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COMPETITION BETWEEN EXOTIC SPECIES: SCALE INSECTS ON HEMLOCK[1]

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Abstract. Two exotic armored scales, *Fiorinia externa* Ferris and *Tsugaspidiotus tsugae* (Marlatt), native to Japan occur sympatrically in the northeastern United States where they often attain high population densities on eastern hemlock, *Tsuga canadensis* Carriere. Both scales preferentially colonize the young needles of the lower hemlock crown, which intensifies competition between them when food and space become limiting at high scale densities. Studies conducted for 2 yr in the greenhouse and in a hemlock forest located in Darien, Connecticut, demonstrated that summer generations of *F. externa* and *T. tsugae* compete intraspecifically and interspecifically at densities occurring in the field. *F. externa* had a greater adverse affect (reduced survival and fecundity) on itself and on *T. tsugae* than did *T. tsugae* have either on itself or on *F. externa*. The superior competitive ability of *F. externa* over *T. tsugae* was likely due to its earlier colonization time. Hatching in early June some 2–4 wk prior to its competitor, *F. externa* is afforded a distinct spatial and nutritional advantage (1) by colonizing young, nitrogen-rich needles at a time during the year when concentrations of foliar nitrogen and water are high, (2) by reducing the amount of foliar nitrogen available to *T. tsugae* nymphs, and (3) by forcing *T. tsugae* crawlers to colonize older, nitrogen-poor foliage where they subsequently suffer significantly greater mortality.

Aspidiotiphagus citrinus Crawford (Hymenoptera: Aphelinidae), a primary internal parasitoid of *F. externa* and *T. tsugae*, exhibited a density dependent response to both scales in single-species infestations in the Darien forest. In mixed infestations, however, the parasitoid did not selectively attack the more abundant species but parasitized each scale in proportion to its frequency. Because it did not discriminate between hosts, *A. citrinus* did not alter the outcome of the competition between summer generations of the two scales.

The geographical distributions of the two scales in Fairfield County, Connecticut, and their population trends for 3 yr at 20 sites where they occur sympatrically indicate that competition has excluded *T. tsugae*. At 18 of 20 sites coinhabited at different densities during 1976, *T. tsugae* was excluded or nearly excluded within 3 yr. Only at two sites, where *T. tsugae* was abundant and *F. externa* was sparse, was *T. tsugae* able to maintain its initial relative density.

Key words: armored scales; Aspidiotiphagus citrinus; *colonization time; Diaspididae; eastern hemlock; fecundity;* Fiorinia externa; *foliar nitrogen; Homoptera; interspecific competition; intraspecific competition; parasitism; survival;* Tsuga canadensis; Tsugaspidiotus tsugae.

INTRODUCTION

Exotic species introduced into habitats with hospitable climates and suitable resources often find conditions conducive to rapid population growth. With abundant food and little discouragement from native competitors and natural enemies, their numbers often increase nearly exponentially until the food supply becomes exhausted. Competition between species can be examined best in such habitats where the influence of numerous regulatory factors characteristic of indigenous communities is minimal. A dramatic example of an exotic phytophagous insect whose populations quickly deplete the food supply is the red pine scale, *Matsucoccus resinosae* B and G (Homoptera: Margarodidae). Deterioration of the food resource with increasing scale density and its deleterious effects on scale survival, development rate, and fecundity (McClure 1976, 1977*a*) vividly illustrate the precarious fate of an introduced species. One of the best-documented examples of interspecific competition resulting in exclusion of inferior species also involved exotic species, namely three aphelinid parasitoids introduced into California for biological control of California red scale, *Aonidiella aurantii* (Maskell) on citrus (DeBach and Sundby 1963, DeBach 1966).

Scale insects (Homoptera: Coccoidea) are well represented among the hundreds of exotic species which have established themselves as serious pests throughout the world. DeBach and Rosen (1976) list 47 exotic scales belonging to the single family of armored scales (Diaspididae). In addition numerous other exotic coccoids have become sufficient pests that biological control projects have been initiated at considerable expense (see DeBach et al. 1971, DeBach 1974).

Two exotic scales of eastern hemlock, *Tsuga canadensis* Carriere, in the northeastern United States are *Fiorinia externa* Ferris and *Tsugaspidiotus tsugae* (Marlatt) (Homoptera: Diaspididae). Both species were introduced into the United States between 1908 and 1910 on exotic hemlocks shipped to the New York City area from Japan, and subsequently became established on native eastern hemlock (Sasscer 1912,

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Weiss 1914, Ferris 1936). The crawlers, or mobile first-instar nymphs of both species preferentially colonize the undersides of hemlock needles where they insert their piercing stylets and suck the fluid from mesophyllic cells. Their feeding causes needles to discolor and drop prematurely and sometimes trees die following sustained and heavy attacks.

Previous studies on *F. externa* (McClure 1979*a* and *b*, 1980) showed that scale survival, development rate, and fecundity on hemlock decrease as its numbers increase, suggesting intraspecific competition. Reduced success accompanying increasing density was attributed to depleted nitrogen and water available to nymphs on the foliage. Another study revealed that *F. externa* and *T. tsugae* frequently feed and breed in the same localities on the same hosts in southwestern Connecticut (McClure and Fergione 1977). At 11 sites where these species occurred sympatrically, densities of *F. externa* and *T. tsugae* were significantly negatively correlated, suggesting interspecific competition.

The physiological status of a host plant is undoubtedly important to the success of populations of phytophagous insects (Southwood 1973, McNeill and Southwood 1978). Numerous studies have established the dynamic nature of host nutritional quality for piercing and sucking insects not only during the season (Dixon 1970, 1975, van Emden et al. 1969, Webb 1977, Webb and Moran 1978, White 1978) but also throughout the course of an infestation (McClure 1977*a*, 1979*a*). Accordingly a factor important to the outcome of interspecific competition between exotic phytophagous insects is the relative degree of compatibility of their phenologies with that of the host. The phenologies of *F. externa* and *T. tsugae* on hemlock differ considerably in Connecticut (McClure 1978). *F. externa* has one complete generation each year with crawlers reaching peak abundance during the 2nd wk of June. Approximately 30% of the progeny of this summer generation initiates an unsuccessful autumn generation whose crawlers hatch in mid-September and subsequently die over winter (McClure 1981). *T. tsugae* has two complete generations each year with crawlers reaching peak abundance during late June to early July (summer generation) and during the last week in September (autumn generation). Therefore, the summer generation crawlers of *F. externa* colonize hemlock needles prior to those of *T. tsugae*.

Another important factor which could alter the outcome of competition between exotic hemlock scales is differential mortality from a natural enemy. The potential impact of a natural enemy on interspecific competition has been demonstrated by Park's (1948) laboratory study with flour beetles (Coleoptera: Tenebrionidae). A small exotic solitary wasp *Aspidiotiphagus citrinus* (Crawford) (Hymenoptera: Aphelinidae) of nearly worldwide distribution is a primary internal parasitoid of both *F. externa* and *T. tsugae*. While 50% parasitism of these hemlock scales is common in forests throughout southwestern Connecticut, parasitism as high as 96% has been observed in some areas (McClure 1978). A previous study (McClure 1978) revealed that the seasonal abundance of ovipositing adults of *A. citrinus* was closely synchronized with that of first-instar nymphs of *T. tsugae*, the stage suitable for parasitism. In addition, both parasitoid and scale were bivoltine and had similar rates of development. The relationship between *A. citrinus* and *F. externa* was quite the contrary due to their sharply contrasting seasonal development. Peak abundance of ovipositing adults of the bivoltine parasitoid and of second-instar nymphs of *F. externa*, the suitable stage of this univoltine host, were asynchronous. Although seasonal development of *A. citrinus* is poorly synchronized with that of *F. externa*, a permanent parasitoid-host relationship could be preserved in areas where *F. externa* and *T. tsugae* occur sympatrically, if adult parasitoids emerging from one host species would readily attack the other (McClure 1978).

Here I report results of field and laboratory studies to examine competition between summer generations of *F. externa* and *T. tsugae* on hemlock and to investigate the impact of colonization time and parasitism by *A. citrinus* on the outcome of interspecific competition.

Materials and Methods

Vertical distribution in the hemlock crown

Studies to determine the vertical distributions of sympatric and allopatric populations of *F. externa* and *T. tsugae* in the hemlock crown were conducted during 1977 and 1978 at three forested sites in Fairfield County, Connecticut. Two of these sites were located in the town of Westport. Hemlocks at one site were infested with *F. externa* only, while trees at the other site located 8 km away were infested with *T. tsugae* only. Both species coinhabited the third site located in New Canaan ≈12 km west northwest of the nearest Westport site. At each site five mature hemlocks 12 m tall were sampled in January by removing five branches with a pole pruner from each crown at 0–4 m, 5–8 m, and 9–12 m aboveground and then counting the number of scales occurring on 100 needles of youngest growth on each branch. Analysis of variance was used to test the significance of differences between the vertical distributions of hemlock scales at sites where they occur solitarily and at sites where they coexist.

Colonization time

To determine the colonization times of summer generation crawlers of *F. externa* and *T. tsugae* and the nutritional quality (foliar nitrogen and water concentrations) of the young hemlock needles at colonization time, a study was conducted during 1978 in hemlock forests located in 10 townships of Fairfield County, Connecticut, where hemlock scales have coexisted for several years at various relative densities. On 26 May and biweekly through 24 July, four hemlock trees were sampled at each site. From each of four branches per tree, 15 young needle clusters were removed and immediately placed on dry ice. Of these, 20 clusters (five per branch) were then stored at −50°C for determination of total nitrogen concentration using a modified Kjeldahl technique (Glowa 1974) while the remaining 40 clusters per tree were weighed, oven dried at 45°C, and then reweighed for determination of water content. The utility of these techniques for estimating the nutritional quality of foliage for hemlock scales has been discussed previously (McClure 1980). The remaining foliage from each branch was examined and the number of eggs unhatched and hatched was counted. Chorions left from hatched eggs, easily distinguished from unhatched eggs, provided a basis for determining the time of peak crawler hatch for each scale at the 10 sites.

Competition in greenhouse populations

Experiments were conducted during 1978 and 1979 in the greenhouse to determine whether summer generations of *F. externa* and *T. tsugae* compete at population densities typical of those observed in the forests of southwestern Connecticut and to determine the importance of the time of colonization by crawlers. On 9 May 1978, 60 4-yr-old hemlocks, obtained from a common stock at the Pachaug State Nursery in Voluntown, Connecticut were potted in equal parts of soil, sand, peatmoss, and wood chips and maintained in the greenhouse. On 7 June during peak colonization of summer-generation *F. externa* (McClure 1978) hemlock branches infested with eggs and crawlers were collected from Westport and were used to infest greenhouse hemlocks as follows: six branches were placed on each tree in one group of 15 hemlocks and three branches on each tree in another group. On 21 June, during peak colonization by summer-generation *T. tsugae* (McClure 1978), hemlock branches infested with eggs and crawlers were collected from New Canaan and were used to colonize greenhouse trees as follows: six branches were placed on each tree in one group of 15 trees and three branches were placed on each tree in the group which was colonized previously with *F. externa*. This produced single-species infestations of each scale and a mixed-species infestation. The sequence of infestation simulated colonization times by crawlers of both species under natural conditions. Branches were left on all trees for 14 d. Using this procedure, approximately equal total scale densities were obtained on all single- and mixed-infestation groups. Total numbers of crawlers which colonized the various experimental groups (100–150 per 100 young needles) are typical of densities observed in the field (McClure and Fergione 1977). One group of 15 hemlocks was left uninfested to serve as a control for effects of scale feeding on the concentration of foliar nitrogen.

Five weeks after hemlocks were infested, two branches were sampled from each of five randomly selected trees in each infested group. The number of nymphs of each species which had colonized 100 young (1978) needles, 100 1-yr-old needles, and 100 2-yr-old needles, and their percent survival, based upon 100 colonists on needles of each age, were determined for each branch by microscopic examination. On 26 July, 40 clusters of young and 1-yr-old needles were sampled randomly within a 1-h period from five trees in all four groups. Of these, 20 clusters were immediately placed on dry ice and later stored at −50°C for nitrogen determination while the remainder were weighed, oven dried, and reweighed for determination of water content.

A similar experiment was conducted in the greenhouse during 1979 to investigate further the importance of colonization time to the success of summer generations of *F. externa* and *T. tsugae* in single- and mixed-species infestations by varying the time when crawlers settled on the hemlock foliage. On 2 May 1979, 60 4-yr-old hemlocks were obtained from a common stock at the State Nursery and were potted and maintained in the greenhouse as described for the previous experiment. On 8 June during peak colonization by summer-generation *F. externa*, hemlock branches infested with eggs and crawlers were collected from Westport. A portion of these branches was used to infest greenhouse hemlocks as follows: six branches were placed on each tree in one group of 12 hemlocks and three branches on each tree in another group. The remainder of the infested branches was refrigerated at 5°C to arrest further development of crawlers and hatching of eggs of *F. externa*. On 22 June during peak colonization by summer-generation *T. tsugae*, hemlock branches infested with eggs and crawlers were collected from New Canaan and were used to infest greenhouse hemlocks as follows: six branches were placed on each tree in one group of 12 uninfested hemlocks and three branches on each tree in the group infested previously with three branches containing *F. externa* and on another group which was uninfested. The branches infested with *F. externa* were removed from refrigeration on that same day (22 June) and were used to infest greenhouse hemlocks as follows: six branches were placed on each tree in one group of 12 uninfested trees and three branches were placed on each tree in the group infested with three branches containing *T. tsugae*. Branches were left on all trees for 14 d. Those which had been held in refrigeration for 14 d were examined microscopically to ensure the vitality of eggs and crawlers of *F. externa*. Approximately equal densities (100–150 total scales per 100 young needles), representative of those observed in the field, were obtained on all single- and mixed-infestation groups.

Five weeks after hemlocks were infested, two branches were sampled from each of five randomly selected trees in each group. The number of crawlers which had colonized 100 young (1979) and 1-yr-old needles and the number alive per 100 colonists were determined for each branch by microscopic examination. Analysis of variance was used to test the significance of differences in foliar nitrogen concentration and scale mortality in single- and mixed-species infestations in the greenhouse.

Competition in forest populations

A study was conducted during 1978 in a hemlock forest in Darien, Fairfield County, Connecticut to examine competition during the summer generation in single- and mixed-species infestations of *F. externa* and *T. tsugae*. In January, 70 hemlocks of approximately equal size and age and growing under similar soil and moisture conditions were sampled to determine the density of their resident scale populations. Four branches were removed with a hand pruner from the lower crown of each tree and the number of each species occurring on 100 youngest needles (1978) of each branch was determined by microscopic examination. Of these, 18 trees were selected for competition studies: six trees infested only with *F. externa*, six only with *T. tsugae*, and six with both species. The six trees in each group were chosen to represent a range of total scale density from lightly infested to heavily infested so that density effects on scale success could be evaluated. Using techniques described and used effectively in a previous study (McClure 1979*a*), survival of colonists, fecundity of third-instar (adult) females, and percent parasitism by *A. citrinus* for the 1977 summer generations were estimated from the January 1978 samples while the corresponding data for the 1978 summer generations were determined from samples taken in October 1978. Percent survival was measured by counting the number of living and dead colonists for the first 100 individuals encountered on young needles of each of four branches. Fecundity was obtained by counting the number of eggs and chorions beneath 25 females on each branch. Percent parasitism was calculated from the number of parasitized scales per 100 individuals on each branch identified using techniques described by Wallner (1965). Relationships between scale density and the success of summer generations of *F. externa* and *T. tsugae* in single- and mixed-species infestations were analyzed by linear regression.

To investigate the consequences of competitive interaction in wild sympatric scale populations, densities of *F. externa* and *T. tsugae* were monitored from 1976 to 1978 at 20 sites (including the 10 discussed previously) located in 20 townships of Fairfield County, Connecticut where these species coexist. In January 1977, 1978, and 1979 four hemlocks at each site were sampled by removing two branches from the lower crown with a hand pruner and counting the number of scales occurring on 100 youngest needles per branch.

TABLE 1. Percent of total *Fiorinia externa* population and total *Tsugaspidiotus tsugae* population occurring on hemlock at three heights in the crown. Allopatric populations were sampled during 1977 at two sites in Westport, Connecticut; sympatric populations were sampled during 1978 in New Canaan, Connecticut. Means (±1 SE) are based upon five trees per site. Numbers in parentheses are total scales occurring on 2000 hemlock needles.

	Allopatric populations		Sympatric populations	
Height (m)	*F. externa*	*T. tsugae*	*F. externa*	*T. tsugae*
0–4	49.5 ± 1.8 (3355)	76.6 ± 4.1 (1101)	44.4 ± 1.9 (6133)	61.9 ± 3.0 (740)
5–8	31.5 ± 1.4 (2141)	27.7 ± 2.7 (335)	32.1 ± 0.9 (4434)	28.5 ± 3.3 (352)
9–12	19.0 ± 0.8 (1301)	2.6 ± 1.3 (39)	23.5 ± 2.2 (3245)	9.6 ± 0.7 (119)

RESULTS

Vertical distribution in the hemlock crown

The vertical distribution of allopatric and sympatric population˜ of *F. externa* and *T. tsugae* in the hemlock crown did not differ significantly (ANOVA; P's > .05; df = 1,8) (Table 1). Crawlers of both scales preferentially colonized the lower crown (0–4 m) with lowest numbers occurring in the upper crown (9–12 m) even though concentrations of foliar nitrogen and water do not vary with crown height in forest hemlocks (McClure 1980). Since crawlers of both species colonize only the lower surface of hemlock needles and feed on the fluid contents of the same mesophyllic cells (McClure and Fergione 1977; this study), overlap of their feeding sites is almost complete.

Colonization time

Colonization of the young hemlock needles by summer generation crawlers extended over a 2-wk period in June for *F. externa* and over a 5-wk period during July and August for *T. tsugae* at the 10 sites (Fig. 1). Peak colonization time (mean for 10 sites) of *F. externa* preceded that of *T. tsugae* by 1 mo. There was a consistent trend among sites for decreasing amounts of nitrogen and water in the young hemlock foliage as the season progressed (Fig. 1). Concentrations of foliar nitrogen and water were highest immediately following needle flush in May, declined rapidly during June, and gradually leveled off during July. Therefore, the nutritional quality of hemlock foliage was greater during colonization by *F. externa* than by *T. tsugae*. Although these differences in concentrations of nitrogen and water during peak colonization times are small, a previous study (McClure 1980) has shown that differences of this magnitude are related to significant differences in survival, development rate, and fecundity of hemlock scales.

Competition in greenhouse populations

A significantly greater number of crawlers of both *F. externa* and *T. tsugae* colonized the young needles than either the 1-yr-old or 2-yr-old needles in single-species infestations (P's < .01; all comparisons in the greenhouse experiment by ANOVA, df = 1,8) (Table 2). However, in the mixed-species infestation where *F. externa* had colonized the young needles 14 d earlier, significantly fewer *T. tsugae* crawlers colonized the young needles than either the 1-yr-old (P < .01) or 2-yr-old needles (P < .05). The presence of *F. externa* nymphs on the young needles apparently discouraged *T. tsugae* crawlers from colonizing these sites.

For all experimental groups including the uninfested trees, nitrogen concentration was significantly higher in the young needles than in the older ones on 26 July (P's < .01; Table 2). The nitrogen concentration of the young needles of hemlocks infested only with *F. externa* was significantly lower than that of the other infested and uninfested trees (P's < .01). Foliar nitrogen concentration was reduced more than 18% after 7 wk of feeding by *F. externa*. For all infestations nymphs incurred significantly greater mortality on 1-yr-old and 2-yr-old needles than on young needles (P's < .05; Table 2). In mixed-species infestations *F. externa* nymphs suffered significantly less mortality than in single-species infestations even though total scale densities (all needles) were higher in mixed infestations (P's < .01; Table 2). In contrast *T. tsugae* nymphs suffered significantly greater mortality in mixed infestations even though total scale densities (all needles) were lower than in *T. tsugae* single-species infestations (P's < .01).

The greenhouse experiment conducted during 1979 confirms the results obtained the previous year and further demonstrates the importance of colonization time to crawler behavior and scale success. As in the 1978 experiment, crawlers of both scales selected young needles over older ones during colonization

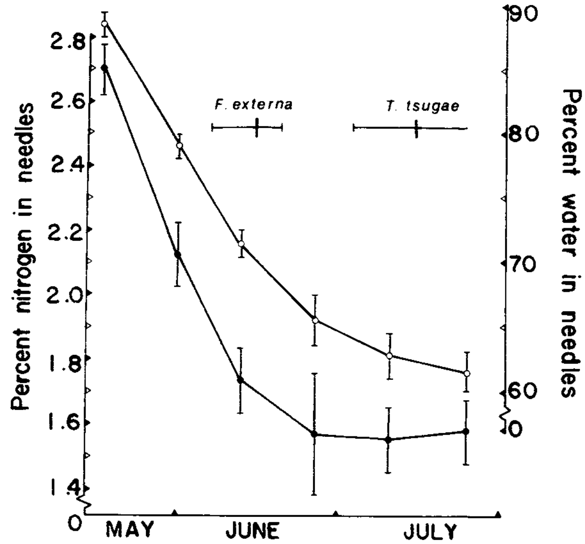

FIG. 1. Mean (±1 SD) percent nitrogen (solid circles) and water (open circles) in the young hemlock needles and the duration and mean (vertical line) of peak colonization of the young needles by summer-generation *Fiorinia externa* and *Tsugaspidiotus tsugae* during 1978 at 10 hemlock forests in southwestern Connecticut.

(P's < .01; Table 3). In mixed infestations, where *F. externa* colonized 14 d earlier, *T. tsugae* crawlers again settled in significantly greater numbers on less preferred 1-yr-old growth (P < .01). However, in the mixed infestation where crawlers of both species colonized needles simultaneously, an unlikely occurrence under natural conditions, a significantly greater number of *T. tsugae* crawlers colonized young growth along with crawlers of *F. externa* (P < .01).

For all infestations, percent mortality after 5 wk was again significantly higher among colonists feeding on the older needles than among those feeding on the younger ones (P's < .05; Table 3). *F. externa* suffered significantly greater mortality for both age classes of needles on hemlocks that were colonized on 22 June than on trees that were colonized on 8 June, the time

TABLE 2. Number of *Fiorinia externa* and *Tsugaspidiotus tsugae* colonizing needles of various ages, nitrogen concentration of those needles, and percent mortality to colonists on hemlocks in the greenhouse during 1978. Trees were infested with *F. externa* on 7 June and with *T. tsugae* on 21 June to simulate natural conditions. Numbers are means (±1 SD) based upon five trees in each group.

	Colonists per 100 needles				Nitrogen (% dry mass)		Mortality (%)		
Treatment	Young	1 yr old	2 yr old	All needles	Young	1 yr old	Young	1 yr old	2 yr old
Single species									
F. externa	124.4 ± 24.3	11.4 ± 7.2	3.8 ± 2.4	136.3 ± 23.4	3.36 ± 0.25	2.92 ± 0.29	12.8 ± 2.5	17.4 ± 0.9	18.0 ± 1.1
T. tsugae	135.6 ± 30.4	83.6 ± 20.0	57.8 ± 9.2	275.5 ± 36.3	4.02 ± 0.72	3.28 ± 0.47	21.4 ± 4.7	28.0 ± 5.2	28.6 ± 4.8
Mixed species									
F. externa	63.2 ± 13.1	23.0 ± 4.3	2.2 ± 2.2	264.8 ± 29.6	4.01 ± 0.16	3.08 ± 0.31	8.2 ± 2.2	12.0 ± 2.7	12.9 ± 1.9
T. tsugae	44.2 ± 9.2	79.8 ± 10.0	54.0 ± 8.1				37.6 ± 4.7	48.0 ± 3.8	50.2 ± 4.1
Uninfested					4.11 ± 0.57	3.03 ± 0.23			

TABLE 3. Number of *Fiorinia externa* and *Tsugaspidiotus tsugae* colonizing young and 1-yr-old needles and percent mortality on greenhouse hemlocks during 1979. Trees were infested with *F. externa* on 8 June and on 22 June and with *T. tsugae* on 22 June to determine the effects of phenology on scale success. Numbers are means (±1 SD) based upon five trees in each group.

Treatment	Date infested	Colonists per 100 needles			Mortality (%)	
		Young	1 yr old	All needles	Young	1 yr old
Single species						
F. externa	8 June	123.4 ± 21.3	12.6 ± 9.3	135.2 ± 19.7	16.2 ± 2.2	18.3 ± 1.2
F. externa	22 June	102.8 ± 19.7	10.3 ± 6.4	114.3 ± 16.8	25.2 ± 2.3	29.7 ± 4.6
T. tsugae	22 June	133.2 ± 23.4	47.8 ± 12.6	183.0 ± 21.6	23.8 ± 3.3	30.6 ± 3.8
Mixed species						
F. externa	8 June	57.8 ± 15.3	21.4 ± 7.3	178.8 ± 24.2	10.6 ± 3.0	13.3 ± 4.3
T. tsugae	22 June	42.6 ± 7.1	59.5 ± 9.3		37.2 ± 4.1	46.4 ± 3.4
F. externa	22 June	51.8 ± 12.2	17.3 ± 8.0	152.6 ± 18.8	18.8 ± 3.3	25.5 ± 6.8
T. tsugae	22 June	58.0 ± 11.6	26.1 ± 9.1		28.6 ± 2.3	35.3 ± 3.6

of peak colonization in the field (P's $< .01$). As in the previous experiment, *F. externa* nymphs suffered significantly less mortality in mixed-species infestations than in single-species infestations for both colonization dates, even though total scale densities (all needles) were higher in mixed infestations (P's $< .01$). Again, *T. tsugae* nymphs suffered significantly greater mortality in mixed-species infestations even though total scale densities (all needles) were lower than in single-species *T. tsugae* infestations ($P < .01$). Mortality incurred by *T. tsugae* nymphs in mixed infestations on both young and 1-yr-old needles was significantly lower on hemlocks colonized by *F. externa* on 22 June than on those colonized on 8 June (P's $< .01$).

Percent mortality of *F. externa* colonists on young and 1-yr-old needles was 36% and 31% lower, respectively, in mixed-species infestations than in single-species infestations during 1978 and 35% and 27% lower during 1979. Percent mortality of *T. tsugae* colonists on young and 1-yr-old needles was 76% and 42% higher in mixed-species infestations than in single infestations during 1978 and 56% and 34% higher during 1979. Therefore, *F. externa* had a greater adverse effect on *T. tsugae* survival than on its own survival and a greater adverse effect on *T. tsugae* survival than did *T. tsugae* have on itself.

All mortality incurred by nymphs in greenhouse experiments resulted from starvation and/or desiccation; none was due to parasitoids.

Competition in forest populations

The success of *F. externa* and *T. tsugae* colonists during the 1977 and 1978 summer generations varied considerably among hemlocks in the Darien forest. On

TABLE 4. Number of *Fiorinia externa* colonizing 100 young needles of six hemlocks infested only with *F. externa* and six infested with *F. externa* and *Tsugaspidiotus tsugae*, percent survival of colonists, fecundity of adult females, and percent parasitism by *Aspidiotiphagus citrinus* for two generations of *F. externa* in a Darien, Connecticut forest. Means for density, percent survival, and percent parasitism were calculated from examination of 100 individuals and for fecundity from examination of 25 individuals on each of four branches per tree.

Infestation	1977 summer generation of *F. externa*				1978 summer generation of *F. externa*			
	Density*	Survival (%)	Eggs/♀	Parasitism (%)	Density*	Survival (%)	Eggs/♀	Parasitism (%)
F. externa	37.5	85.0	16.6	17.0	52.5	90.5	14.4	17.0
	48.5	93.0	15.5	18.0	71.5	88.5	12.3	18.5
	50.5	90.0	15.9	16.5	74.0	89.0	12.5	24.0
	87.5	70.0	16.0	25.0	76.5	85.5	12.7	26.0
	92.5	65.5	13.8	26.5	86.5	73.0	10.0	25.0
	153.5	54.5	12.5	28.5	170.5	55.0	9.4	32.0
Mixed species	79.0 (99.5)	75.5	15.8	15.5	22.0 (38.0)	91.5	13.3	14.0
	81.0 (191.5)	69.5	14.0	26.0	44.5 (75.5)	93.0	13.4	12.5
	104.5 (174.0)	73.5	13.3	19.5	62.0 (74.5)	85.5	11.3	14.5
	147.5 (189.0)	57.5	12.9	23.0	93.0 (252.5)	87.5	11.7	21.5
	148.5 (169.0)	56.5	11.8	18.5	137.0 (147.0)	63.5	9.7	19.5
	157.0 (219.5)	61.0	12.8	26.5	218.0 (288.0)	60.0	7.8	20.5

* Numbers in parentheses are total scales, both species combined.

the six trees infested only with *F. externa*, percent survival and fecundity for 2 yr were highest on the trees supporting the lowest scale densities and lowest on the most heavily infested tree (Table 4). Percent parasitism of *F. externa* by *A. citrinus* was highest where scales were most abundant and lowest where scales were fewest, suggesting a density-dependent response. On the six hemlocks infested with both hemlock scales there was a similar trend of reduced survival and fecundity of *F. externa* as its density increased for both years (Table 4). Percent parasitism of *F. externa* by *A. citrinus* did not increase with *F. externa* density as in the single-species infestations but did increase with the density of both hemlock scales combined.

On the six trees infested only with *T. tsugae*, there was a similar trend for reduced survival and fecundity and increased parasitism by *A. citrinus* with increasing scale density for 2 yr (Table 5). However, in mixed-species infestations percent survival and fecundity of *T. tsugae* did not show an obvious trend with either its density or that of both scales combined. Percent parasitism of *T. tsugae* did not increase with its own density in mixed infestations but did increase with total scale density as in the previous case of *F. externa*.

Analyses of the data gathered for 2 yr in the Darien forest indicate that *F. externa* has a significant deleterious effect on its own success and on that of *T. tsugae* (Table 6). Significant negative correlation coefficients were obtained for the relationships between *F. externa* density on six hemlocks and the survival and fecundity of *F. externa* and *T. tsugae* in both single- and mixed-species infestations. The density of *T. tsugae*, however, was not significantly correlated with its own success or that of its competitor. Neither survival nor fecundity of *F. externa* and *T. tsugae* was significantly related to total scale density under mixed-species conditions. Percent parasitism of *F. externa* and *T. tsugae* by *A. citrinus* was significantly correlated with their densities on the six hemlocks in single-species infestations, indicating a density-dependent response by the parasite for both hemlock scales. Percent parasitism in mixed-species infestations was significantly correlated only with total scale density suggesting that adult parasitoids respond positively to scale density without differentiating between species. Indeed the portion of the parasitoid population attacking each scale species in mixed infestations does reflect

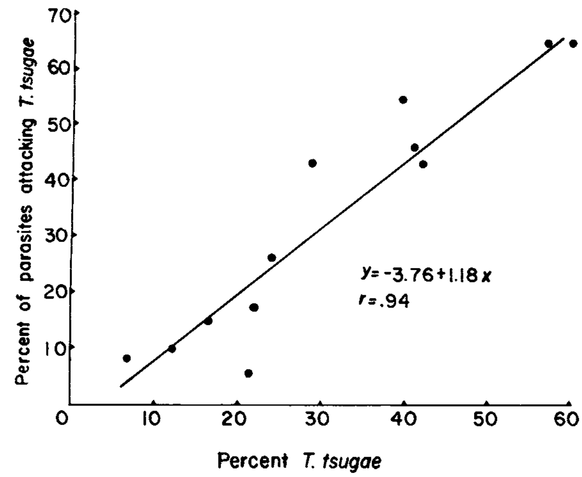

FIG. 2. Relationship between the percent in the total scale population of *Tsugaspidiotus tsugae* coinhabiting with *Fiorinia externa* on each of 12 hemlocks in the Darien, Connecticut forest (data for the 1977 and 1978 summer generations combined) and the percent of the total *Aspidiotiphagus citrinus* on each tree which parasitized *T. tsugae* ($P < .001$).

TABLE 5. Number of *Tsugaspidiotus tsugae* colonizing 100 young needles of six hemlocks infested only with *T. tsugae* and six infested with *T. tsugae* and *Fiorinia externa*, percent survival of colonists, fecundity of adult females, and percent parasitism by *Aspidiotiphagus citrinus* for two generations of *T. tsugae* in a Darien, Connecticut forest. Means are as in Table 4.

	1977 summer generation of *T. tsugae*				1978 summer generation of *T. tsugae*			
Infestation	Density*	Survival (%)	Eggs/♀	Parasitism (%)	Density*	Survival (%)	Eggs/♀	Parasitism (%)
T. tsugae	19.5	80.0	51.3	6.0	18.0	90.5	52.8	10.0
	51.5	63.0	41.6	17.5	35.5	75.0	44.9	14.5
	64.5	73.5	48.5	13.1	49.0	75.0	29.3	16.0
	98.5	76.0	37.7	14.5	57.5	82.0	36.5	14.5
	136.5	44.5	43.0	20.0	80.5	81.0	37.0	21.5
	138.0	48.5	37.4	23.0	126.5	65.5	26.6	24.0
Mixed species	20.5 (169.0)	45.0	24.2	16.0	10.0 (147.0)	50.0	22.0	22.5
	21.5 (99.5)	60.0	35.8	11.5	12.5 (74.5)	58.5	38.1	12.5
	42.0 (189.0)	44.0	24.4	17.0	16.0 (38.0)	81.5	42.3	14.5
	62.5 (219.5)	36.5	24.3	26.0	31.0 (75.5)	83.5	45.9	15.5
	69.5 (174.0)	55.0	26.3	18.0	70.0 (288.0)	45.5	26.3	22.5
	110.5 (191.5)	59.0	33.3	20.5	159.5 (252.5)	64.0	37.3	24.0

* Numbers in parentheses are total scales, both species combined.

TABLE 6. Correlation coefficients obtained from analysis of the relationship between *Fiorinia externa*, *Tsugaspidiotus tsugae*, and total scale density on six hemlocks in the Darien, Connecticut forest and percent survival, fecundity, and percent parasitism by *Aspidiotiphagus citrinus*.

Infestation	Species correlated with	Survival (%) 1977	Survival (%) 1978	Eggs/♀ 1977	Eggs/♀ 1978	Parasitism (%) 1977	Parasitism (%) 1978
Single species							
F. externa	self	−.94**	−.95**	−.89*	−.82*	.92**	.86*
T. tsugae	self	−.80	−.74	−.72	−.78	.86*	.95**
Mixed species							
F. externa	self	−.90*	−.92**	−.83*	−.96**	.31	.76
	T. tsugae	.27	.06	.04	−.11	.73	.66
	both	−.57	−.61	−.71	−.74	.89*	.90*
T. tsugae	self	.24	−.12	.18	.01	.60	−.01
	F. externa	−.97**	−.87*	−.92**	−.84*	.44	.72
	both	−.66	−.67	−.66	−.58	.91*	.87*

* $P < .05$.
** $P < .01$.

relative scale abundance, as indicated by a highly significant positive correlation (Fig. 2).

F. externa showed superior competitive ability over *T. tsugae* at 18 of 20 sites in southwestern Connecticut where populations were monitored for 3 yr (Table 7). At 14 of the 20 sites, *F. externa* excluded *T. tsugae* after 2 or 3 yr even over a wide range of initial relative scale densities. *T. tsugae* was eliminated from all 12 sites where densities in 1976 were <10 scales per 100 needles even though at five of these sites densities of its competitor, *F. externa*, were equally low. *T. tsugae* was also excluded from two of the six sites where densities during 1976 were between 28 and 32 scales per 100 needles; it is nearing extinction at the other four of these sites. In only the two sites where densities of *T. tsugae* were >80 scales per 100 needles and of *F. externa* were <9 scales per 100 needles has *T. tsugae* maintained its initial relative abundance.

TABLE 7. Density of *Fiorinia externa* and *Tsugaspidiotus tsugae* during 1976, and percent of the total scale population comprised by *T. tsugae* from 1976 to 1978, at 20 coinhabited sites in southwestern Connecticut. Densities are mean numbers (± 1 SD) of scales occurring on 100 youngest needles for four trees per site. Asterisks indicate sites where *T. tsugae* was eliminated.

Site	Density during 1976: *T. tsugae*	Density during 1976: *F. externa*	Percent *T. tsugae* 1976	1977	1978
1	1.3 ± 0.9	25.0 ± 4.8	4.9	0.3	*
2	1.5 ± 0.6	107.0 ± 12.1	1.4	1.2	*
3	2.0 ± 0.8	6.5 ± 2.6	23.5	16.0	*
4	2.3 ± 1.1	3.0 ± 2.1	43.4	2.1	*
5	2.3 ± 0.9	2.8 ± 1.0	45.1	5.3	*
6	2.5 ± 1.1	2.0 ± 0.9	55.6	33.3	*
7	3.0 ± 1.3	2.0 ± 1.1	60.6	13.6	*
8	3.0 ± 1.1	96.5 ± 7.6	3.0	3.1	*
9	3.8 ± 1.1	43.8 ± 6.1	8.0	*	*
10	4.0 ± 0.3	111.0 ± 9.9	3.5	3.2	*
11	6.3 ± 2.1	121.5 ± 9.3	4.9	1.9	*
12	9.0 ± 2.6	50.3 ± 5.3	15.2	4.6	*
13	28.5 ± 6.3	9.5 ± 3.1	75.0	37.8	16.1
14	28.8 ± 7.8	9.8 ± 4.1	74.6	1.4	*
15	28.8 ± 4.6	31.0 ± 3.5	48.2	37.8	6.0
16	29.0 ± 3.7	3.8 ± 1.1	88.4	34.2	13.0
17	29.3 ± 4.6	7.3 ± 2.1	80.1	2.6	*
18	31.5 ± 1.0	42.5 ± 7.3	42.6	22.9	0.9
19	80.5 ± 7.1	5.8 ± 2.3	93.3	98.0	97.0
20	81.0 ± 8.3	8.3 ± 1.3	90.7	97.1	92.7

DISCUSSION

Competition

Earlier studies revealed that *F. externa* and *T. tsugae* overlap extensively in their geographical distributions, in their feeding and breeding hosts (McClure and Fergione 1977), and in their phenology on hemlock (McClure 1978). Their spatial distributions on hemlock as shown in this study also overlap considerably as both scales colonized primarily the young needles of the lower crown. This similarity of resource utilization by the hemlock scales intensified competition among them when resources, probably food and space, essential for growth and development, became limiting at high scale densities. Indeed the greenhouse and forest studies demonstrated that summer generations of *F. externa* and *T. tsugae* do experience intraspecific and interspecific competition at densities commonly encountered in Connecticut forests. Data gathered from the greenhouse experiments conducted during 1978 and 1979 indicate that *F. externa* density has a deleterious effect on survival of *F. externa* and on that of *T. tsugae*, which supports the findings of earlier investigations (McClure 1979*a* and *b*, 1980). Comparison of the mortality data for single- and mixed-species infestations revealed that *F. externa* has a greater adverse effect on the survival of its competitor than *T. tsugae* has on itself, while *T. tsugae* has a less adverse effect on *F. externa* survival than *F. externa* has on itself (Tables 2 and 3). Therefore intraspecific competition was more important in regulating *F. externa* populations while interspecific competition had a greater regulatory impact on *T. tsugae* populations. Differences in magnitude of increases and reductions in percent mortality to each species in single- and mixed-species infestations suggest that competition has a more severe impact on *T. tsugae* survival than on *F. externa* survival.

The results of the field study in the Darien forest support those obtained from the greenhouse experiments, indicating that summer generations of *F. externa* and *T. tsugae* compete intraspecifically and interspecifically. High scale density had profound deleterious effects on the success of both hemlock scales for 2 yr. Linear regression analysis of the relationships between scale density and scale survival and fecundity in single- and mixed-species infestations confirms the greenhouse findings that *F. externa* has a greater adverse effect on *T. tsugae* success than on its own and is the superior competitor.

The superior competitive ability of *F. externa* likely results from the nutritional and spatial advantage conferred by its earlier colonization time. By colonizing the young hemlock foliage in early June some 2–4 wk prior to its competitor, *F. externa* is afforded a distinct competitive advantage as follows: (1) Survival, development rate, and fecundity of hemlock scales exhibit a significant positive correlation with concentrations of foliar nitrogen and water (McClure 1979*b*, 1980). Because concentrations of nitrogen and water decline during the season as the foliage matures, the earlier colonization time of *F. externa* provides nymphs with a nutritional advantage over *T. tsugae*. The significantly greater survival of *F. externa* which colonized greenhouse hemlocks during its natural colonization time compared to scales which settled 2 wk later (Table 3) attest to the nutritional advantage of early colonization. (2) Feeding by *F. externa* nymphs significantly reduces the amount of nitrogen in the young hemlock foliage available to *T. tsugae* nymphs which colonize 2–4 wk later (McClure 1979*b*; Table 2). Consequently, *T. tsugae* nymphs in mixed-species infestations will have even less food available for their survival, growth, and development. Indeed the significantly greater mortality suffered by *T. tsugae* nymphs on greenhouse hemlocks colonized by *F. externa* 2 wk earlier, relative to trees colonized with both scales simultaneously (Table 3), suggests that *F. externa* reduces the quality and/or availability of the food for its competitor. (3) Previous colonization by *F. externa* of young hemlock needles with high concentrations of nitrogen forces *T. tsugae* crawlers to colonize older foliage with low nitrogen concentrations where the crawlers subsequently suffer significantly greater mortality (Tables 2 and 3). *T. tsugae* crawlers did not shift their colonization sites to older foliage on greenhouse hemlocks when both scales colonized simultaneously (Table 3). This suggests that it is the previous establishment of *F. externa* nymphs

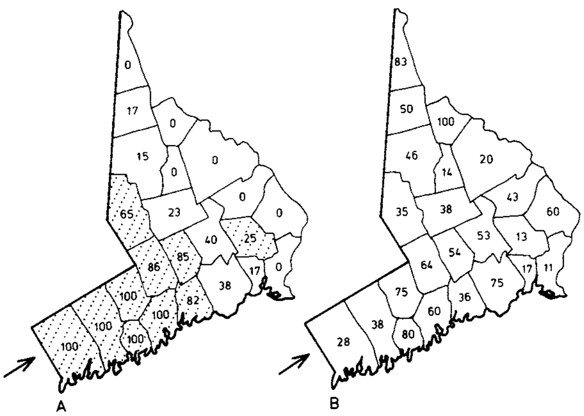

FIG. 3. Percent of the hemlock sites sampled in each of the 23 townships of Fairfield County, Connecticut, which were inhabited by *Fiorinia externa* (A) and by *Tsugaspidiotus tsugae* (B). Stippled townships are those in which *F. externa* was present at more of the sampled sites than was *T. tsugae*. A total of 232 sites was sampled (minimum of five sites per township). The arrows indicate the direction of prevailing winds, the likely path of scale invasion from New York City.

rather than the presence of crawlers that elicits the behavioral response in *T. tsugae* crawlers, giving *F. externa* a distinct spatial and nutritional advantage over its competitor. Clearly under natural conditions where hemlock scales coexist, the later colonization time of *T. tsugae* and the behavioral shift to older, low-nitrogen foliage will further reduce the scale's competitive ability.

Results of the Darien, Connecticut forest study show that the parasitoid, *A. citrinus* responds density dependently to summer generations of both hemlock scales in single-species infestations (Tables 4, 5, and 6). These data confirm the density-dependent nature of the parasite-hemlock scale interaction reported previously (McClure 1977*b*, 1978). However, in mixed-species infestations the parasitoid concentrated its attack on hemlocks supporting the highest total scale densities and did not discriminate between host species (Table 6; Fig. 2). *A. citrinus* did not key in on the most abundant species in mixed-species infestations but rather attacked each scale in the same frequency in which it occurs in the infestation. Because of its nondiscriminatory host-seeking behavior, *A. citrinus* will likely have little if any appreciable effect on the outcome of interspecific competition between hemlock scales during the summer generation. However, this parasitoid does adversely affect the autumn generation of *T. tsugae*, accelerating the population decline of this scale in forests in which it coexists with *F. externa* (McClure 1981).

Competitive exclusion

Because of the competitive superiority of *F. externa* over *T. tsugae* during summer and the inability of *A.*

citrinus to discriminate between host species, one might expect *F. externa* to outcompete and eventually exclude *T. tsugae* from mixed-species infestations. Two pieces of evidence suggest that competitive exclusion has occurred under natural conditions where these species occur sympatrically. The first derives from a comparison of the distributions of *F. externa* and *T. tsugae* in Fairfield County, Connecticut (see McClure and Fergione 1977 and Fig. 3). Following their introduction into the New York City area some 70 yr ago, both species subsequently expanded their distributions through dispersal as airborne crawlers primarily northeastward in the direction of the prevailing winds and probably invaded Connecticut at its extreme southwestern corner in Greenwich, Fairfield County (see Felt 1933, McClure 1977*c*). The further extension of *T. tsugae* into the county (Fig. 3) suggests that it invaded Connecticut prior to *F. externa.*

F. externa has a typical fanlike distribution in Fairfield County with the highest incidence in the townships first invaded and less and less incidence in areas farther from this infestation center (Fig. 3A). Although we would expect a similar fanlike distribution for *T. tsugae,* such is not the case. Instead there is relatively low incidence of *T. tsugae* in areas where *F. externa* is widespread, high incidence in a transition zone at the edge of the *F. externa* infestation center, and medium to high incidence of *T. tsugae* where *F. externa* incidence is low (Fig. 3B). This peculiar distribution of *T. tsugae* in Fairfield County could be the result of ongoing competitive exclusion of *T. tsugae* from areas where *F. externa* has subsequently invaded and established extensive infestations.

Additional evidence of the ability of *F. externa* to exclude *T. tsugae* competitively derives from the trends in relative abundance of hemlock scales from 1976 to 1978 at 20 coinhabited sites in southwestern Connecticut (Table 7). At 14 of the 20 sites *F. externa* excluded *T. tsugae* after 2 or 3 yr even over a wide range of initial relative densities, and at four of the remaining sites *F. externa* demonstrated a distinct competitive advantage after 3 yr.

Results of the greenhouse experiments and forest studies reported here indicate that summer generations of *F. externa* and *T. tsugae* on eastern hemlock experience intraspecific and interspecific competition at densities typical of those occurring in forests throughout southwestern Connecticut. Competition results in reduced scale survival and fecundity which is likely due to reduced concentrations of foliar nitrogen and water and spatial limitations at high densities.

Due to its early seasonal colonization time, *F. externa* has a distinct spatial and nutritional advantage over *T. tsugae* by colonizing nitrogen-rich young needles at a time during the season when concentrations of foliar nitrogen and water are high. Because *F. externa* has a more adverse effect on *T. tsugae* success than on its own and because their parasitoid, *A. citrinus,* is not likely to alter the outcome of interspecific competition due to its nondiscriminatory host-seeking behavior, *F. externa* was able to outcompete and exclude its competitor over a wide range of initial relative densities.

The direct consequences of competition and factors influencing the outcome of competition can be appraised best in relatively young and simple communities, such as the exotic scales on hemlock, where resources are abundant and factors regulating population growth are few compared to indigenous communities. Indeed such communities of introduced species offer great potential for insight into competition and coexistence among similar organisms.

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