BIOLOGY AND POPULATION DYNAMICS OF TEA SCALE,
Fiorinia theae GREEN
(DIASPIDIDAE:COCCOIDEA:HOMOPTERA)

By

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DEDICATION

This dissertation is dedicated to my father, Choudhry Murad Ali, whose support, love, and goodwill enabled me to complete this work.

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Abstract of Dissertation Presented to the Graduate
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Tea scale, Fiorinia theae Green, is the most important pest of camellias and hollies in the eastern United States. Because chemical control is costly and otherwise less than satisfactory, an attempt was made to import natural enemies for biological control of this pest. Two aphelinids, Aphytis theae (Cameron) and Aspidiotiphagus sp., were imported from India and cultured in greenhouses at Gainesville. Both species attack male nymphs of tea scale. Field releases of A. theae and Aspidiotiphagus sp. were made in May 1976 and January 1977, respectively. A. theae was colonized but failed to survive the second winter; Aspidiotiphagus sp. seems to have become established.

A mite and a thrips feed on settlers, while male nymphs are preyed on by 3 species of predators. A local parasite that attacks female nymphs is very rare and consequently ineffective in population regulation of tea scale.

Biology of tea scale was studied. Development in males and females is asynchronous, the species being protandrous. Dimorphism is exhibited in the immature as well as mature stages. Females deposited an average of 28.82 eggs which were retained under the armor where they hatched in 9-10 days. Male nymphs molt 4 times; females 2 times. Male adults emerged in 34 days; females began ovipositing in 65 days.

Data generated by field and laboratory studies are utilized to construct 12 monthly and 1 annual life tables. Generation mortality ranged from 92.65% in April to 96.92% in February, with an annual average of 95.15%. Index of population trend varied from 0.71 to 1.39, with an average of 0.98. Major mortality factors were dispersion loss at crawler stage and parasitization of male nymphs by A. theae. Mortality in male nymphs did not affect the overall population level because of male biased sex-ratio and polygyny. Survivorship curves and fertility tables for tea scale were also prepared. Net replacement rate (R_0) ranged from 1.80 in February to 4.45 in May, with an annual average of 2.86. Specific sex-ratio in the tea scale varied at all stages; there were more males at nymphal stages but females were more abundant as adults. Crude sex-ratio indicated a constant preponderance of males. Major cause of variation in sex-ratio was mortality of the male nymphs by A. theae. Age composition figures for tea scale were prepared for each month and for mean annual populations. A schematic representation of life cycle depicting the salient features of biology and population dynamics of tea scale was developed. Methods to calculate the survival rates of males and females are described.

INTRODUCTION

The tea scale, Fiorinia theae Green, is a member of Diaspididae, a family that contains many damaging and unmanageable pests of perennial crops and ornamentals. Tea scale is regarded as one of the principal armored scale insect pests of the world (Beardsley & Gonzalez, 1975). In North Florida and a large part of the Southeastern United States, including Alabama, Georgia, and South Carolina, it is placed among the 10 most important pests of nurseries and home landscape plantings (Dekle, 1965).

Tea scale is a polyphagous insect and at least 43 different ornamentals and fruit trees are known to serve as its hosts. The most seriously affected plants are camellias and hollies which are highly desirable broad-leaf evergreen ornamentals.

Being stenomerous, it feeds only on leaves of the host plants. The feeding on lower surfaces of leaves invariably results in discoloration on the upper side, followed by defoliation. Infested camellias assume an unthrifty appearance and flower poorly. In cases of severe infestations, dieback of twig terminals occurs and ultimately results in the death of the plants.

Tea scale is known to have originated in the Oriental region, where it is associated with tea and related plants. Nowhere in the region from India to Japan has the tea scale been found to be a serious pest. This suggests that natural control factors provide effective control of tea scale in that area. Although a number of natural enemies have been found

in association with tea scale in Florida, they are not effective in keeping the populations at non-economic levels.

Efforts to control tea scale infestations have, so far, been confined to chemical control; a number of insecticides have been tested, utilized, and recommended by various workers. However, chemical control is not a suitable long-term strategy for suppression of pests such as tea scale. The fact that tea scale is a pest of ornamentals, normally grown around homes, offices, and other public buildings, makes use of chemical insecticides undesirable, for more people, especially children, are likely to come into physical contact with the toxic compounds. Moreover, the nature of tea scale infestations is such that chemical control does not offer much promise of success. For instance, camellia and holly plants are usually quite large and densely foliated, with tea scale colonies located on the underside of leaves. These characteristics render many insecticides ineffective because of poor spray coverage. Also, new foliage in some varieties of host plants is sensitive to certain chemicals. In addition, chemical treatments are costly, especially for homeowners, and must be repeated at regular intervals.

Despite the fact that tea scale is a pest of foreign origin, belonging to a group that provides numerous examples of successful control by introduced natural enemies, and is an unsuitable candidate for chemical control, no effort was made to introduce exotic natural enemies. Various species of Aphytis have proved to be key agents in regulating the densities of numerous diaspid pests of citrus and other crops in various parts of the world (Rosen, 1973). In Florida similar scale pest problems on citrus have been eliminated through the action of introduced parasites of the genus Aphytis, the two most notable examples being the control of Florida

red scale by A. holoxanthus DeBach, and of purple scale by A. lepidosaphes Compere. These were the circumstances that prompted initiation in 1976 of an effort to introduce parasites of tea scale from India. As a result of a joint IFAS-ARS-CIBC effort, A. theae and a still unidentified species of Aspidiotiphagus were obtained and released in Gainesville. Both species proved specific to male nymphs of tea scale. Although the limitations of male specific parasites were recognized, it was hoped that male mortality would be sufficient to prevent fertilization of females and thus bring about reductions in tea scale populations. Had such proved the case, it would have been the first example of control through the agency of male specific mortality caused by parasites.

The initiation of a biological control program and subsequent evaluation of its results require detailed information on the biology, seasonal history, and population dynamics of the candidate pest species. In Florida such information for the tea scale was at best fragmentary, and no attempt has ever been made anywhere in the world to study bionomics of the species in the detail needed for purposes of biological control.

Post-colonization studies designed to assess the efficacy of introduced natural enemies are very useful in understanding the success or failure of biological control programs. Such studies provide information on the role of various mortality factors in regulating the population of pest species, and, if the previously introduced species are proven ineffective, demonstrate the need for introduction of different species of natural enemies. Although there are many examples of successful biological control programs, a larger number have met with failure. Seldom has it been possible to adequately document reasons for either success or failure, and in the words of Krebs (1972), "biological control will remain an art until we can do so" (p. 374).

Biology of tea scale was studied in the laboratory, and observations on the seasonal changes and population dynamics were carried out at Wilmot Garden, Gainesville, Florida. The data obtained through these studies were utilized in the construction of life tables, survivorship curves, fertility tables, and age composition. These are very convenient and useful methods to describe the dynamics of populations.

Ecological life tables are one of the most useful methods of description and analysis of population dynamics of an insect. These tables contain a series of sequential measurements that indicate changes in the population in its natural environment. These measurements, when related to the mortality factors and presented in the form of life tables, reveal the presence of successive processes that operate in the populations. Life tables were initially developed for the quantitative analysis of human populations. Their importance lies in the fact that each stage in the life history of a species is affected by different mortality factors and at different rates.

Life tables for humans and insects fundamentally differ only in objectives. In human life tables the objective is to determine the average expected life remaining for an individual and therefore the most important feature is the e_x column. In the case of insects, the major interest lies in the mortality factors and their rates, and therefore the most important features are the d_x and d_x^F columns. Life tables for non-human populations are termed ecological life tables because of the emphasis on mortality factors and the actual numbers used. The ecological life table is really an organized summary of the life of a typical cohort of individuals in a population. It describes in precise detail the stages in the life history and reveals which contribute most to the population, and at the same time

reveals the mortality factors-- biotic or abiotic-- responsible for regulation of the population. Trends in populations can be better understood once the causes of mortality during each age interval are quantified.

An ecological life table usually consists of 6 columns. The first column is labeled x and lists the pivotal age for the age class or age interval under consideration. For insects it consists of various stages, i. e., egg, nymph or larva, pupa, and adult. The next column labeled l_x contains the number of individuals of the original cohort which were alive at the beginning of age class x . Mortality factors are listed in the third column which is labeled $d_x F$. The fourth column, which represents the number of individuals dying during the age interval, is labeled d_x . The fifth column, headed $100q_x$, is the proportion of individuals dying by cause listed in $d_x F$ expressed as the percentage of l_x . The last column is labeled $100d_x/N_1$ and gives the percentage of the generation mortality; in some life tables, this column is labeled s_x and records the survival at age interval x .

Three types of data are used in the construction of life tables:

- 1) Survival of a reasonably large cohort born more or less simultaneously is followed at fairly close intervals throughout its existence. Since this does not involve the assumption that the population is stable in time, this is considered the best form of information.
- 2) Age at death is directly observed for a large and reasonably random sample of individuals in the population. This requires the assumption that the population is stable in time and that the birth and death rates remain constant.

3) Age structure is obtained directly from a random sample of population and the number of dead individuals is inferred from the reduction in the number of living individuals between successive age intervals. It requires the assumption that the population has a stable age distribution.

Data for the construction of tea scale life tables were obtained by the combination of the above techniques in order to avoid unnecessary assumptions. Death in different age intervals can be accurately determined because dead individuals remain attached to leaves and can be easily counted. Because of stable age distribution, all stages are present simultaneously, thus age structure can be observed directly. The only assumption made was that the ovipositing females represent the terminal individuals of a cohort that contained all dead individuals of each age interval found on the sampled leaves. In view of the fact that life cycle of the tea scale lasts for about 2 months, and that only new colonies were sampled, this assumption does not seem unreasonable.

In general, there are 2 types of life tables, the age-specific and the time-specific. These 2 kinds are different in meaning and form except under unusual circumstances. The age-specific life tables are also called cohort, generation, or horizontal life tables, and are constructed on the basis of data obtained by following a cohort or designated members of a population with discrete generations. The time-specific life tables are also called stationary, static, current, or vertical life tables. Data for these are collected on the basis of a cross-section of a multivoltine population with overlapping generations.

Among diaspid, life tables are available only for the oystershell scale, Lepidosaphes ulmi (L.) in Quebec, Canada, where this species is univoltine and undergoes diapause in the egg stage. Tea scale, on the other hand, is a multivoltine species and does not undergo diapause at any stage.

Life tables are very useful in understanding the dynamics of animal and plant populations. Their concise and organized form presents much information that is otherwise difficult to handle and comprehend. They also help in determining the survival strategies of species, and evolution of characteristics, such as fecundity and parental care. Data for life tables are utilized by population theorists to test the validity of their conceptual models. Life tables of pest species reveal the most vulnerable stage in the life history and leads to emphasis on control at that stage in order to influence survival rates of pests through management strategies.

In order to understand the effect that any one environmental factor has on the trend of a population, a series of age-specific life tables is required covering a number of generations. The analysis of a series of this sort enables one to assess the effect of each component of the environment. A number of different techniques have been used to analyze life table data. One method in particular is now widely used, namely, the "K" factor analysis of Varley and Gradwell (1960). The other popular methods involving regression analysis were developed by Morris (1963) and Watt (1963).

Adequate sampling techniques to study changes in population density and interaction of various factors were not available for tea scale, which is a multivoltine, bisexual, and dimorphic species. Sampling techniques are further complicated by the fact that distribution of tea scale on host plants is not uniform. Both interplant and intraplant variations are large. Many potential host plants are not infested, while on infested plants 1 or 2 twigs may be infested, the rest of the plant being free of the scale. Inensive survey and sampling of small, arbitrarily

delineated populations on individual plants over time, is therefore necessary.

The parasites Aphytis theae (Cameron) and Aspidiotiphagus sp., originally imported from India and later released in Gainesville, exhibited a marked preference for male nymphs of tea scale. This necessitated ascertaining the importance of males in the reproductive biology of tea scale. Consequently, an experiment was designed to determine if females were capable of reproducing without fertilization. Results of this experiment also provided information on relative survival of tea scale at different temperatures and preference of crawlers to settle on lower sides of leaves. All information on biology and population dynamics of tea scale obtained through these studies was summarized in a schematic representation. The data and information on the biology and ecology of tea scale obtained in these studies will prove very valuable as a foundation for future attempts to control this pest through importation of additional enemy species and for comparing results of such attempts.

LITERATURE REVIEWS

Fiorinia theae, Green

General Review

The published history of Fiorinia theae Green contains 3 major landmarks: its discovery as a pest of tea in India by Watt in 1898, a formal description as a new species by Green in 1900, and comprehensive studies on its biology in India by Das and Das in 1962. The remainder of the articles on tea scale contains either original records or reviews on local and geographical distribution, host plants, descriptions of female and male armors, and chemical control measures. Borchsenius (1966), Fernald (1903), Lobdel (1937), Merrill and Chaffin (1923), and Riddick (1955) included F. theae in their lists of coccids; while Kuwana (1925) and MacGillivray (1921) presented keys to separate species of Fiorinia, including theae.

Description

Green's (1900) original description of F. theae was based on specimens from Kangra Valley, India. He stated, "when this insect was first submitted to me I supposed it to be merely a local form of the world-wide F. fioriniae. A more critical examination shows me that it is quite distinct. It differs from fioriniae in the absence of lateral lobes on the pygidium; in the form of the antenna which has no stout spine, and in the presence between the antennae of a proboscis-like projection. The scale also is larger, stouter and more opaque. I now describe the species under the name F. theae" (p. 3).

He described the female armor as "consisting of the indurated pellicle of the second stage which completely encloses the adult insect and is without any secretory margin. Elongate; narrow; with a moderately distinct median longitudinal carina. Colour bright castaneous to dark ferruginous brown, median longitudinal area darkest; opaque; not revealing the form of the insect beneath. First pellicle colourless or very pale yellow; projecting from anterior extremity of scale. Length 1.25 to 1.50 mm. Breadth 0.50 mm" (p. 3-4).

In his description of the adult females, he wrote:

Antennae close together, on anterior margin; each antenna consisting of an irregular tubercle with a single curved bristle on one side. From between the antennae springs a stout spatulate process . . . which is not chitinous but of the same consistency as the surrounding parts of the body. Margin of thorax and abdomen with a series of minute spinneret ducts opening on to small conical tubercles. Pygidium . . . with a conspicuous median cleft, on the margins of which are situated the moderately large serrate thickenings of the margin; second lateral lobes obsolete. Spines normal, the dorsal series rather long; one pair springing from within the median cleft. Circumgenital glands in five groups; the median and upper lateral groups together forming an almost continuous arch. Median group with 4 or 5 orifices; upper laterals 10 to 13; lower laterals 15 to 18. A very few circular pores with accompanying ducts, on dorsal surface, near the margin. Length 0.50 to 0.75mm. (p. 3-4).

Neither the male scale nor the male armor were represented in the material examined by Green.

Sasscer (1912) published the first descriptive account of the male armor. Later, many workers provided descriptions of females and males

and their armor, and keys to separate F. theae from other species of Fiorinia. Das and Das (1962) were the first workers to describe the immature stages of tea scale in detail.

Tippins (1970) described the second instar males of F. theae, F. externa, and F. pinicola, and presented a key to separate these species on the basis of morphological differences in the second instar males.

Distribution

Tea scale is widely distributed in the warmer parts of the world except Africa and Australia. According to Das and Das (1962), it is present in all of the tea growing districts of India. Tapia (1968) was the first to record the tea scale damaging camellias in Argentina. In the United States, Sasscer (1912) stated that tea scale was present in Alabama, the District of Columbia, Georgia, Louisiana, North Carolina, and South Carolina, and Lawson (1917) reported it from Kansas. Tea scale has also been recorded from Japan (Ferris, 1942), China, Taiwan, Mexico, and Costa Rica (Merrill, 1953), and Sri Lanka (Ceylon) and the Philippines (Sasscer, 1912).

F. theae is considered to have originated in the Orient. On the basis of the number of described species, Takagi (1970) concluded that the origin of the genus was evidently centered in eastern Asia, with most of the species occurring in India through China to Japan. He stated that none of the genuine members of the genus was native to the New World and the Ethiopian region. Commenting on the introduction of the tea scale in the United States, Sasscer (1912) remarked that "since no (tea) plants have been introduced from Asiatic regions, all being grown from seed, it is extremely probable that its (tea scale) introduction was through the agency of the camellias, which have been for a number of years greatly in demand as ornamental plants in this country" (p. 10).

Sasscer (1914) reported interception of F. theae at quarantine in the District of Columbia in a shipment of mango plants from Java.

Host Plants

Tea scale is a polyphagous species and has, so far, been found to feed on some 43 species of plants in 25 genera belonging to 16 families (Table 1).

Economic Importance

Watt and Mann (1903) regarded the tea scale as a destructive pest of tea in India, but Das and Das (1962) disagreed and maintained that it was destructive only in rare instances. With the exception of Argentina, where Camellia japonica was reported as seriously damaged (Tapia, 1968), there are no published records describing tea scale as a serious pest in parts of the world other than the United States. Sasscer (1912) reported that in the northwestern Himalayas, tea scale infestations on the olive, Olea grandulifera, frequently caused leaves to turn yellow and drop off.

In the United States, specialists on insects of ornamentals are unanimous in their opinion that scale insects are the most important group of pests infesting camellias. Tea scale holds a prominent position within the group and is, in all likelihood, the most important pest of camellias (Kouskolekas, 1971). Sasscer (1912) reported that tea scale was a serious pest of camellias and warranted frequent application of control measures. English and Turnipseed (1940) considered the tea scale as the most important pest of camellias and stated that infestation by tea scale impaired the vitality of the plant and production of bloom, thereby greatly reducing the sale value of the plants. Merrill (1953) remarked that the tea scale was a serious pest in Florida

TABLE 1
Host Plants of Tea Scale, Fiorinia theae

Family	Species	Common Name	Source
Anacardiaceae	<u>Mangifera indica</u> L.	mango	Merrill, 1953
Aquifoliaceae	<u>Ilex aquifolium</u> L.	English holly	Dekle, 1965
	<u>I. cassine</u> L.	dahoon holly	Dekle, 1965
	<u>I. cornuta</u> Lindl. & Paxton	Chinese holly	Merrill, 1953
	<u>I. cornuta</u> Burfordii	Burford holly	Dekle, 1965
	<u>I. latifolia</u> Thunb.	lusterleaf holly	Kuitert & Dekle, 1972
	<u>I. opaca</u> Ait.	American holly	Kuitert & Dekle, 1972
	<u>I. rotunda</u> Thunb.	--	Kuitert & Dekle, 1972
Buxaceae	<u>I. vomitoria</u> Ait	yaupon	Merrill, 1953
	<u>Buxus</u> sp.	--	Murakami, 1970
Celastraceae	<u>Euonymus</u> sp.	burning bush, strawberry bush	Merrill, 1953
Compositae	<u>Senecio confusus</u> Britt.	Mexican flame vine	Dekle, 1965
Cornaceae	<u>Aucuba japonica</u> Thunb. & Gold dust	Japanese aucuba	Dekle, 1965
	<u>Cornus</u> sp.	dogwood	Merrill, 1953
Dioscoriaceae	<u>Dioscorea</u> sp.	--	Beshear, Tippins & Howell, 1973
Euphorbiaceae	<u>Ostodes zeylandica</u> Muell.	--	Sasscer, 1912
Malpighiaceae	<u>Malpighia</u> sp.	malpighia	Dekle, 1965
Myrtaceae	<u>Callistemon</u> sp.	bottlebrush	Merrill, 1953
	<u>Malaleuca quinquenervia</u> (Cav.)	cajeput, punk tree	Dekle, 1965

TABLE 1-continued

Family	Species	Common Name	Source
Oleaceae	<u>Olea grandulifera</u> Wall.	olive	Watt, 1898
	<u>Osmanthus fragrans</u> Lour.	sweet olive, tea olive	Dekle, 1965
Palmae	<u>Caryota</u> sp.*	caryota palm	Sasscer, 1912
Rubiaceae	<u>Cardenia</u> sp.	cape jasmine	Dekle, 1965
	<u>Thysanosperrum diffusum</u> Champ.	--	Takagi, 1970
Rutaceae	<u>Citrus</u> sp.	citrus	Watt, 1898
	<u>C. limon</u> Burm.	lemon	Kuiter & Dekle, 1972
	<u>C. paradisi</u> Macf.	grapefruit	Dekle, 1965
	<u>C. reticulata</u> Blanco	satsuma	Merrill, 1953
	<u>C. sinensis</u> Osbeck	orange	Merrill, 1953
	<u>Fortunella</u> sp.	kumquat	Kuiter & Dekle, 1972
	<u>Poncirus trifoliata</u> Raf.	trifoliate orange	Merrill, 1953
Symplocaceae	<u>Symplocos tinctoria</u> (L.)	common sweetleaf	Dekle, 1965
Theaceae	<u>Camellia caudata</u> Griff.	--	Das & Das, 1962
	<u>C. irrawadiensis</u> Barua.	--	Das & Das, 1962
	<u>C. japonica</u> Wall.	camellia	Das & Das, 1962
	<u>C. kissi</u> Wall.	--	Sasscer, 1912
	<u>C. sasanqua</u> Thunb.	sasanqua	Merrill, 1953
	<u>C. (Thea) sinensis</u> (L.)	tea plant	Watt, 1898
	<u>Cleyera ochracea</u> DC.	--	Murakami, 1970
	<u>Eurya</u> sp.	--	Das & Das, 1962
	<u>E. japonica</u> Thunb.	--	Takagi, 1970
	<u>Gordonia</u> sp.	loblolly bay	Dekle, 1965
	<u>G. excelisa</u> Bl.	--	Das & Das, 1962

*Caryola vide Sasscer, 1912. Probably Caryota, as there is no genus Caryola in botanical literature.

and required frequent application of chemical insecticides. Kuitert and Dekle (1972) considered it to be the most destructive pest of camellias and hollies in Florida. Because of the importance of camellias and hollies in landscape plantings in Alabama, Florida, Georgia, and South Carolina, the tea scale is clearly one of the 10 most important pests of nurseries and ornamental shrubs in the southeastern United States.

Collins (unpublished) claimed that the natural enemies kept tea scale under control in other parts of the world, and it was because of the absence of natural enemies that the tea scale was an economic pest in Florida.

My studies on tea scale, in which infested potted camellias were held in a greenhouse from which all natural enemies were excluded, confirm Collins' view. Within weeks both sides of the leaves on these plants were densely covered with colonies of tea scale. Subsequent death of the plants was attributed to the curtailment of photosynthetic activity of the leaves and ultimate loss of all foliage. Under field conditions, leaf drop results from the scale infestations, which greatly depreciates the ornamental value of the plants, but seldom causes death.

Biology

English and Turnipseed (1940) published a partial life history of F. theae on camellia in Alabama. They stated that each female deposited 10-16 eggs which hatched within 7-21 days. Crawlers settled within 2-3 days and secreted thin white coverings. Later, they secreted great quantities of white woolly filaments which covered the undersides of leaves. Nymphs molted within 13-36 days after hatching. Second molt occurred a week later. The females started laying eggs within 41-65 days, and life cycle was completed in 60-70 days.

Das and Das (1962) carried out comprehensive studies on the biology of tea scale on potted tea plants in India. They found that pre-oviposition periods lasted 12-14 days. Females laid 22-43 eggs with an average of 32.1 eggs per female. Males molted 4 times and completed development in 22-24 days, while females molted 2 times and completed the life cycle in 24-27 days. They also described the eggs, crawlers, nymphs, and adults of both sexes in some detail.

Laboratory Rearing

Accounts of rearing tea scale in the laboratory on artificial hosts are scanty. Nagarkatti (personal communication, 1977), Collins (unpublished), and Chiu and Kouskolekas (1978) experienced considerable difficulties in establishing laboratory colonies.

Nagarkatti (personal communication, 1977) commented that tea scale colonies could be established on pumpkin if relative humidity was maintained at about 70%. Chiu and Kouskolekas (1978) tested a number of artificial hosts and found that butternut squash was the most suitable laboratory host for tea scale.

Natural Enemies

Watt (1898) reported on a fungus parasitizing a tea scale female which was sent to him by Green, probably from Ceylon. He also commented that the fungus was not present in India and that "it certainly would be worthwhile to obtain a supply if the blight (tea scale) becomes serious" (p. 325).

In the United States, Sasser (1912) reported that the Darjeeling tea, which was grown in moist lowlands in South Carolina, was frequently found covered with a brown fungus which was apparently parasitic on tea scale and was quite effective in holding the pest in check. He also listed Chilocorus bivulnerus Muls., Microwisea misella Lec. (Coccinellidae), and Cybocephalus nigrutilus Lec. (Cybocephalidae) as predators of the tea scale.

Das and Das (1962) stated that in India an aphelinid, Aphytis sp., parasitized the second instar nymphs. They noticed that about 38% of the males and 4% of the females in the field were killed by this parasite. They also reported Scymnus sp. and Jauravia quadrinotata Kapur (Coccinellidae) as predators of the immature stages of tea scale and a fungus that occasionally attacked second instar female nymphs and mature females.

Nagarkatti (personal communication) informed that Aphytis sp. and Aspidiotiphagus sp. parasitized male nymphs, while a species of Prospaltella attacked the female nymphs of tea scale in India.

In Florida, Collins and Whitcomb (unpublished) conducted a survey of natural enemies and observed Aspidiotiphagus sp. nr. lounsburyi (Berlese & Paoli) and Aphytis sp. nr. lignanensis (Compere) (Aphelinidae), Aleurodothrips fasciapennis (Franklin) (Phlaeothripidae), Chrysopa bicarnea (Banks), C. claveri (Navas), C. harrisii (Fitch), and

C. rufilabris (Burm.) (Chrysopidae), Cybocephalus nigrutilus (Cybocephalidae), Chilocorus stigma (Say), Lindorus lophanthae (Blaisdell), and Microwisea coccidivora (Ashmead) (Coccinellidae), and a parasitic fungus, Aschersonia aleyrodalis (Webber) (Zythiaceae) associated with tea scale.

Chemical Control

Of the literature concerning tea scale, by far the largest part concerns chemical control. English and Turnipseed (1940), and Kuitert (1949) in Alabama; Tippins (1969) and Kouskolekas (1971) in Georgia; Kuitert and Dekle (1972) and Vaughan, Short and McConnell (1976) in Florida; and Das and Das (1962) in India offered suggestions and recommendations for suppressing the tea scale infestations by means of insecticides. Kouskolekas (1973) and Kouskolekas and Self (1973) conducted experiments designed to improve methods of application of insecticides, while Tippins and Dupree (1973) evaluated the effectiveness of different types of sprayers.

Aphytis theae (Cameron)

Description

Cameron (1891) described an aphelinid which was "bred from the tea scale insect Aspidiotus theae from Janygo (India)" (p. 3). His description was based on a single specimen mounted in balsam that was so flattened that its exact shape could not be seen satisfactorily. Although he placed the specimen in the genus Aphelinus, but because of certain peculiarities, he was confident that on further examination of fresh specimens the peculiarities would prove to be of generic value and that the species would form the type of a new genus.

Redescription

On the basis of the original description, Compere (1955) transferred Aphelinus theae to the genus Aphytis. He stated that Aphytis and Aphelinus were not closely related to each other. He further elaborated that members of the two genera differed from each other in basic structural characters of the abdomen and ovipositor. According to him, Aphytis and Aphelinus differed also in the manner of oviposition which was correlated with fundamental differences in the structural features of the abdomen and ovipositor. He observed that when Aphelinus oviposited, the entire ovipositor everted and the whole apparatus swung outward. On the other hand, when Aphytis oviposited, only the shaft swung downward, but the other components of the ovipositor did not evert.

Rosen and DeBach (1977) redescribed Aphytis theae from a female neotype and a male allotype, because the original type was lost, and the description and figures presented by Cameron were very confusing. They established the group Funicularis for the species of Aphytis with 5-segmented antenna and reduced mouth parts. The group includes Aphytis funicularis, A. gordonii, A. ulianovi, and A. theae. A key for the identification of the 4 members of the new group was also presented.

Life Tables

Life tables were originally devised by demographers to study human populations. They were used extensively in the field of life insurance to determine the average expected life of clients. Pearl and Parker (1921) introduced the life tables to ecologists by studying the population fluctuations of Drosophila in the laboratory cultures. Leopold (1933) was the first ecologist to recognize the value of the life tables in the study of natural populations, and although he used the term "life

equation," he was indeed talking about life tables. Pearl and Miner (1935) attempted to formulate a general theory of mortality of lower organisms on the basis of life tables. However, they gave up the attempt after realizing that the environmental detriments of life duration could not, at least then, be disentangled from such biological detriments as genetic constitution and rate of living. They pleaded for more observational data, carefully and critically collected for different species that will follow throughout the life of each individual in a cohort. Deevey (1947) also recognized the difficulty of comparing life tables of different species because the basic data of life tables were sometimes of the "age-specific" type and sometimes of the "time-specific" type; the point of origin of life tables was also different—birth for mammals, egg laying for insects, etc. He was the first worker to apply the life tables technique to growing populations in nature. His paper includes many examples of the life table format.

The first life table for an insect species was prepared by Morris and Miller (1954) for the spruce budworm, Choristoneura fumiferana in Canada. They were more interested in the causes of mortality at particular age intervals, and therefore used the stages of life cycle, i.e., eggs, larvae, pupae, etc., instead of dividing the age interval into equal lengths of time. They also added the d_xF column to the life table which listed all quantifiable mortality factors at each age interval.

There are only 3 reviews in the literature that deal with the development of insect life tables; the monograph by Morris (1963), the textbook on ecological methods by Southwood (1966), and the review article by Harcourt (1969).

As for the diaspidids, life tables are available for only one species. Samarasinghe and LeRoux (1966) prepared the life tables of Lepidosaphes ulmi (L.) which is a univoltine species and undergoes diapause in the egg stage during winter in Quebec, Canada. Atkinson (1977) proposed a method of making life tables for Aonidiella aurantii (Mask.) in Swaziland where the generations of the scale were more or less discrete in spring but became increasingly overlapped as the season advanced.

METHODS

Biology

The biology of tea scale was studied in the laboratory at $25 \pm 1.5^{\circ}\text{C}$ and $69 \pm 6.5\%$ relative humidity. Colonies of the scale insect were established on butternut squash using the method described by Chiu and Kouskolekas (1978). Infested leaves of Camellia japonica were collected at Wilmot Garden, Gainesville, Florida. In the laboratory these leaves were lightly brushed to remove natural enemies, contaminants and male tea scales, and then placed on cleaned butternut squash. After 4 days the leaves were removed from the squash. During this interval enough eggs hatched to allow completion of life cycle observations.

Details of development were obtained by daily removal of 20 individuals for microscopic examination. However, when nymphs became distinguishable as males and females, 10 individuals of each sex were examined daily. Since the tea scale is a protandrous species, males emerge long before females become receptive to mating. To ensure fertilization of females some infested leaves containing abundant males near emergence were placed around the squash to provide mates as the females became sexually mature.

Fecundity of the females was estimated by counting the number of egg shells, unhatched eggs, and eggs still present in the ovaries of 40 field collected females.

The incubation period was studied by removing the last egg from under the armor of actively ovipositing females. The removed eggs were kept in

covered plastic dishes for hatching. The incubation period of eggs allowed to remain under the armor was also studied. Gravid females were removed from leaves and placed in plastic dishes. Once removed, the females could lay only 2 more eggs before dying. Laying and hatching dates were recorded to determine the incubation period under more or less natural conditions.

Parthenogenesis

To study the possibility of parthenogenetic reproduction by the tea scale females, 5 potted Camellia japonica plants of uniform size and vigor were implanted with field collected gravid females. The females were placed on pieces of cheesecloth and secured on the upper surfaces of leaves with hairpins. Each plant was supplied with 100 females at 20 females per leaf. Plants were kept in different environators individually set at temperatures of 15, 20, 25, and 35°C. The relative humidity was about 70%, with a light period of 15 hours and dark period of 9 hours in each environator. The cheesecloth was removed after 10 days. Males were counted and removed as soon as they could be recognized. Females were also counted but left on the leaves undisturbed to determine if they could reproduce without fertilization. The number of immatures settled on upper and lower surfaces of the leaves was also recorded to evaluate the site preference. The experiment was repeated a second time, but only 4 plants were used at temperatures of 15, 20, 25, and 30°C.

Population Dynamics

Studies on population dynamics were conducted on the natural field populations of tea sclae on Camellia japonica at Wilmot Garden, Gainesville, Florida. The garden covers approximately 5 acres of a 10-acre green belt; the remaining 5 acres are natural woodland. In addition to numerous

varieties of camellias, azaleas, and hollies, the garden contains many other groups represented by one or more genera.

Populations of A. theae and male F. theae adults were studied in the field. Five Camellia japonica plants growing in a row at Wilmot Garden were selected for regular observations. Each week, 20 infested leaves on each of the 5 plants were randomly selected and thoroughly examined with the aid of a 10x lens. The number of A. theae and male F. theae adults present on the leaves was recorded.

Since both A. theae and male F. theae adults migrate to other locations, their populations were studied by another technique also. At regular intervals, 5 infested leaves of C. japonica were picked up 10 times each month from September 1977 - August 1978. The leaves were placed in covered plastic containers, and kept in the laboratory for 7 days, and then placed in the freezer for a day to kill the emerged adults to facilitate counting. The number of A. theae, male F. theae adults, mites, thrips, Lindorus, and Microweisea, was recorded. Afterward, the leaves were lightly brushed to remove male scales and other contaminants, and an area of 3 cm² was delineated in the center of each leaf with a circular corer. The number of mature females present in the 3 cm² area was recorded.

For studying the population structure of tea scale and its natural enemies, 10 infested leaves containing new colonies of tea scale were picked up at random during the month. In the laboratory, a 3 cm² area was marked in the center of each leaf and examined under a microscope. Each tea scale individual was probed and examined to record its age class (crawler, settler, etc.), sex, and whether it was dead or alive.

The data for life tables were obtained by counting the number of dead and live individuals of all stages present in a 3 cm^2 area per leaf on 10 leaves each month. Ovipositing females were regarded as the final survivors of a cohort which contained all the dead members in previous stages. The number of crawlers that settled successfully was obtained by adding up numbers of all dead individuals backward in time. For example, the total number of successfully settling crawlers = the number of live ovipositing females + the number of dead females (preoviposition stage) + the number of dead female nymphs + the number of male pupae + the number of dead male nymphs + the number of dead settlers. The number of crawlers is assumed to be the same as the number of eggs because all eggs hatch successfully due to protection provided by the females. The amount of eggs was obtained by multiplying the number of live ovipositing females in the previous generation with the average fecundity value (28.82). The number of crawlers lost during dispersion was calculated by subtracting the number of settlers from the number of eggs.

RESULTS AND DISCUSSION

Biology

Biology of the tea scale has been studied in some detail by Das and Das (1962) in India. An earlier less complete life cycle study was made in Alabama by English and Turnipseed (1940). The following studies on biology of tea scale were made in the Biocontrol Laboratory at the Division of Plant Industry, Gainesville, Florida.

Mating

There is no recorded account of mating between male and female tea scale. In the course of these studies, mating was observed only once, when, during examination of an infested leaf, a male was seen attempting to mate, but mating behavior could not be recorded in detail.

The male is probably attracted by a sex pheromone emanating from the raised posterior end of the receptive female. Antennae of the male, which are well developed and as long as the body, are probably used to detect the pheromone.

The presence of a sex pheromone has so far been demonstrated in only two species of armored scale insects. The first suggestion that males of armored scale insects locate the females in response to sex pheromones was that of Bodenheimer (1951), who noted the chemotactic response of California red scale males to virgin females. The conclusive evidence of the sex pheromones in the California red scale, Aonidiella aurantii (Maskell), was provided by Tashiro and Chambers (1967). Their results were confirmed in the laboratory by Rice and Moreno (1969) and in the

field by Rice and Moreno (1970). Later on Moreno et al. (1972) also demonstrated the presence of a sex pheromone in the yellow scale, Aonidiella citrina (Coquillett).

Males of armored scale insects are polygamous. Tashiro and Moffitt (1968) conducted laboratory tests on Aonidiella aurantii and found that individual males were able to inseminate up to 30 females. The average number of females fertilized per male was 11.9.

Oviposition

Eggs are extruded from the body of the female, but retained under the armor, and arranged in 2 rows, probably with the aid of the pygidial plates and lobes. Before depositing any eggs the female occupies the greater part of the space under the armor, but as eggs are laid the body begins to shrivel, ultimately occupying only a small part of the anterior end.

Das and Das (1962) stated that eggs were deposited singly at intervals, at a rate of not more than 4 per day; the rate was highest at the beginning but declined gradually. By following the oviposition activity of a single female they found that 39 eggs were laid in 21 days.

Oviposition by tea scale is typical oviparity. In oviparous insects the eggs are extruded from the genital tract and deposited outside the body. In ovoviviparous insects the eggs are retained in the genital tract until larvae hatch or are ready to hatch. In the case of tea scale, the eggs are laid outside the genital tract but retained under the armor. Thus parental care and a suitable incubation environment is provided for the eggs to a certain extent.

Fecundity

Fecundity of the tea scale was calculated by counting the number of eggshells, unhatched eggs and eggs still present in the ovaries of 40

field collected females (Table 2). Females lay from 17-43 (average 28.82 ± 7.82) eggs during their life span.

In India, Das and Das (1962) studied the tea scale fecundity by daily removal of eggs from the posterior part of the armor. Contending that the method did not appreciably affect the oviposition potential, they found that the average fecundity of 14 females was 29. They also counted the eggshells under the armor of 15 females that had met natural death and recorded 22-43 (average 32.1) eggshells per female. English and Turnipseed (1940) reported from Alabama that tea scale females laid 10-16 eggs. Vaughan (1975), commenting on this discrepancy between fecundity figures given by the above authors, noted that Das and Das (1962) conducted their studies on potted tea plants in the laboratory, whereas English and Turnipseed (1940) observed natural field populations on camellias, and believed this explained the discrepancy. However, the more probable explanation for this discrepancy may relate to the amount of space under the female armor. This can accommodate not more than 17 unhatched eggs. Room for additional eggs is made when the earlier eggs hatch and crawlers emerge. The casual observer can easily and erroneously conclude that the maximum number of unhatched eggs present is the actual total fecundity.

Egg

The newly laid egg is shiny yellow, more or less oval in shape and broader at one end. It measures 0.21 mm in length and 0.13 mm in width at the broadest point. Near hatching, the color changes to dull yellow, and the pinkish eyes can be seen through the chorion. Shortly before hatching, the fully formed crawler is visible through the flattened eggshell. The crawler hatches out by splitting the chorion, and empty

TABLE 2
Total Fecundity of tea scale, Fiorinia theae

Female #	# Eggshells	# Eggs OSO*	# Eggs ISO**	Total Eggs
1	14	8	3	25
2	13	9	5	27
3	9	8	2	19
4	24	0	2	26
5	21	3	2	26
6	22	11	0	33
7	41	1	0	42
8	13	8	1	22
9	14	10	3	27
10	32	7	0	39
11	32	0	0	32
12	20	4	0	24
13	30	0	0	30
14	36	3	0	39
15	37	6	0	43
16	14	6	1	21
17	32	8	0	40
18	15	6	0	21
19	36	7	0	43
20	30	4	0	34
21	9	11	0	20
22	9	8	0	17
23	24	0	0	24
24	22	4	0	26
25	11	10	0	21
26	12	7	0	19
27	22	5	0	27
28	16	10	0	26
29	23	1	2	26
30	40	2	0	42
31	15	8	0	23
32	30	9	0	39
33	34	7	0	41
34	10	9	0	19
35	19	8	0	27
36	14	8	1	23
37	24	5	0	29
38	31	0	0	31
39	13	8	3	24
40	35	1	0	36

* - outside the ovary

** - inside the ovary

Mean = 28.82
Std. Dev. = 7.82

eggshells are pushed to the rear and compressed in rows, one on either side in the posterior space under the armor.

Incubation Period

The incubation period of the 14 eggs that were removed from under the female armor ranged from 10-14 days (average 11.2 ± 1.3). In the case of the eggs that were left undisturbed under the armor, the incubation period for 10 eggs lasted for 9-10 days (average 9.8 ± 0.4). The latter figures are closer to the natural conditions and indicate that the female provides not only protection and care but also a suitable environment to incubate the eggs. The difference in the two incubation periods was statistically significant at a 95% level.

According to English and Turnipseed (1940), temperature appears to be an important factor in determining the length of incubation periods. They recorded an incubation period of 7-21 days for the tea scale. Das and Das (1962) working in India, reported that tea scale eggs hatched in 4-6 days at 30-32.7°C and 73.5-80.7% relative humidity.

Crawler (Free-Living First Instar)

Immediately after hatching, the crawler emerges from under the female armor through the raised posterior end. It is flat and somewhat oval in shape, yellow in color, and measures 0.26 mm in length and 0.14 mm in width. It has 6 well-developed legs and two normal antennae.

After emergence, the crawlers move around for 1-4 days. On finding a suitable place, they insert the mouth part stylets into the plant tissue and settle down. Crawlers from the same female tend to settle in close proximity to each other, forming a new colony.

As in the other diaspidids, the crawler represents an important stage in the life history of the tea scale, since only through crawlers can

infestations actively spread. They are said to be dispersed by other insects and birds, but the dispersal of crawlers by means of the often airborne silken mass secreted by male nymphs is also a possibility. Although the amount of dispersion by this method has not been estimated, some live crawlers were found entangled in masses of gossamer-like waxy thread flying about on windy days. Another method of dispersal and colonization is, of course, through the transfer of infested host material.

No sex-differentiation can be made at crawler stage. However, Ferris (1942) believed that some armored scales might exhibit some differences at this stage, and Stickney (1934) observed an additional spur on the legs of the male of first instar larva of Parlatoria blanchardi Targioni-Tozzetti. Stoetzel and Davidson (1974) stated that sexual dimorphism in the crawlers of certain aspidiotine species could be differentiated by the difference in the dorsal setal patterns of both sexes.

Settler (Sedentary First Instar)

Soon after successfully inserting their stylets, the crawlers change into settlers. Both the free-living crawler and the sedentary settler belong to the same stage, the first instar. In other words, the first instar has 2 phases, being first motile then sedentary. The first instar changes into the second instar (first molt) after 10 days, i. e., 14 days after hatching. As in other diaspidids, the legs disappear and antennae are much reduced during the first molt.

Second Instar (Male) Nymphs

The second instar nymph is yellowish in color and measures 0.53 mm in length and 0.25 mm in width. The armor is thin and felted white. The pale yellow exuvia remains attached to its anterior end. This stage molts into third instar after about 11 days, i. e., 25 days after hatching.

Third Instar (Male) Prepupa

At this stage the rudimentary wing pads become visible. The prepupa is 0.68 mm in length and 0.35 mm in width. The armor is almost rectangular with parallel sides. There is a prominent ridge along the mid dorsal line. One less-prominent ridge is also present laterally on either side. Because of the presence of the rudimentary wing pads, this stage is termed a prepupa. The prepupa molts into pupa in 5 days, i. e., 30 days after hatching.

Fourth Instar (Male) Pupa

In the beginning, the color of the pupa is yellow like that of the prepupa, but later the color changes to orange-yellow. Wing pads become elongated and a conical stylus develops at the end of the abdomen.

The pupa, including the stylus, measures 0.72 mm in length and 0.21 mm in width. Armor is similar to that of the third instar. The pupa changes into a pharate adult in 2 days, i. e., 32 days after hatching, and, on day 34, the adult male emerges from under the posterior end of the armor.

Adult Male

Adult male measures on an average 0.72 mm in length and 0.21 mm in width, with a wing span of 1.4 mm. It is a gnat-like creature of orange-yellow color, and has one pair of glassy, white forewings with reduced venation. The hind pair of wings is represented by a pair of halteres. A long stylus, or penis sheath, is present at the end of the abdomen.

Tea scale males are probably nocturnal, as are the males of other armored scales (Bodenheimer, 1951). Since the mouth parts are non-functional, adult males do not feed, their only purpose being to fertilize the females. According to Das and Das (1962), adult males live for 2-3 days.

Second Instar (Female) Nymph

After the first molt, a thin membranous covering is formed over the body of the female nymph. As in the male, pale yellow exuvia of the first stage remains attached to the anterior end of the female armor. In the early second instar, the body is light yellow and measures 0.59 mm in length and 0.28 mm in width. This stage lasts for 6 days, i. e., 20 days after hatching. Following the second molt, the skin of the second instar female is not shed but remains intact, forming a cover that completely encloses the adult insect which shrinks, thus leaving a vacant space at the posterior end of the armor.

Female (Mature)

The body of the female starts increasing on day 22 and becomes fully elongated by day 26.

The covering of the female is at first thin and light yellow in color, but after sclerotization becomes hard and covered with a thin film of wax. Sclerotization occurs between day 31-36 after hatching. The armor is narrow and elongate with a distinct median longitudinal carina, and is dark brown, the median longitudinal area being the darkest. The female armor measures 1.2 mm in length and 0.43 mm in width. The yellow female lies under this protective armor. Because of shrinkage to provide room under the armor for the forthcoming eggs, the adult female is shorter in length than the mature nymph.

During maturation, the armor of the female adheres firmly to the leaf surface. Upon reaching maturity on or about day 46, the posterior end of the armor becomes slightly raised. This change may be for emanating pheromones to attract males. Raising of the posterior end may serve some additional purposes as well, such as facilitating the intromission of the penis and egression of crawlers.

Eggs become mature in the ovaries in about 62 days after hatching, and females start laying eggs on or about day 65, completing the life cycle. English and Turnipseed (1940) reported that tea scale completed its life cycle in 60-70 days in Alabama. In India, the life cycle was completed in 24-27 days (Das and Das, 1972).

During the maturation of females, it was noticed that some individuals had liquified bodies under the armor. No such individual was found when females had matured. This liquified stage may be an interval of re-organization of nymphal body into adult body, i. e., an incipient pupal stage. Comprehensive studies, however, are required to confirm this finding.

The asynchronous maturation of males and females of the same brood effectively prevents the fertilization of females by males of the same colony. Males emerge much earlier and are extremely short-lived; when females of the same brood mature, males are not available to fertilize the females in the laboratory colonies. To establish successful cultures, a succession of implantations at suitable intervals, preferably weekly, is essential to ensure the availability of males to fertilize the females.

Parthenogenesis

Results of the experiments indicated that unmated females of tea scale are unable to reproduce, because no crawlers developed on any of the plants. The plant kept at 35°C was killed by heat; therefore no plant was used at this temperature in the replication of the experiment.

Sex-ratio in the absence of natural mortality factors was 1.9:1 at 15°C, 1.8:1 at 20 and 25°C, and 1.4:1 at 30°C.

A multiple regression analysis of the data indicated that the temperature (15-30°C) failed to produce any effect on the sex-ratio.

Relative survival of the immatures at different temperatures was also evaluated. Maximum survival was observed at 25°C, while the lowest survival

occurred at 30°C. Data are presented in Appendix 1. Number of immatures present on the upper and lower surfaces of the leaves indicated that the lower surface was preferred by tea scale. Of 865 nymphs examined, 315 (36.4%) had settled on upper surfaces, whereas, 550 (63.6%) had settled on the lower surfaces. There were, on an average, 8.75 nymphs per leaf on the upper surfaces and 15.28 nymphs per leaf on the lower surfaces (Appendix 2). A 't' test indicated that the difference in these values was significant at 95% level of confidence.

Population Dynamics

General Characteristics of Tea Scale Populations

Tea scale colonies, in general, have a whitish appearance caused by the white armors and the profuse white wax secretions of the males. This characteristic cottony mass usually occurs on the under side of the leaves and, in heavy infestations, hangs from the leaves, especially on the lower parts of the plants.

On camellias the tea scale usually behaves as a stenomorous species because the only part of the plant attacked is the leaf. However, in cases of heavy infestations, some individuals may be found on the upper side of the leaves as well as on the buds. In the greenhouse, where natural control is non-operative, both lower and upper sides of camellia leaves became profusely covered with tea scale colonies. In nature, the upper surface of the leaves is kept clean probably by the rain, sunlight, and various natural enemies.

During 1977 some 10,589 leaves on 1320 randomly selected twigs of Camellia japonica at Wilmot Garden were examined for tea scale infestations. Of these, 1450 (13.69%) were found to be infested. Rate of infestation varied from 1.75-88.14% of leaves on individual plants.

Tea scale is a polyphagous species with a host list consisting of 43 species of plants in 25 genera belonging to 16 families. In spite of the long host plant list, it occurs in high numbers only on camellias and hollies, and on these plants it exists virtually without any competition from other phytophagous insects. It may be that on these hosts it eliminates the competitors, while on other host plants, it is eliminated; for instance, as on Euonymus sp. by Coccus hesperidum and on Citrus sp. by whiteflies.

The life history is markedly different in both sexes. Except for the egg and possibly the first instar, all other stages, including adults, exhibit sexual dimorphism. During most of its life span, tea scale remains attached to the leaf. Only crawlers and male adults are the mobile stages. Both of these stages, however, last only for a short time. Non-feeding stages include the egg, crawler, and pre-pupa (third instar male nymph), and male pupa, while the feeding stages include the settlers (sedentary first instar), male nymphs, and all stages of the female.

The most conspicuous sign of feeding is the irregular, yellowish splotches on the upper surface of the leaves. These discolored areas correspond to the tea scale colonies present directly on the lower side, and are obviously caused by their feeding on the leaf tissue. On heavily infested leaves, these splotches coalesce and the entire upper surface of the leaves becomes mottled or discolored. Sometimes males and females were found developing on portions of leaf that had earlier been nibbled by some caterpillars. This obviously means that stylets are inserted into the vascular strands of the leaf for feeding.

Tea scale is a multivoltine species with several overlapping generations breeding more or less uninterruptedly throughout the year in Florida. Though cold weather decreases developmental activity, hatching does occur during the winter. During any part of the year all developmental stages can be found in the field. In the winter, camellias and hollies appear to be heavily infested. This is because no new foliage appears during winter and crawlers must settle on the same leaves near the mother colonies. Crawler dispersal may also be reduced by effects of temperature during the cold season. In India, Das and Das (1962) also found the same pattern of higher levels of infestation during winter.

Tea scale populations are characterized by highly male-biased sex-ratios and marked sexual dimorphism; the males being white, soft-bodied, and ultimately emerging as winged adults, while the less conspicuous, heavily armored females remain in place as neotenic adults. These attributes would appear well suited to divert attention of predators away from the less expendable and better protected females. Aspidiotiphagus sp. nr. lounsburyi is the only native parasite that attacks females but it is very rare, killing no more than 1.25% of the females by direct parasitization and destroying about 19% of the females by host feeding. As a result of diversion of predation to the more numerous soft-bodied males, and the resistance of the less conspicuous, heavily armored females to both predation and parasitization, and protection of the eggs during incubation, the tea scale has developed a remarkably successful strategy for survival.

Tea scale is a protandrous species, males emerging long before the females of the same brood become sexually mature. Despite the shorter developmental period, males molt 4 times while females molt only twice. This asynchrony in the life cycles of the sexes creates some problems in the study of population dynamics. In the interest of clarity and consistency, the following simplified terminology has been adopted:

Egg

Crawler - free-living first instar nymph

Settler - sedentary first instar nymph

Male nymph - second and third instar nymph

Female nymph - second instar nymph with unsclerotized armor

Male pre-reproductive - intact pupa (fourth instar)

Female pre-reproductive - second instar with fully sclerotized armor, pre-oviposition stage

Male reproductive - emerged adult (empty pupal armor)

Female reproductive - ovipositing female

Populations of Adult Males

The population surveys of adult male tea scale were carried out at Wilmot Garden during March 1977 through August 1978. Under field conditions, males began to emerge in April when new foliage was appearing on host plants. Adults were present in fluctuating numbers during April - January, with peaks of population occurring in May, July, and November.

The curves representing the adult male populations shown in Fig. 1 and Fig. 2 do not conform due to the difference in sampling techniques. In Fig. 2 the curve for adult population indicates the presence of males throughout the year because of continuous emergence of males from pupae in the laboratory. In Fig. 1 the curve represents the number of adult males observed on leaves and shows an absence of males during February - April, indicating a disruption of emergence from pupae in the field.

Male populations were greatly affected by the destruction of nymphs due to parasitism following introduction of Aphytis theae and Aspidiotiphagus sp. During September - December 1977, when A. theae was present, male populations were much smaller than those of the corresponding months in 1979 when A. theae was no longer present (Table 3). Average number of adult males emerging from 200 leaves (50 leaves per month) was 650 in 1977, and 1625 in 1979. A 't' test indicated that the difference in means was statistically significant at 95% level of confidence.

Figure 1. Adult Populations of Aphytis theae and Male Fiorinia theae Observed on Leaves of Camellia japonica at Wilnot Garden, Gainesville

Figure 2. Number of Male Adults of Fiorinia theae, Adults of Aphytis theae, Larvae of Microgaster coccidivora and Lindorus lophanthae on Leaves of Camellia japonica, and Percent Parasitism by A. theae at Wilnot Garden, Gainesville.

TABLE 3
 Comparison of Numbers of Male F. theae Adults Emerged from Colonies on
 Leaves of Camellia japonica at Wilmot Garden in 1977 and 1979.

Month	Number of males emerged per 50 leaves	
	1977	1979
Sept.	295	1439
Oct.	786	2071
Nov.	675	1398
Dec.	843	1591
Total	2599	6499
Mean	650	1625

Populations of Mature Females

Populations of mature females fluctuated through the season. Peak of population occurred during January (Fig. 3). This peak was the result of decreased reproductive activity which causes accumulation of females during winter. The percent of ovipositing females in the total female population varies from 49.24 in November to 66.48 in April, with an average of $56.54 \pm 6.1\%$. The number of mature females in pre-oviposition, oviposition, and post-oviposition is given in Table 4.

Mortality in the mature females occurs mostly in the pre-oviposition stage by parasitization and host feeding of Aspidiotiphagus sp. nr. lounsburyi, and ranges from 14.28% in May to 23.94% in October, with an annual average of $19.7 \pm 3.1\%$.

Life cycle and survival of different stages are summarized graphically in Fig. 4.

Figure 3. Number of Ovipositing Females of Tea Scale, *Fiorinia theae*, on Leaves of *Camellia japonica* at Wilmot Garden, Gainesville.

TABLE 4
 Number of Mature Females of F. theae in Pre-Oviposition, Oviposition,
 and Post-Oviposition Stages

Month	Number of females/30 cm ²			Total	
	Pre-Oviposition live	dead	Oviposition Post-Oviposition		
Sep. 77	20	38	98	13	169
Oct. 77	12	51	137	13	213
Nov. 77	53	41	97	6	197
Dec. 77	61	41	121	11	234
Jan. 78	62	68	160	11	301
Feb. 78	49	50	126	9	234
Mar. 78	32	30	113	9	184
Apr. 78	24	28	121	9	182
May 78	26	19	86	2	133
Jun. 78	27	28	66	9	130
Jul. 78	17	25	71	15	128
Aug. 78	38	36	85	11	170
Total	421	455	1281	118	2275
Mean	35	38	107	10	190
Std. Dev.	17.3	13.6	27.9	11.8	50.8

Figure 4. Life Cycle and Survival of Different Stages of Tea Scale, *Florinia theae* Green, at Gainesville. The Area of Circles is Proportioned to the Size of Populations. Decrease in Size of Circles is Due to Mortality Occurred Between Successive Stages.

Introduced Parasites

Aphytis theae (Cameron)

A. theae was introduced into Florida from Jorhat, India, in 1976. It was successfully cultured in a greenhouse and then released at several locations in Gainesville during May 1976. Population surveys during the summer indicated that it was rapidly increasing in numbers and dispersing to other locations. However, with the advent of winter, its populations started declining, and during late winter only dead pupae were encountered in the field, indicating that the parasite failed to survive the winter (Fig. 5).

Re-colonization of A. theae was initiated in March 1977. For this purpose infested Camellia japonica leaves harboring pupae and adults of A. theae from the greenhouse culture were securely placed on infested leaves of C. japonica at Wilmot Garden. Results of intensive surveys indicated a rapid increase in population numbers reaching a peak in October 1977. A sudden decline in population occurred during the second week of November when adults were killed in large numbers by freezing temperatures at night. The decline in population continued until January (Fig. 1). No adults were seen in the field during January - March. However, A. theae adults did emerge in the laboratory from the 50-leaf sample collected in January and March. No adult emerged from the material sampled in February.

Live larvae and pupae were present in the field during January and February, but most of the live pupae seen during this period had been denuded (host scale removed) by the predators. A few eggs were recorded in March, indicating that A. theae had barely survived the winter of 1977 - 1978. This seems to have been a consequence of momentum imparted

Figure 5. Larval and Pupal Populations of Aphytis theae on Leaves of Camellia japonica at Wilmot Garden, Gainesville.

by the extremely high numbers of A. theae present in late fall, the small percent surviving winter mortality being sufficient to maintain a viable population.

The larger population present in the fall of 1977 may be explained by the date of re-colonization which was about 6 weeks earlier than the first release in 1976. This provided time for about 3 more generations during the 1977 season.

During 1978, adults were not seen in the field until late May (Fig. 1). The subsequent pattern of population increase was similar to that of the two preceding seasons; however, intensive survey was terminated in August 1978. No adult of A. theae was seen in the field during January - March 1979, and later observations revealed that A. theae failed to survive the winter of 1978 - 1979.

Mortality of A. theae larvae ranged from 0 in September to 57.14% in February. Average larval mortality was 7.16%. Pupal mortality ranged from 8.33% in June to 100% in March. The major cause of larval and pupal death was cold, seemingly accentuated in the case of pupae by activity of predators which resulted in removal of the protective host scale cover from many of the parasites. Details of larval and pupal mortality are presented in Table 5.

The failure of A. theae to survive in Gainesville can be attributed to the winter weather conditions. A comparison of 20-year averages of minimum temperatures and rainfall in Jorhat (India) and Gainesville (Florida) is presented in Fig. 6. The curves for temperature and rainfall indicate that winters are cooler and wetter in Gainesville. Another striking feature exhibited by the temperature curves is the straight line representing the months from December through February

TABLE 5
Larval and Pupal Mortality of *Aphytis theae*
per 30 cm² of leaves of *Camellia japonica* at Wilmot Garden

Month	No. of larvae live	No. of larvae dead	% mortality	No. of pupae live	No. of pupae dead	% mortality
Sep. 77	29	0	0.00	24	5	17.24
Oct. 77	42	1	2.33	38	11	22.45
Nov. 77	49	0	0.00	67	12	15.19
Dec. 77	119	10	7.75	61	32	34.41
Jan. 78	42	11	20.75	11	33	75.00
Feb. 78	6	8	57.14	4	30	88.23
Mar. 78	0	0	-	0	22	100.00
Apr. 78	0	0	-	1	19	95.00
May 78	3	3	50.00	5	7	58.33
Jun. 78	51	2	3.77	33	3	8.33
Jul. 78	83	0	0.00	41	9	18.00
Aug. 78	43	1	2.32	40	8	16.66
Total	467	36		325	191	
Average	38.9	3	7.16	27.1	15.9	37.00

Figure 6. Average Monthly Rainfall and Minimum Temperature at Jorhat (India) and Gainesville (Florida). Data for Jorhat were Obtained from CIBC (Indian Station), and for Gainesville from Agronomy Department, University of Florida.

at Gainesville and indicating a prolonged period of low temperatures. The corresponding portion of the Jorhat temperature curve indicates that winter temperatures are somewhat warmer and the period of adverse temperatures is of shorter duration. This difference no doubt accounts for failure of A. theae to persist at Gainesville.

In the field, mating was observed in the morning and forenoon. In the laboratory, 10 matings lasted for 25-53 seconds with an average of 39.5 seconds. Egg laying occurs during evening hours. The egg is deposited under the armor on the dorsal side of the second instar male nymph. On hatching, the parasite larva migrates to the ventral side and starts feeding ectoparasitically. On completion of feeding, it molts into the pupal stage; two black fecal pellets (meconia) are excreted before the molt. At this stage the head of the parasite pupa can be seen protruding from under the posterior end of the host armor. Adults emerge after a week. For emergence, adults do not drill any holes, but crawl out from under the host armor. The life cycle is completed in about 2 weeks.

Because of the atrophied mouthparts, adult A. theae is not capable of host feeding.

Aphytis theae exhibits host relationships of more than usual interest as it shows a marked preference for parasitizing male nymphs of its host species. While originally collected from tea scale it is not in any sense restricted to this species. Near the end of the 1977 season it was observed to attack male nymphs of the false oleander scale, Pseudaulacaspis cockerelli (Cooley) as readily as those of tea scale. A. theae appears, therefore, to be a representative of a group of scale parasites that are adapted to exploit the male sex of diaspine

scales. This kind of host-parasite association may represent another example of resource partitioning (Schoener, 1974) in which other related parasite species are restricted to the host females. Direct competition between parasites would thus be minimized by host sex rather than host species specificity. As an alternative explanation, restriction of a parasite such as A. theae to males of host species may have evolved as regulative mechanism facilitating coexistence of host and parasite.

Such sex specific parasites also afford an interesting opportunity to investigate the effect of male mortality on host populations. Although there is no documented evidence that such mortality has significant generation to generation effects on host populations, two possible effects can be hypothesized. First, the population of host species will decline due to reduced mating. This effect would most likely occur if females were polyandrous and normally the more numerous sex. Secondly, the host species might in due time evolve a uniparental strain.

Failure of A. theae to produce any effect on tea scale populations in spite of high male mortality can be attributed to the fact that male tea scale, like other male diaspidids, is polygamous, and normally present in numbers that considerably exceed the number of females.

Tashiro and Moffitt (1968) proved that males of the California red scale are polygamous. They found that a single male could fertilize up to 30 females, with an average of 11.9 females per male.

Effect of A. theae on tea scale populations was studied during September 1977 through August 1978. This period can be divided into two parts. First, the period lasting from January through May when A. theae was inactive due to winter, and second, the period lasting from June through December when A. theae was active. Comparison of

numbers of live male nymphs in the two intervals was made. On the average, there were 167 live male nymphs per 30 cm² of leaf surface present during January through May, whereas, the corresponding number during June through December was 80. A 't' test indicated that the difference in numbers of live male nymphs was statistically significant at 95% level of confidence.

A similar test on numbers of female nymphs present in the respective periods indicated a statistically insignificant difference.

Comparison of numbers of male F. theae emerging from the colonies present on 50 leaves during each month of the 2 seasonal periods was also made. On the average, 1320.8 males per 50 leaves emerged during January - May, and the corresponding numbers during June through December was 699.2. The difference was found to be statistically significant.

On rare occasions adults of Aphytis sp. nr. lignanensis were found in the 5-leaf samples. These were probably chance visitors which happened to be present on the leaves at the time of collection. There are many Aphytis species attacking different species of armored scales in Florida, but there is no local species of Aphytis specific to tea scale in North America. A systematic search of Asian areas where the tea scale originated would almost certainly reveal a species of Aphytis adapted to fill this vacant niche.

Aspidiotiphagus sp.

Aspidiotiphagus sp. (Indian) is uniparental species; no males are present in this species, and unfertilized females produce only female progeny. A culture was established in the laboratory at Gainesville using Aspidiotus nerii Bouche as host which was in turn bred on Irish potato tubers.

To record the duration of life cycle and fecundity, 30 females were released individually on A. nerii on potatoes. Females were observed ovipositing, and took 70-140 (average 103) seconds to deposit a single egg. The progeny started emerging after 28 days. Each female produced 11-41 (average 22.1 ± 8.5) daughters. When Aspidiotiphagus sp. was released on tea scale on potted camellia in the laboratory, females were seen ovipositing in both male and female nymphs of tea scale.

Field releases were made in Gainesville during January - June 1977.

No data on population dynamics of tea scale were collected during September 1978 - August 1979, but observations were resumed in September 1979 and carried out through December 1979.

During this period, Aspidiotiphagus sp. emerged in abundant numbers. From a 50-leaf sample per month, 204 Aspidiotiphagus sp. adults emerged in September, 398 in October, 247 in November, and 55 in December. The percent of parasitism on males was 12.4 in September, 16.1 in October, 15.0 in November, and 3.3 in December 1979. The decrease in numbers was due to overwintering of the parasite in the pupal stages. All emerging adults were females. Adult parasites emerge from male nymphs of tea scale by making a hole on the dorsal side of the armor.

Although re-colonization of A. theae and releases of Aspidiotiphagus sp. (Indian) were made during the same period in 1977, there was no evidence that the latter had established until September 1979. In the meantime, A. theae increased rapidly during 1977 - 1978, and maintained high population levels until winter. This indicates the superiority of A. theae as a competitor of Aspidiotiphagus sp., which did not increase to detectable levels until relieved of competition from A. theae.

Life Tables

In developing the life tables, 5 age intervals are used, namely, egg, crawler, settler, pre-reproductive, and reproductive. Since tea scale exhibits distinct sexual dimorphism, nymph, pre-reproductive, and reproductive age intervals are divided into male and female categories.

Egg. The number of eggs was estimated as the product of the average fecundity value (28.82) and the number of live ovipositing parent females. Since the number of such females was not known for September, 1977, it was arbitrarily calculated as the average number of live ovipositing females for 11 months (October 1977 - August 1978). This is the only assumed number in the life table figures for September, 1977. All other numbers in the rest of the life tables are real figures. All eggs under the female armor hatched successfully and emerged as crawlers.

Crawler. Since crawlers are mobile, their number cannot be accurately estimated by the sampling method used to calculate numbers of the sedentary stages. Any other sampling technique employed to estimate the number of crawlers would have been statistically inappropriate. Because all eggs hatch successfully, their number also represents the number of crawlers.

A large number of crawlers die before settling. They are probably blown away by wind, washed away by rain, and lost by misadventure during dispersal and leaf fall. Their mortality ranged from 62.41% in July to 86.44% in September with an annual average of 77.35%. This high early mortality is a characteristic of all species with free-living and exposed individuals. Samarasinghe and LeRoux (1966) found the same trend of crawler mortality for Lepidosaphes ulmi (L.) in Quebec, Canada.

Settler. These are sedentary individuals with thin armors. As sex differentiation is not apparent at this stage, the numbers in the l_x and d_x columns represent the density of settlers of both sexes. They are preyed upon by a phytoseiid mite, Iphiseides sp., and a thrips, Aleurodothrips fasciapennis (Franklin) (Phalaeothripidae).

The extent of mortality caused by each species could not be ascertained. Combined mortality caused by these 2 predators ranged from 16.50% in July to 36.76% in October with an annual average of 24.08%.

Nymph. Dimorphism is quite distinct at this age, and male and female nymphs can be distinguished from each other.

Male nymphs: This stage includes both second and third instar nymphs. The major cause of mortality was the temporarily established introduced parasite, A. theae. The percentage of nymphs parasitized by A. theae ranged from 8.78 in May to 58.52 in December with an annual average percentage of 37.47. However, this parasite was not most active in December as indicated by the rate of parasitism for that month. The figures were obtained by counting the number of dead nymphs containing all stages of the parasite, namely, eggs, larvae, pupae, and exuviae of the emerged adults. Peak numbers of the adult parasite were observed during October, but populations started declining with the advent of winter.

Major predators feeding on male nymphs are 2 species of coccinellids, namely, Lindorus lophanthae (Blaisdell) and Microweisea coccidivora (Ashmead). These are regularly present among the tea scale colonies. Usually a single larva of L. lophanthae is found feeding on tea scale. It ploughs through the colonies, denuding and destroying more male nymphs that it feeds on. This habit of Lindorus probably slows down the

growth rate of Aphytis populations because of indiscriminate destruction of unparasitized as well as parasitized tea scale nymphs. Most of the dead pupae of A. theae in winter had been denuded by Lindorus. On the other hand, 2 or more larvae of Microweisea feed together. This coccinellid consumes the host nymphs individually by making an irregular hole in the male armor.

The peaks of Lindorus and Microweisea populations more or less alternated with each other during the season (Fig. 2). This may be the result of competition between the 2 species. A multiple regression analysis indicated that variations in the populations of male tea scale were caused by the activity of these 2 predator species acting together as well as individually.

A complex of Chrysopa spp. and 2 coccinellids, Cybocephalus sp. and Chilocorus stigma (Say), which feed on male nymphs, are also occasionally present among the tea scale colonies. But because of their extremely low populations and irregular occurrence during the season, these predators did not play any significant role in the population dynamics of tea scale. The combined mortality of male nymphs caused by predators ranged from 3.40% in September to 25.09% in May, with an annual average of 13.22%.

A considerable number of male nymphs were found dead but the cause of death could not be ascertained. Diseases and some other physiological reason may be responsible for this mortality which ranged from 4.76% in September to 34.31% in February, with an annual average of 14.08%. The highest rates of mortality occurred during January - March indicating that cold may be the major cause of death in this category.

Female nymphs: This stage includes both unelongated and elongated nymphs with unsclerotized armor. A local species of parasites, Aspidiotiphagus sp. nr. lounsburyi (Berlese and Paoli) (Aphelinidae), attacks the female nymph. It oviposits in the body of the second instar nymphs, and the larva feeds endoparasitically. Pupae are black and can be seen through the thin covering of the dead host. A round hole near one end of the unsclerotized armor is made by the emerging adult. A few hosts with fully sclerotized armor also contained emergence holes. This parasite is very rare with rates of parasitization ranging from 0 in May to 3.93% in November with an annual average of 1.57%.

Female nymphs were also parasitized by A. theae. Rate of parasitism by A. theae on female nymphs ranged from 1.37% in June to 5.06% in July, with an average of 1.05% during the year. Death in the majority of female nymphs can be attributed to diseases. Bodies of such nymphs became liquified under the armor. In later studies, it appeared that liquification might be due to reorganization of the body tissue preliminary to pupation. Nevertheless, in the absence of experimental evidence to the contrary, these nymphs have been assumed dead due to disease. Mortality by this cause ranged from 11.87% in October to 31.01% in July, with an average of 21.46% during the year.

Pre-reproductive. Male pre-reproductives: This is the fourth instar or pupal stage. Although neither A. theae nor predators were found attacking the pupae, many dead individuals were encountered in the field. Most of the dead pupae had died as pharate adults. Direct cause of death was desiccation caused by the denudation of pupae by the predators, which removed the armors while probing for food but left the pupa intact. Mortality in male pupae ranged from 4.05% in June to 48.39% in February,

with an annual average of 15.09%. Very high mortality in February indicates that cold may also be responsible for death of pupae. In population surveys, the pupal stage is the most appropriate index of population density. Duration of this stage is very short and, therefore, the extent of generation overlap is minimal.

Female pre-reproductives: In this stage females have fully sclerotized scales. A large number of females were found dead apparently because of hostfeeding by Aspidiotiphagus sp. nr. lounsburyi. Some of the dead female nymphs may have died of this cause also. It is possible that Aspidiotiphagus adults may be parasitizing the nymphs but hostfeeding on pre-reproductives. Rate of mortality ranged from 18.80% in April to 29.02% in January with an average of 26.21% during the year.

Reproductive. **Male reproductives:** This stage was sampled by counting the number of empty pupal armors which indicated the successful emergence of male adults. Cause of death is recorded in the life tables as senility which, in fact, means natural death after mating.

Female reproductives: All ovipositing females that survived to reproduce are included in this category. Generation mortality ranged from 92.65% in February to 96.92% in April with an annual average of 95.15%.

Population trend index (I) is the most practical measure of population changes obtained from the life tables. It was calculated as the ratio of number of eggs in 2 successive generations. Stable populations have population trend index (I) value equal to 1. A value of (I) greater or less than 1 indicates increasing or decreasing population trends.

Population trend index (I) of tea scale varied from 0.70 in November to 1.39 in October with an annual average of 0.98. This shows that on an average tea scale populations were on decline during the year

1977 - 1978. This finding is in agreement with the fluctuating population trends reported by other workers for all species studied to date. This should occasion no surprise as all species have good years and bad years.

To determine the relationship of variation in population trend index (I), and other variables such as sex-ratio, male and female densities, and the generation mortality, data were subjected to a multiple regression analysis. The results of analysis showed that the generation mortality was the main factor responsible for fluctuations in the values of population trend index (I).

The column headings of the life tables (Table 6) are similar to those proposed by Morris and Miller (1954) except that the last column, labeled as $100d_x/N_1$ represents generation mortality. A brief description of column headings follows:

x	=	The age interval
l_x	=	The number alive (l) at the beginning of the age interval (x)
d_x^F	=	The factor responsible for the death of individuals (d_x) within each age interval
d_x	=	The number dying (d) within the age interval stated in the (x) column
$100q_x$	=	Percentage mortality (d_x as percentage of l_x)
$100d_x/N_1$	=	The percentage of generation mortality

The figures in l_x and d_x columns represent the number of individuals per 30 cm² of the infested leaves; figures in other columns were calculated from these numbers. In d_x^F column, parasites are mentioned individually by name, whereas, the predators are grouped together. This

is because it is possible to distinguish deaths caused by each species of parasites, while it is not possible to quantify the damage caused by the individual species of predators.

TABLE 6
Monthly and Annual Life Tables for Tea Scale, Florinia theae,
at Wilmot Garden, Gainesville

September 1977											
x	males	1x females	total	d _y F	males	females	d _x	total	males	females	100d _x /N ₁ total
Egg			3142	-				0			0.00
Crawler			3142	Dispersion loss			2716				86.44
Settler			426	Thrips and mites			107				3.40
Nymph	147	172	319	Aburhis these	113	0	113	76.87	0.00	35.42	3.60
				<u>Epilobium</u> sp.	0	2	2	0.00	1.16	0.63	0.06
				Preductors	5	0	5	3.40	0.00	1.57	0.16
				Disease	0	34	34	0.00	19.77	10.66	1.08
				Unknown	7	0	7	4.76	0.00	2.19	0.22
				Total	125	36	161	85.03	20.93	50.47	5.12
Pre-reproductives	22	136	158	Desiccation	5	0	5	22.73	0.00	3.16	0.16
				lost feeding	0	38	38	0.00	27.94	24.06	1.21
				Total	5	38	43	22.73	27.94	27.22	1.37
Reproductives	17	98	115	Senility	17	98	115				
Generation							3027				96.33

Number of females	98
Number of potential eggs	$(98 \times 28.82) = 2824$
Index of population trend	$2824/3142 = 0.9$

TABLE 6-continued

December 1977									
x	males	1_x females	total	d_x^F	males	d_x females	total	100q _x males	100q _x / N_1 females
Egg			2796	-			0	0.00	0.00
Crawler			2796	Dispersion loss			1803	64.48	64.48
Settler			983	Thrips and mites			171	17.22	6.12
Nymph	593	229	822	Aphytis thrae	476	5	481	80.27	2.18
				<u>Aspidiotiphagus</u> sp.	0	4	4	0.00	1.75
				Predators	34	0	34	0.49	0.00
				Disease	0	58	58	0.00	4.14
				Unknown	49	0	49	7.06	1.22
								0.00	2.07
								5.96	0.00
				Total	559	67	626	94.26	1.75
Pre-reproductives	34	162	196	Desiccation	2	0	2	29.26	2.39
				Host feeding	0	41	41	0.00	2.39
				Total	2	41	43	0.00	0.00
Reproductives	32	121	153	Senility	32	121	153	1.02	0.07
Generation								20.92	1.47
Number of females			121					25.31	1.47
Number of potential eggs (121 X 28.82) =			3487					21.94	1.54
Index of population trend 3487/2796 =			1.25						94.52

TABLE 6-continued

January 1978

x	x	i _x	d _x F	d _x	100g _x	100d _x /i ₁
	males	females	total	males	females	total
Eggs			3487			0.00
Crawler			3487			72.64
Settler			954			5.82
Nymph	464	287	751			
				260	56.03	7.45
				0	0.00	0.00
				3	1.04	0.09
				62	13.36	1.78
				56	0.00	1.61
				117	25.22	3.35
				439	94.61	12.58
				59	20.55	1.70
				4	16.00	0.11
				68	25.82	1.95
				72	16.00	1.95
				181	28.46	2.06
				3306		94.80

Number of females

160

Number of potential eggs (160 X 28.82) = 4611

Index of population trend 4611/3487 = 1.32

TABLE 6-continued

March 1978		1x		dx		100qx		100qx/1	
x	males	females	total	males	females	total	males	females	total
Egg			3631						0.00
Crawler			3631						83.67
Settler			593						4.82
Nymph	238	180							
				69	0	28.99	0.00	0.00	1.90
				3	3	0.00	1.67	0.00	0.08
				31	0	13.02	0.00	0.00	0.85
				34	34	0.00	18.89	0.00	0.94
				61	0	25.63	0.00	0.00	1.68
				161	37	67.64	20.56	1.02	5.45
				14	0	18.18	0.00	0.00	0.38
				0	30	0.00	20.98	0.00	0.82
				14	30	18.18	20.98	0.82	1.20
				63	113				
Pre-reproductives	77	143	220						
Reproductives	63	113	176						
Generation									
Number of females			113						95.14
Number of potential eggs (113 X 28.82) =			3256						
Index of population trend 3256/3631 =			0.89						

TABLE 6-continued

April 1978		I_x		d_x^F		d_x		$100\%x$		$100\%x/N_1$	
x	males	females	total		males	females	total	males	females	males	total
Egg			3256	-			0	0.00		0.00	0.00
Crawler			3256	Dispersion loss			2599	79.82		79.82	
Settler			657	Thrips and mites			171	26.03			5.25
Nymph	296	190	486	Aphytis thomae	69	0	69	23.31	0.00	14.20	2.12
				<u>Aspidiotiphagus</u> sp.	0	2	2	0.00	1.05	0.41	0.06
				Predators	45	0	45	15.20	0.00	9.26	1.38
				Disease	0	39	39	0.00	20.52	8.02	1.20
				Unknown	46	0	46	15.54	0.00	9.47	1.41
				Total	160	41	201	54.05	21.57	41.35	6.17
Pre-reproductives	136	149	285	Desiccation	18	0	18	13.23	0.00	6.32	0.55
				Host feeding	0	28	28	0.00	18.08	9.82	0.86
				Total	18	28	46	13.23	18.08	16.14	0.55
Reproductives	118	121	239		118	121	239				
Generation							3017				92.65
Number of females			121								
Number of potential eggs (121 X 28.82) =			3487								
Index of population trend 3487/3256 =			1.07								

TABLE 6-continued

May 1978		1x		d _x F		d _x		100q _x		100d _x /N ₁	
x	males	females	total	males	females	males	females	males	females	males	females
Egg			3487					0.00			0.00
Crawler			3487					84.37			84.37
Settler			545					24.77			3.87
Nymph	263	147	410								
				36	0	36	13.69	0.00	0.00	1.03	0.00
				0	0	0	0.00	0.00	0.00	0.00	0.00
				66	0	66	25.09	0.00	0.00	1.90	0.00
				0	42	42	0.00	28.57	10.24	0.00	1.20
				44	0	44	16.73	0.00	10.73	1.26	0.00
				Unknown							
				146	42	188	55.51	28.57	45.85	4.19	1.20
				Total							5.39
Pre-reproductives	117	105	222								
				20	0	20	17.09	0.00	9.01	0.57	0.57
				0	19	19	0.00	18.09	8.56	0.00	0.55
				Host feeding							
				Total							
				20	19	39	17.09	18.09	17.57	0.57	1.12
Reproductives	97	86	183								
				97	86	183					
				Senility							
				Generation							
				3304							94.75
Number of females			86								
Number of potential eggs			(86 X 28.82) = 2479								
Index of population trend			2479/3487 = 0.71								

TABLE 6-continued

[illegible]

TABLE 6-continued

August 1978		1x		dxF		dx		100qx		100d/N;	
x	males	females	total	males	females	total	males	females	total	males	females
Egg			2046	-		0			0.00		0.00
Crawler			2046	Dispersion loss		1420			69.40		69.40
Settler			626	Thrips and mites		151			24.12		7.38
Nymph	303	172	475	anhydria theae	214	3	70.63	1.74	45.68	10.46	0.15
				anidictybanus sp.	0	2	0.00	1.16	0.42	0.00	0.09
				Predators	62	0	20.46	0.00	13.05	3.03	0.00
				Disease	46	46	0.00	26.75	9.68	0.00	2.25
				Unknown	15	0	4.95	0.00	3.16	0.73	0.00
				Total	291	51	96.04	29.65	72.00	14.22	2.49
Pre-reproductives	12	121	133	Desiccation	1	0	8.33	0.00	0.75	0.05	0.00
				Host feeding	0	36	0.00	29.75	27.07	0.00	1.76
				Total	1	36	8.33	29.75	27.82	0.05	1.76
Reproductives	11	85	96	Senility	11	85					
Generation											
Number of females			85								95.30
Number of potential eggs	(85 X 28.82) =		2450								
Index of population trend	2450/2046 =		1.20								

TABLE 6-continued

Annual (Sept. 1977 - August 1978)										
x	i_x		d_x^F		d_x		$100d_x$		$100d_x/N_1$	
	males	females	total		males	females	total	males	females	total
Egg			3134	-			0	0.00		0.00
Crawler			3134	Dispersion loss			2425	77.35		77.35
Settler			710	Thrips and mites			171	24.08		5.45
Nymph	348	191	539	Aphytis theae	200	2	202	57.47	1.05	37.47
				Aspidiotiphagus sp.	0	3	3	0.00	1.57	0.56
				Predators	46	0	46	13.22	0.00	8.53
				Disease	0	41	41	0.00	21.46	7.61
				Unknown	49	0	49	14.08	0.00	9.09
				Total	259	46	341	84.77	24.08	63.26
Pre-reproductives	53	145	198	Desiccation	8	0	8	15.09	0.00	4.04
				Host feeding	0	38	38	0.00	26.21	19.19
				Total	8	38	46	15.09	26.21	23.23
Reproductives	45	107	152	Semility	45	107	152			
Generation							2982			
Number of females			107							95.15
Number of potential eggs (107 X 28.82) =			3084							
Index of population trend 3084/3134 =			0.98							

K-Factor Analysis of Life Tables

Varley and Gradwell (1960) described a method of analyzing life table data that reveals factors responsible for changes in population density. By this method, the killing power, or k-value, of each mortality factor is measured by taking the difference between the logarithm of population numbers before and after its action (Appendix 3). Since a series of mortality factors act successively in a population, their total killing power, or K-value, equals the total killing power of the individual factors. Its application to tea scale is as follows:

k_1 = mortality of crawlers during dispersal

k_2 = mortality of settlers due to predators

k_3 = mortality of nymphs due to parasites, predators,
diseases and unknown causes

k_{3a} = mortality of male nymphs due to A. theae, (contained
in k_3)

k_4 = mortality of the pre-reproductives due to parasite,
host feeding, and desiccation

Using these k-values, generation mortality (K) can be expressed as follows: $K = k_1 + k_2 + k_3 + k_4$

The k-values for different age intervals and K-value for each month (Appendix 3) were plotted in Fig. 7, where the contribution of each mortality factor to variation in K can be seen by visual inspection. From the figures it is quite apparent that there are two main types of mortality factors; the first is for dispersion loss of crawlers (k_1) and the second is the action of natural enemies on nymphs (k_3). Both k-values followed, more or less, the same pattern as did the generation mortality (K). Action of A. theae is shown separately as k_{3a} , which is similar to k_3 but somewhat lower in magnitude. Since A. theae failed to become

Figure 7. Key Factor Analysis. The Recognition of Key Factors in the Life Tables for Tea Scale, *Fiorinia theae*, by Visual Correlation of Various Mortality Factors (k_s) with the Generation Mortality (K).

permanently established, it is no longer operating as a mortality factor affecting tea scale populations in Gainesville.

Survivorship Curves

A survivorship curve is the simplest graphical description of a life table and is obtained by plotting the number in the l_x column on the ordinate against age on the abscissa (Fig. 8). Lotka (1925) pointed out that survivorship curves become more informative if l_x is plotted on a logarithmic scale. A straight line would indicate a constant mortality throughout life, while other shapes would measure the different "force of mortality" at different age intervals. Pearl and Miner (1935) and Deevey (1947) recognized 3 general types of survivorship curves: Type I, "the negatively skew rectangular" or convex curve is shown by members of a cohort which, having been born at the same time, die more or less simultaneously after a life span characteristic of the species. In other words, mortality acts heavily on old individuals. Type II is the "diagonal" curve and represents a constant mortality rate at all age intervals. That is, there is no greater probability of death at one stage than at another. Type III, "the positively skew rectangular" or concave curve indicates very high mortality in the young stages, but the few individuals which survive to advanced ages have a relatively high probability of further life. This is the most common type of survivorship curve met with in animals. Most invertebrates and lower vertebrates exhibit this trend of mortality. In the higher vertebrates, the survivorship curve is of Type I because of greater parental care to their offspring.

Most survivorship curves known so far tend to be rather intermediate, in varying degree, between Type I and Type II. Price (1975) analyzed the survivorship curves of 22 insect species and found that there were 2 basic types of curves, although intermediates also occurred. In insects, mortality occurs in distinct stages; therefore, their survivorship curves show a number of distinct steps (Ito, 1961).

Figure 8. General Types of Survivorship Curves.

In tea scale, the eggs are retained under the female armor until hatching. This is a sort of parental care comparable to the higher vertebrates with Type 1 curves. The shape of the tea scale survivorship curve (Fig. 9) is somewhat convex in the beginning because of the high survival of eggs. The latter portion of the curve conforms to the typical stepped appearance of insect survivorship curves. Survivorship curve for females shows a consistent pattern throughout the year, while that for the males indicates variation in the survival which is directly affected by absence or presence of A. theae. Data for the survivorship curves are presented in Appendix 4. In the preparation of survivorship curves, actual numbers were converted to begin at 1000.

The shape of survivorship curves of insect pests helps in determining the vulnerable stage of each species and may lead to the emphasis of control efforts on that stage. For instance, in the case of tea scale, the most vulnerable stage is the female nymph. If a species of natural enemy can be found that attacks this stage, the tea scale population can be reduced to non-economic levels.

Figure 9. Monthly and Annual Survivorship Curves of Tea Scale, Florinia theae, at Wilmot Garden, Gainesville.

Figure 9-continued.

Figure 9-continued.

Figure 9-continued.

Fertility Tables

Knowledge of sex-ratio is a pre-requisite for species fertility tables. Tanner (1978) stated that sex-ratio can be categorized into the specific sex-ratio and the crude sex-ratio. The former relates to the ratio of the numbers of each sex within a particular age group; the latter is the ratio of the number of each sex in the entire population.

The specific sex-ratio in tea scale varied greatly during different months because of the differential activity of natural enemies. Aphytis theae was the major mortality factor acting on the second instar male nymphs. Populations of A. theae also fluctuated during the season. During summer months it killed a major portion of male nymphs, but during the winter period, A. theae was wiped out by prolonged cold. Absence of A. theae released the pressure on the male nymphs of tea scale, and the sex-ratio swung further in favor of male sex. For instance, during March through September, when A. theae was active, the sex-ratio at nymphal stage ranged from 2.75:1 to 4.87:1, while during October through February, when Aphytis was inactive or absent, the sex-ratio at nymphal stage ranged from 6.02:1 to 8.43:1 (Table 7). Data are presented in Appendix 5.

The effect of fluctuations in A. theae populations was also reflected by the varying sex-ratio in the subsequent stages of tea scale. Although the specific sex-ratios at the pre-reproductive and reproductive stages were in favor of females (except during March - May in the case of pre-reproductives, and May and June in the case of reproductives), the crude sex-ratio consistently remained in favor of males (Fig. 10). A delayed effect of A. theae on sex-ratio is also depicted by Fig. 10. The highest proportion of males occurred in February at the nymphal stage, in April at pre-reproductive stage, and in May at reproductive stage.

TABLE 7
Specific and Crude Sex-Ratios of Tea Scale, Florinia theae

Month	Nymph	Sex-ratio (male:female)		Crude
		Pre-Reprod.	Reproductive	
Sep. 77	3.53:1	0.12:1	0.17:1	1.03:1
Oct. 77	6.44:1	0.51:1	0.20:1	1.62:1
Nov. 77	6.46:1	0.07:1	0.47:1	2.00:1
Dec. 77	6.32:1	0.16:1	0.26:1	2.22:1
Jan. 78	6.02:1	0.73:1	0.13:1	1.92:1
Feb. 78	8.43:1	0.76:1	0.13:1	2.07:1
Mar. 78	4.87:1	1.31:1	0.56:1	1.97:1
Apr. 78	3.35:1	1.63:1	0.98:1	1.89:1
May 78	2.75:1	1.27:1	1.13:1	1.87:1
Jun. 78	2.78:1	0.07:1	1.10:1	1.67:1
Jul. 78	3.44:1	0.09:1	0.24:1	1.99:1
Aug. 78	3.03:1	0.22:1	0.13:1	1.41:1
Average	4.52:1	0.55:1	0.42:1	1.83:1

Figure 10. Specific and Crude Sex-Ratio of Tea Scale, *Fiorinia theae*, at Wilmot Garden, Gainesville.

Females of a species are capable of reproducing only during a certain age span. Much of their life is spent as either immature (pre-oviposition) or too old (post-oviposition). To estimate the growth of populations with overlapping generations, it is essential to know the number of female individuals that are present at each age interval (Table 8) and the number of female offspring produced by an average female at different intervals in her reproductive life. Once these parameters are known, the calculation of fertility rate (m_x) becomes an easy process. Fertility rate (m_x) and sex-ratio are used in preparing the fertility tables.

A fertility table describes, in a summarized fashion, the net replacement rate (R_0) of an average female. R_0 is defined as the number of daughters that replace an average female in the course of a generation. The usual method of calculating R_0 is from tables of age survivorship (l_x) and fecundity (m_x). The sum of all products of l_x and m_x denotes R_0 . A value of R_0 equal to 1, indicates a stable population; greater than 1 indicates an increasing population; and less than 1 indicates a decreasing population.

R_0 is used in the calculation of reproduction or instantaneous rate of population growth (r). Here $r = \log R_0/T$, where T is the generation time. According to Price (1975), in the case of populations with overlapping generations, each month can be considered as a breeding season. Therefore, for purposes of generation time T of the tea scale assumed as one month is used. Then $r = \log R_0/1$ or $r = \log R_0$.

A stable population will have $r = 0$, while a value more than 0 will indicate an increasing population, and a minus value of r will

TABLE 8
 Number of Female Tea Scale, Fiorinia theae, per 30 cm² area of leaves
 of Camellia japonica at Wilmot Garden, Gainesville

Month	Number of Females				
	Nymphs		Pre-reproductives		Reproductives
	survived	died	survived	died	survived to reproduce
Sep. 77	172	36	136	38	98
Oct. 77	219	31	188	51	137
Nov. 77	178	40	138	41	97
Dec. 77	229	67	162	41	121
Jan. 78	287	59	228	68	160
Feb. 78	214	38	176	50	126
Mar. 78	180	37	143	30	113
Apr. 78	190	41	149	28	121
May 78	147	42	105	19	86
Jun. 78	146	52	94	28	66
Jul. 78	158	62	96	25	71
Aug. 78	172	51	121	36	85
Total	2292		1736		1281
Mean	191		141		107
Std.Dev.	40.5		39.7		27.9

represent a decreasing population. Values of R_0 and r for tea scale during September 1977 - August 1978 are presented in Table 9.

TABLE 9
Monthly and Annual Fertility Tables for Tea Scale, F. theae

September 1977
Sex-ratio - 3.53:1

x	l_x	m_x	$l_x m_x$
Nymphs	1.00	0	0
Pre-reproductives	0.79	0	0
Reproductives	0.57	$28.82/4.53 = 6.36$	3.63
			$R_0 = 3.63$
			$r = .56$

October 1977
Sex-ratio - 6.44:1

x	l_x	m_x	$l_x m_x$
Nymphs	1.00	0	0
Pre-reproductives	0.85	0	0
Reproductives	0.62	$28.82/7.44 = 3.87$	2.40
			$R_0 = 2.40$
			$r = .38$

November 1977
Sex-ratio - 6.46:1

x	l_x	m_x	$l_x m_x$
Nymphs	1.00	0	0
Pre-reproductives	0.77	0	0
Reproductives	0.52	$28.82/7.46 = 3.86$	2.01
			$R_0 = 2.01$
			$r = .30$

TABLE 9-continued

December 1977
Sex-ratio - 6.32:1

x	l_x	m_x	$l_x m_x$
Nymphs	1.00	0	0
Pre-reproductives	0.71	0	0
Reproductives	0.53	$28.82/7.32 = 3.94$	2.08
		$R_0 =$	2.08
		$r =$	.32

January 1978
Sex-ratio - 6.02:1

x	l_x	m_x	$l_x m_x$
Nymphs	1.00	0	0
Pre-reproductives	0.79	0	0
Reproductives	0.56	$28.82/7.02 = 4.10$	2.29
		$R_0 =$	2.29
		$r =$	.36

February 1978
Sex-ratio - 8.43:1

x	l_x	m_x	$l_x m_x$
Nymphs	1.00	0	0
Pre-reproductives	0.82	0	0
Reproductives	0.59	$28.82/9.43 = 3.06$	1.80
		$R_0 =$	1.80
		$r =$	.26

TABLE 9-continued

March 1978
Sex-ratio - 4.87:1

x	l_x	m_x	$l_x m_x$
Nymphs	1.00	0	0
Pre-reproductives	0.79	0	0
Reproductives	0.63	$28.82/5.87 = 4.91$	3.09
			$R_0 = 3.09$
			$r = .49$

April 1978
Sex-ratio - 3.35:1

x	l_x	m_x	$l_x m_x$
Nymphs	1.00	0	0
Pre-reproductives	0.78	0	0
Reproductives	0.64	$28.82/4.35 = 6.62$	4.24
			$R_0 = 4.24$
			$r = .62$

May 1978
Sex-ratio - 2.75:1

x	l_x	m_x	$l_x m_x$
Nymphs	1.00	0	0
Pre-reproductives	0.71	0	0
Reproductives	0.58	$28.82/3.75 = 7.68$	4.45
			$R_0 = 4.45$
			$r = .65$

TABLE 9-continued

June 1978
Sex-ratio - 2.78:1

x	l_x	m_x	$l_x m_x$
Nymphs	1.00	0	0
Pre-reproductives	0.64	0	0
Reproductives	0.45	$28.82/3.78 = 7.62$	3.43
			$R_0 = 3.43$
			$r = .53$

July 1978
Sex-ratio - 3.44:1

x	l_x	m_x	$l_x m_x$
Nymphs	1.00	0	0
Pre-reproductives	0.61	0	0
Reproductives	0.45	$28.82/4.44 = 6.49$	2.92
			$R_0 = 2.92$
			$r = .46$

August 1978
Sex-ratio - 3.03:1

x	l_x	m_x	$l_x m_x$
Nymphs	1.00	0	0
Pre-reproductives	0.70	0	0
Reproductives	0.49	$28.82/4.03 = 7.15$	3.50
			$R_0 = 3.50$
			$r = .54$

TABLE 9-continued

Average: September 1977 - August 1978

Sex-ratio - 4.53:1

x	l_x	m_x	$l_x m_x$
Nymphs	1.00	0	0
Pre-reproductives	0.76	0	0
Reproductives	0.55	$28.82/5.53 = 5.21$	2.86
			$R_0 = 2.86$
			$r = .45$

Age Composition

The age pyramids are constructed in order to determine whether populations are increasing, decreasing, or stable in time. It is therefore essential to know the age distribution in the population. In the natural populations with overlapping generations, at each interval dead members are being replaced by the addition of new members. Because of this, the populations with overlapping generations are a complex of individuals representing all possible age groups. Difference in the age composition of populations at different intervals becomes quite apparent from the shape of the age pyramids. By following a series of age pyramids, changes in the age structure of a population can be ascertained with reasonable accuracy.

Age composition of tea scale is presented in Fig. 11. As in survivorship curves, female populations are more or less stable. Male populations show variations through the season. Adult males were in the lower proportions during July - September and December - February. The first reduction was caused by A. theae, while the second reduction was caused by cold, as low temperatures prevented the pupae from becoming adults. Data for Fig. 11 are presented in Appendix 6.

Figure 11. Monthly and Annual Age Composition of Tea Scale,
Fiorinia theae, at Wilmot Garden, Gainesville.

Figure 11-continued.

Figure 11-continued.

Figure 11-continued.

Methodology to Calculate Survival Rates of Female and Male
Tea Scale Populations

Females. Male and female armors remain attached to the leaf even after the death of tea scale. Accumulation of the females of successive generations gives the impression of heavy infestations. In reality, however, only a proportion of the female population is alive. Since pest management strategies require a precise estimation of potential damage, it becomes necessary to determine the proportion of gravid females in the total population. A procedure to derive the reproductive value of tea scale females present on leaves is described below:

1) A sample of 60 field collected leaves of Camellia japonica was examined to determine the number of dead and live females in pre-oviposition, oviposition, and post-oviposition stages. The following data were obtained:

Total number of females	6269
number of live females in pre-oviposition stage	889
number of dead females in pre-oviposition stage	1161
number of females in oviposition stage (live)	3546
number of females in post-oviposition stage (dead)	673

2) A 40-leaf sample was examined to determine the number of females in oviposition stage and to record the following information:

Total number of females in oviposition stage	2469
number of females (ovipo- sition stage) with no hatched eggs (i.e., eggs were present but none had yet hatched)	482

number of females (oviposition stage) with some hatched eggs 1987

3) Average fecundity of 40 females was determined by counting the number of eggshells, unhatched eggs, and eggs still present inside the ovaries (Table 2).

4) A sample of 40 ovipositing females was examined to determine the reproductive value (average number of remaining eggs) by counting the number of eggshells and deducting this number from the average fecundity (28.82) of females (Appendix 7). The average number of remaining unlaidd and unhatched eggs per female was 12.45

5) Expected progeny of ovipositing females
with no hatched eggs = 482×28.82 = 13891

Expected progeny of ovipositing females
with some hatched eggs = 1987×12.45 = 24738

Total expected progeny of ovipositing females = 38629

Average expected progeny of ovipositing
females = $39629/2469$ = 15.65

6) There were 6269 females on 60 leaves, and if all were alive would deposit (6269×28.82) 180,673 eggs. But there are only 889 (pre-oviposition stage) and 3546 (oviposition stage) live females.

Expected progeny of live females in
pre-oviposition stage = 889×28.82 = 25621

Expected progeny of live females in
oviposition stage = 3546×15.65 = 55495

Total progeny of live females = 81116

Average progeny of live females = $81116/4435$ = 18.29

Average progeny of all (dead and live)
females = $81116/6269$ = 12.94

This is the reproductive value of each female present on the leaf. Total number of eggs on a leaf can be calculated by multiplying the number of

females present on a leaf by 12.94. This also means that for every 100 females present on a leaf, only 44.9 ($12.94/28.82 \times 100$) are potential producers.

Two simple methods to determine the total number of females on infested leaves were developed and are described below.

The area of randomly selected uninfested leaves of Camellia japonica was measured with a leaf-area measuring machine. The average of 100 leaves was $21.7 \text{ cm}^2 \pm 6.7$. Then 50 infested leaves were procured from the field and cleaned with a soft brush to remove scales. On each leaf an area of 3 cm^2 was delineated in the center with a circular corer. The number of mature females was counted in the 3 cm^2 area first, and then the number of females present on the whole leaf was counted (Appendix 8).

One method to calculate the total number of females on a leaf is to multiply the number of females in 3 cm^2 by a factor of 7.23 ($21.7/3$). The second method would be to multiply the number of females in 3 cm^2 by factor (number on whole leaf/number in 3 cm^2). This factor obtained from a 50-leaf count was $8647/1596 = 5.42$ (see Appendix 8). A comparison of the two methods indicates that only the second method is accurate and should be employed in sampling future populations. The difference between the two methods is due to the fact that distribution of tea scale on leaves is clumped. If distributions were random, both methods would conform.

Males. Sex-ratio in tea scale can be used in estimation of the total population and the survival rate of the males. During September - December 1979, the number of males emerging from a 50-leaf sample per month was recorded. The number of females present on the leaves was also counted.

The absolute population of tea scale and male mortality was estimated as follows:

Number of females on 200 leaves
(50 leaves per month) = 32356

Crude sex-ratio (Table 7)
males:females = 1.83:1

Therefore, the potential number of
males on 200 leaves = 32356×1.83 = 59212

Total population of tea scale
on 200 leaves = $32356 + 59212$
or, 32356×2.83 = 91568

Number of males actually emerged
from 200 leaves = 6499

Survial rate of males =
 $6499/91568 \times 100$ = 7.097%

SUMMARY AND CONCLUSIONS

Tea scale is the most serious pest of camellias and hollies in the eastern United States. In Florida it breeds continuously with several overlapping generations throughout the year. Both immature and mature stages exhibit well marked sexual dimorphism. Males molt 4 times and complete development in about 34 days. Their armors are soft in texture and white in color. Females are neotenic and molt twice before commencing oviposition in about 65 days. They have well sclerotized armors of brown color. Effective protection is provided to eggs by the female armor during incubation periods. Asynchronous maturation of males and females effectively prevents mating between individuals of the same brood. Unfertilized females cannot lay fertile eggs, but male biased sex-ratio and polygamous nature of males ensure fertilization. Comparison of rates of development of tea scale in different areas indicates that higher temperatures expedite the development of different stages.

A complex of native predators feeds on male nymphs, while a local parasite attacks female nymphs. These native natural enemies, however, are ineffective in keeping the host populations below economic levels. Because chemical control is costly and otherwise less satisfactory, two species of parasites from India were introduced into Florida. Both parasites proved to be specific to male tea scale. One species, Aphytis theae, could not become permanently established because of prolonged cold periods during winter, but was an important mortality factor during the period of

study; the other parasite, Aspidiotiphagus sp., has become established. In spite of very high rates of parasitism, these sex-specific parasites failed to reduce tea scale populations, thus confirming a long held view of biological control workers regarding efficacy of male-specific natural enemies.

Field collected data are utilized to construct 12 monthly and 1 annual life tables. These life tables are the first of their kind for a sexually dimorphic, multivoltine species with overlapping generations. The methods developed for tea scale life tables will prove suitable for constructing the life tables for species with characteristics similar to tea scale. According to tea scale life table analysis, the major mortality factors were dispersion loss at crawler stage and parasitization of male nymphs by A. theae. Analysis of survivorship curves for males and females indicates that tea scale populations can be reduced if a natural enemy attacking female nymphs is introduced.

Specific sex-ratio in the tea scale varied at all stages; there were more males at nymphal stages but females were more abundant as adults. Crude sex-ratio indicated a constant preponderance of males. Major cause of variation in sex-ratio was mortality of the male nymphs by A. theae. Variations in the relative populations of males and females in all stages are presented in the form of 12 monthly and 1 annual age pyramids. Methods to calculate the survival rates of males and females are developed and will provide useful guidelines in future population surveys of the tea scale. Data generated by field and laboratory studies will provide valuable basic information for comparison of results of future attempts on the biological control of tea scale.

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APPENDIX 1

Number of Male and Female Tea Scale, Fiorinia theae, survived
on Camellia japonica at different temperatures

Plant No. & Temp.	# scales	1	2	3	4	5	Total
1	males	71	2	24	28	32	157
15°C	females	9	7	15	11	21	63
	Total	80	9	39	39	53	220
1-A	males	43	27	14	39	25	148
15°C	females	4	57	4	22	9	96
	Total	47	84	18	61	34	244
2	males	32	12	36	54	27	161
20°C	females	19	14	18	42	9	102
	Total	51	28	54	96	36	263
2-A	males	28	101	37	1	15	182
20°C	females	6	35	32	12	3	88
	Total	34	136	69	13	18	270
3	males	36	70	6	59	64	235
25°C	females	58	17	22	13	44	154
	Total	94	87	28	72	108	389
3-A	males	16	27	34	98	82	257
25°C	females	13	18	18	40	28	117
	Total	29	45	52	138	110	374
4	males	15	24	9	60	10	118
30°C	females	7	5	4	32	10	58
	Total	22	29	13	92	20	176
4-A	males	22	2	10	40	16	90
30°C	females	46	15	6	8	20	95
	Total	68	17	16	48	36	185
5	males	--	--	--	--	--	---
35°C	females	--	--	--	--	--	---
	Total	--	--	--	--	--	---

5-A not used.

APPENDIX 2
Side Preference of Tea Scale, Fiorinia theae

Leaf #	Number of Crawlers Settled		Total
	upper side	lower side	
1	7	3	10
2	7	12	19
3	1	4	5
4	5	7	12
5	0	3	3
6	2	0	2
7	5	1	6
8	6	0	6
9	1	0	1
10	2	3	5
11	6	8	14
12	2	2	4
13	2	3	5
14	15	60	75
15	18	29	47
16	44	49	93
17	30	39	69
18	0	2	2
19	7	4	11
20	2	1	3
21	0	1	1
22	0	1	1
23	1	5	6
24	5	0	5
25	0	5	5
26	0	1	1
27	36	42	78
28	19	32	51
29	13	37	50
30	14	39	53
31	0	3	3
32	6	33	39
33	7	30	37
34	13	32	45
35	33	54	87
36	6	5	11
Total	315	550	865

APPENDIX 3
Values (log) of Various Mortality Factors (k's) and the Generation
Mortality (K) for Tea Scale, Florinia theae, at
Wilnot Garden, Gainesville

Month	Egg/Crawler log #/30 cm ²	Settler log #/30 cm ²	Nymph log #/30 cm ²	Pre-reproductive log #/30 cm ²	Reproductive log #/30 cm ²	K-value
Sep. 77	3.497	2.629	2.503	2.198	2.060	0.138
Oct. 77	3.451	2.890	2.691	2.340	2.217	0.123
Nov. 77	3.596	2.911	2.911	2.274	2.155	0.119
Dec. 77	3.446	2.996	2.914	2.292	2.184	0.108
Jan. 78	3.542	2.979	2.875	2.403	2.257	0.146
Feb. 78	3.663	2.863	2.744	2.315	2.152	0.163
Mar. 78	3.560	2.773	2.621	2.342	2.245	0.097
Apr. 78	3.512	2.817	2.686	2.454	2.378	0.076
May 78	3.542	2.736	2.612	2.346	2.262	0.084
Jun. 78	3.394	2.833	2.687	2.225	2.136	0.089
Jul. 78	3.279	2.854	2.775	2.064	1.944	0.120
Aug. 78	3.310	2.796	2.676	2.123	1.982	0.141

APPENDIX 4

Data for the Survivorship Curves.

Number of Tea Scale, Fiorinia theae, per 30 cm² area of leaves
of Camellia japonica at Wilmot Garden, Gainesville

Month	Eggs	Crawlers	Settlers	Number Survived			Pre-reproductives			Reproductives		
				Male	Nymphs Female	Comb.	Male	Female	Comb.	Male	Female	Comb.
Sep. 77	3142	3142	426	147	172	319	22	136	158	17	98	115
Oct. 77	2825	2825	778	273	219	492	31	188	219	28	137	165
Nov. 77	3948	3948	816	470	178	648	50	138	188	46	97	143
Dec. 77	2796	2796	993	593	229	822	34	162	196	32	121	153
Jan. 78	3487	3487	954	464	287	751	25	228	253	21	160	181
Feb. 78	4611	4611	730	341	214	555	31	176	207	16	126	142
Mar. 78	3631	3631	593	238	180	418	77	143	220	63	113	176
Apr. 78	3256	3256	657	296	190	486	136	149	285	118	121	239
May 78	3487	3487	545	263	147	410	117	105	222	97	86	183
June 78	2479	2479	681	341	146	487	74	94	168	71	66	137
July 78	1902	1902	715	439	158	597	20	96	116	17	71	89
Aug. 78	2046	2046	626	303	172	475	12	121	133	11	85	96
AVERAGE	3134	3134	710	348	191	539	53	145	198	45	107	152

APPENDIX 5

Number of Male and Female Tea Scales, Florinia theae, per 30 cm² area of
Camellia japonica at Wilmot Garden, Gainesville

Month	Nymphs		Pre-reproductives		Reproductives		Total	
	male	female	male	female	male	female	male	female
Sep. 77	194	55	7	58	17	98	218	211
Oct. 77	354	55	32	63	28	137	414	255
Nov. 77	478	74	7	94	46	97	531	265
Dec. 77	689	109	16	102	32	121	737	332
Jan. 78	650	108	95	130	21	160	766	398
Feb. 78	497	59	76	99	16	126	589	284
Mar. 78	336	69	81	62	63	113	480	244
Apr. 78	285	85	85	52	118	121	488	258
May 78	283	103	57	45	97	86	437	234
Jun. 78	315	113	4	55	71	66	390	234
Jul. 78	482	140	4	42	17	71	503	253
Aug. 78	370	122	16	74	11	85	397	281
Totals	4933	1092	480	876	537	1281	5950	3249

APPENDIX 6

Data for the Age Composition.

Number of Live Male and Female Tea Scales, Florinia theae, per 30 cm² area of Leaves of Camellia japonica at Wilnot Garden, Gainesville

Period	Total # of individuals*	Eggs		Settlers		Nymphs		Pre-reproductives		Reproductives							
		#	%	#	%	Male #	Female %	Male #	Female %	Male #	Female %						
Sep. 77	1555	976	62.8	354	22.8	69	4.4	19	1.2	2	0.1	20	1.3	17	1.1	98	6.3
Oct. 77	2105	1365	64.8	398	18.9	112	5.3	24	1.1	29	1.4	12	0.6	28	1.3	137	6.5
Nov. 77	1516	966	63.7	259	17.1	58	3.8	34	2.2	3	0.2	53	3.5	46	3.0	97	6.4
Dec. 77	1900	1205	63.4	295	15.5	130	6.8	42	2.2	14	0.7	61	3.2	32	1.7	121	6.3
Jan. 78	2548	1594	62.6	360	14.1	211	8.3	49	2.0	91	3.6	62	2.4	21	0.8	160	6.2
Feb. 78	2009	1255	62.5	294	14.6	187	9.3	21	1.0	61	3.0	49	2.4	16	0.8	126	6.2
Mar. 78	1985	1126	56.7	377	19.0	175	8.8	32	1.6	67	3.4	32	1.6	63	3.2	113	5.7
Apr. 78	2065	1205	58.4	361	17.5	125	6.1	44	2.1	67	3.2	24	1.2	118	5.7	121	5.9
May 78	1554	857	55.2	253	16.3	137	8.8	61	4.0	37	2.4	26	1.7	97	6.2	86	5.5
June 78	1144	657	57.4	213	18.6	48	4.2	61	5.3	1	0.1	27	2.4	71	6.2	66	5.8
July 78	1153	707	61.3	199	17.3	63	5.5	78	6.8	1	0.1	17	1.5	17	1.5	71	6.2
Aug. 78	1370	847	61.8	224	16.4	79	5.8	71	5.2	15	1.1	38	2.8	11	0.8	85	6.2
TOTAL	20904	12760		3587		1394		536		388		421	2.0	537	2.6	1281	
AVERAGE	1742	1063	61.0	299	17.2	116	6.7	45	2.6	32	1.8	35	2.0	45	2.6	107	6.1

*Number/30cm²

APPENDIX 7

Reproductive Value of the Ovipositing Females of the Tea Scale,
Fiorinia theae, at Wilmot Garden, Gainesville

Female #	# Eggshells	Avg. # Eggs	$\pm$ Remaining Eggs
1	14	28.82	+ 14.82
2	13	"	+ 15.82
3	9	"	+ 19.82
4	24	"	+ 4.82
5	21	"	+ 7.82
6	22	"	+ 6.82
7	41	"	- 12.18
8	13	"	+ 15.82
9	14	"	+ 14.82
10	32	"	- 3.18
11	32	"	- 3.18
12	2	"	+ 26.82
13	20	"	+ 8.82
14	30	"	- 1.18
15	36	"	- 7.18
16	37	"	- 8.18
17	14	"	+ 14.82
18	32	"	- 3.18
19	15	"	+ 13.82
20	36	"	- 7.18
21	30	"	- 1.18
22	9	"	+ 19.82
23	9	"	+ 19.82
24	6	"	+ 22.82

APPENDIX 7-continued

Females	# Eggshells	Avg. # Eggs	$\pm$ Remaining Eggs
25	11	28.82	+ 17.82
26	9	"	+ 19.82
27	11	"	+ 17.82
28	24	"	+ 4.82
29	10	"	+ 18.82
30	22	"	+ 6.82
31	1	"	+ 27.82
32	3	"	+ 25.82
33	11	"	+ 17.82
34	12	"	+ 16.82
35	4	"	+ 24.82
36	22	"	+ 6.82
37	24	"	+ 4.82
38	22	"	+ 6.82
39	11	"	+ 17.82
40	12	"	+ 16.82
41	22	"	+ 6.82
42	16	"	+ 12.82
43	23	"	+ 5.82
44	40	"	- 11.18
45	15	"	- 13.82
46	30	"	- 1.18
47	34	"	- 5.18
48	10	"	+ 18.82
49	19	"	+ 9.82
50	14	"	+ 14.82

Reproductive Value: Mean = 12.45

APPENDIX 8
 Number of Female Tea Scale, Fiorinia theae, in 3 cm² area, and on
 Whole Leaves of Camellia japonica at Wilmot Garden, Gainesville

Leaf	# Females/3 cm ²	# Females/whole leaf	Ratio
1	27	182	6.74
2	16	114	7.13
3	13	68	5.23
4	33	210	6.36
5	78	287	3.68
6	11	73	6.64
7	23	136	5.91
8	26	166	6.38
9	43	221	5.14
10	52	290	5.58
11	29	72	2.48
12	20	86	4.30
13	46	234	5.09
14	37	186	5.03
15	37	251	6.78
16	31	170	5.48
17	7	37	5.29
18	5	22	4.40
19	36	257	7.14
20	33	269	8.15
21	5	34	6.80
22	22	61	2.77
23	49	407	8.31
24	54	360	6.67
25	18	93	5.12
26	78	200	2.56
27	70	357	5.10
28	29	130	4.48
29	22	193	8.77
30	35	232	6.63

APPENDIX 8-continued

Leaf	# Females/3 cm ²	# Females/whole leaf	Ratio
31	13	108	8.31
32	18	138	7.67
33	52	342	4.67
34	25	231	9.24
35	41	191	4.66
36	28	103	3.68
37	20	189	9.45
38	23	97	4.22
39	25	80	3.20
40	33	117	3.55
41	40	238	5.95
42	15	86	5.73
43	42	230	5.48
44	24	149	6.21
45	7	47	6.71
46	63	366	5.81
47	56	255	4.55
48	49	227	4.63
49	9	30	4.44
50	28	114	4.10
Total	1596	8647	5.42
Mean = 31.92	Mean = 172.94	Mean = 5.65	
Std.Dev. = 18.05	Std.Dev. = 95.43	Std.Dev. = 1.67	

BIOGRAPHICAL SKETCH

Badar Munir was born on April 7, 1938, at Rawalpindi, Pakistan. He completed his high school education at the Islamia High School, Rawalpindi, in 1955, and then joined the Gordon College, Rawalpindi, whence he obtained his B.S. degree in biology in 1961. He received his M.Sc. degree in Zoology from the University of Punjab in 1963. He joined the Pakistan Station of the Commonwealth Institute of Biological Control in 1963 as Junior Entomologist and worked on the ecology of high altitude forest pests and their natural enemies in Pakistan. In 1968 he was promoted to Senior Entomologist and in that capacity studied the ecology of fruit flies. In 1971 he proceeded to Barbados, West Indies, to take up an appointment as Government Entomologist. There he worked on the biological control of vegetable pests. He left Barbados in 1976 to join the University of Florida as a graduate student. He is presently working for his Ph.D. degree in entomology. Mr. Munir has published 4 technical papers and has presented papers at various entomological meetings. He is a member of the International Organization of Biological Control, Entomological Society of America, Florida Entomological Society, Caribbean Food Crops Society, and the International Organization for Ecology.

He is married to Rafia Sultana and has a daughter, Saliha, and a son, Hummayum.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

R. I. Sailer, Chairman
Graduate Research Professor
of Entomology and Nematology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

T. E. Freeman
Professor of Plant Pathology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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This dissertation was submitted to the Graduate Faculty of the College of Agriculture and to the Graduate Council, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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