistent with the values obtained here for development time and fecundity at comparable densities.

Overwinter mortality of *F. externa* and its parasite, *A. citrinus* did not differ significantly among trees, which supports the generally accepted view that climatic factors operate on individuals of a population independent of their density. However, mortality to nymphs due to parasitism and to inadequate procurement of the necessary energy for growth and development were significantly correlated with scale density. In a previous study conducted in a Westport, CT forest (McClure, 1977d) *A. citrinus* responded density-dependently to *F. externa* both within the hemlock crown and among trees and percent parasitism increased from 28.5 to 42.1 in a single year. As we have seen (Fig. 1) there were significant changes in scale density on individual hemlocks from 1976 to 1977 at Ridgefield. But, the range of densities among the 10 trees in autumn 1976 and in autumn 1977 remained relatively constant as did the range of percent parasitism. This implies that a shift in percent parasitism occurred concurrently with the shift in scale density on the 10 trees. This supports the conclusion drawn from previous findings (McClure, 1977d) that during oviposition *A. citrinus* females select trees with the highest scale densities. Thus, on any given hemlock the current percent parasitism does not necessarily reflect the level of parasitism on that tree during a previous year.

Unlike the Westport study (McClure, 1977d) mean percent parasitism at Ridgefield did not increase significantly in one year. The relatively high percent mortality suffered by *A. citrinus* ($\bar{x}=62.4$) compared with that of its host ($\bar{x}=30.7$) during the abnormally cold winter of 1976-77 is a likely explanation.

The observed differences in the success of *F. externa* on hemlocks supporting various scale densities is likely due to differences in the quality and availability of essential resources for feeding nymphs. As we have seen (McClure, 1977b) edaphic conditions and their subsequent effect on the vigor of hemlock had

a profound influence on the development rate and survival of resident *F. externa* nymphs by altering the nutritional quality of their food. Similarly scale induced stress of red pine, indicated by resinosis from feeding wounds, and its subsequent deleterious effects on food quality had a profound influence on the development, fecundity, survival, and dispersal of the red pine scale (McClure, 1977a). Stress induced by excessive feeding, likewise, may have reduced the nutritional quality of hemlock resulting in the differential success of nymphs on trees supporting various scale densities at Ridgefield.

Density could also have a more direct influence on the success of feeding nymphs through competition if and when essential resources (likely food and space) became exhausted. Because a nymph becomes sessile once it has settled, the food available to it is that contained within the cells of a single needle which are within reach of its sucking mouthparts. Wallner (1964) reported that *F. externa* nymphs feed by inserting a long feeding tube (fused mandibular and maxillary stylets) through the cuticle or via a stomatal opening and then sucking juices from cells which the tube penetrates as it moves parallel to the longitudinal axis of the needle. He determined that this feeding tube may be from seven to eight times the length of the nymph's body. Using Wallner's determination of stylet length, a second instar nymph, whose body length is roughly 0.5 mm, has a feeding tube of approximately 4 mm. Thus, a single nymph could conceivably exploit a circular area of 50 mm², which is more than three times the average area of a hemlock needle (15.2 mm²) (McClure and Fergione, 1977).

One might expect that as scale density increased competition became increasingly important in determining the success of feeding nymphs. But as is characteristic of a scramble-type competition, such as this would be, success is commonly not achieved, since available resources are divided among individuals in such a way that few or none may obtain a sufficient amount of energy for survival (see Nicholson, 1954). We have seen that when mean scale densities on hemlock approximated 6 nymphs per needle survival was only 43%; at 10 nymphs per needle survival was less than 16%. Interference between nymphs feeding on the same needle is likely common and would certainly affect the ability of coexisting nymphs to acquire necessary energy for growth and development. The observed reductions in fecundity with increasing scale density on individual needles, although insignificant, might well be indicative of interference competition. Ongoing studies will examine the relative importance of changes in the nutritional quality of hemlock induced by scale feeding and of intraspecific competition in the self-regulation of *F. externa* populations.

Decreases in development, fecundity, and survival with increasing scale density suggest that the essential resources needed for normal growth and development became reduced in quality, depleted, or, at least, less available due to interference by other nymphs. The sharp reduction after a single year in the number of scales on hemlocks which had supported high densities the previous year indicated that populations of *F. externa* are to some extent, self-regulated. However, it is apparent from the high incidence of mortality among infested trees that these self-restraints are insufficient to maintain populations below the level at which control measures are unnecessary. Even though crawlers did not disperse more readily from hemlocks supporting the higher scale densities (this

study), they were able to disseminate for considerable distances on the wind and colonize hemlocks on which they fell (McClure, 1977 b). Through dispersal the elongate hemlock scale is able to escape the self-regulatory influence imposed at high densities and establish new population centers.

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