Thermal Requirements for Development, Population Trends, and Parasitism of Azalea Lace Bug (Heteroptera: Tingidae)

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ABSTRACT Duration of development of azalea lace bug, *Stephanitis pyrioides* (Scott), measured at six temperatures ranged from ≈22 d at 30°C to 97 d at 15°C. Development was not successful at 33°C. Estimated threshold temperatures (T_0) and calculated thermal unit requirements (K) for development of egg, nymphal, and complete development were, respectively: 10.2, 12.2, 11.2°C and 213.1, 179.2, 394 degree-days (DD). Four generations of azalea lace bug occurred in central Georgia. Phenology of the first generation developing from overwintered eggs was closely predicted in the landscape using these parameters. A mymarid parasitoid, *Anagrus* sp., emerged from eggs collected at intervals during the season. Greatest parasitoid-induced mortality was observed in the overwintering generation.

KEY WORDS Insecta, *Stephanitis pyrioides*, temperature, development

AZALEA LACE BUG, *Stephanitis pyrioides* (Scott), is indigenous to Asia and has likely attained its current wide distribution via accidental introductions on imported nursery stock (Weiss 1916, Drake & Ruhoff 1965). Although several species of lace bugs in the genus *Stephanitis* attack ericaceous plants (Bailey 1951, Mead 1967), *S. pyrioides* is the major pest of cultivated azaleas. Nymphs and adults colonize the undersides of leaves and damage their hosts by piercing the leaves and destroying the mesophyll. Infested leaves have a stippled appearance from above and are discolored with dark, varnishlike excrement and exuviae underneath. Plant vitality is reduced and the visible damage produced by lace bugs may reduce sale value (English & Turnipseed 1950).

Few natural enemies are known to attack tingids (e.g., Oliver et al. 1985). Neal et al. (1991) reported on the biological control potential of *Stethoconus japonicus* Schumacher (Heteroptera: Miridae), an introduced predator of the azalea lace bug. The mymarid egg parasitoid *Anagrus takeyanus* Gordh has been reared from eggs of a lace bug, *Stephanitis takeyai* (Drake & Maa), in Connecticut (Dunbar 1974, Gordh & Dunbar 1977).

Azaleas are among the most abundant landscape ornamentals (Holmes & Davidson 1984, Raupp & Noland 1984). Raupp et al. (1988) discuss the lack of decision-making rules for pests causing aesthetic damage as an impediment to implementing urban pest management. As the landscape industry increasingly adopts integrated pest management for ornamental plants, the need for such guidelines for pests causing aesthetic injury will increase. Predictive capabilities that minimize time spent monitoring for pests and optimize timing of control efforts are needed.

Neal & Douglass (1988) described the life history of *S. pyrioides* in Maryland. Four generations occurred following early spring eclosion from overwintered eggs in leaf tissue. Development of eggs and nymphs evaluated at three temperatures was nonlinear.

The objective of our research was to define more closely the relationship between temperature and development of *S. pyrioides* to permit the prediction of occurrence of damaging stages on landscape plants. Degree-day (DD) models are valuable tools in pest management programs (Pruess 1983). Applications of the degree-day approach in predicting phenology of urban landscape pests has been demonstrated (e.g., Potter & Timmons 1983, Akers & Nielsen 1984, Potter et al. 1989). Potter (1986) emphasized the need for such tools in urban landscape integrated pest management.

Use of this approach requires the estimation of a lower developmental threshold and the calculation of thermal units above that base temperature required to reach a certain phenological stage. We investigated the developmental biology of the azalea lace bug to allow the construc-

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tion of a temperature-dependent predictive model. We further studied the seasonal phenology of the azalea lace bug in Georgia and determined the relationship of lace bug phenology to degree-day accumulations based on laboratory-determined developmental rate data. Finally, we report the seasonal activity of a parasitoid attacking the eggs of this introduced pest.

Materials and Methods

Controlled Temperature Studies. Specimens for experiments were obtained from a colony initiated with adults collected from a landscape planting of 'Delaware Valley White' evergreen azaleas (form of *Rhododendron mucronatum*) in Griffin, Ga. The colony was periodically supplemented with additional field-collected individuals. *S. pyrioides* were maintained in cages in the laboratory at approximately 24°C and a 15:9 (L:D) photoperiod on evergreen azalea ('Delaware Valley White', 'Snow', and 'Morningstar') in 3.8-liter containers.

Cuttings were obtained from potted 'Delaware Valley White' azaleas grown in an outdoor screenhouse. Female lace bugs were caged on individual cuttings, placed in environmental chambers (Percival Manufacturing Company, Boone, Iowa) and allowed to oviposit for 24 h at each experimental temperature except at 15°C. Eggs incubated at 15°C were oviposited at 18°C because no oviposition occurred at 15°C. Eggs and the emerging nymphs were monitored for development twice daily at each of seven constant temperatures: 15, 18, 21, 24, 27, 30, and 33 ± 1°C. Photoperiod was maintained at 15:9 (L:D). First instars were transferred individually to an azalea cutting extending through a plastic lid into a 32-ml plastic cup of water. A second cup was modified by replacing the bottom with organdy screen to allow ventilation. That cup was inverted and placed over the azalea cutting, and the union of the cups was secured with Parafilm M (American National Can, Greenwich, Conn.). Duration of development of males and females was compared at each temperature (Student's *t* test).

Linear Development Model. Least squares linear regression was used to establish the relationship between development rate and temperature over the linear portion of the development curves. Threshold temperatures (T_o) were obtained by extrapolating this line through the x axis (Arnold 1959). Mean thermal unit requirements (K) for each stage were calculated by taking the mean (among all temperatures) of K_t, which was calculated by the following equation:

$$K_t = (T - T_o) * D_t,$$

where T was 15, 18, 21, 24, 27, or 30°C; T_o was the temperature threshold for a particular stage; D_t was the mean development time (in days) for a particular stage at temperature T. Only the developmental times of nymphs that became adults were used in the threshold determination and calculation of thermal requirements. Although nonlinear methods of threshold estimation have been developed (Wagner et al. 1984), linear methods have been proven effective for practical applications (Pruess 1983, Wilson & Barnett 1983).

Field Phenology Studies of *S. pyrioides*. Landscape plantings naturally infested with *S. pyrioides* were sampled during 1989 and 1990. At site 1 (Griffin, Spalding County, Ga.), 12 'Delaware Valley White' azaleas (10 yr old) in a contiguous landscape planting were sampled at approximately weekly intervals from 15 March through 23 December 1989 and from 2 January through 5 November 1990. Two sets of 10 infested leaves were randomly selected within each of three strata (upper, middle, and lower) and placed in plastic bags, resulting in a total of six groups of 10 leaves from the site per sample date. Samples were taken between 1000 and 1300 hours (EST).

Leaves were taken to the laboratory where the number of early-instar (first through third), late-instar (fourth and fifth), male, and female lace bugs per 10-leaf sample were determined. Leaves were then washed with warm water to remove the lacquerlike excrement deposited over the eggs. Leaves were backlighted to improve visibility of lace bug eggs inserted into plant tissue. Eggs present were counted and categorized as intact or hatched.

Weather service data were used to calculate local degree-day accumulations following the method presented by Hartstack et al. (1976). Thresholds and thermal units required for development used in the calculation of degree-day accumulations were derived from the previously described controlled temperature studies and linear model development. Population trends and observed timing of phenological events of interest determined at site 1 were compared with the temperature-dependent model predictions.

Field Phenology Studies of Parasitism. During 1990, additional samples were taken in Spalding County (central Georgia, site 2), Clarke County (northern Georgia, site 3), and Tift County (southern Georgia, site 4). Azaleas at each site were well-established plantings and had a history of repeated infestation by *S. pyrioides*. Parasitized eggs had been observed at each site before sampling was initiated. Six sets of 10 infested leaves randomly selected within each landscape planting were collected periodically from each location: 14 dates from March through November at site 2, 19 dates from February through November at site 3, and 12 dates from March through October at site 4.

Samples were processed in the laboratory as described previously except that eggs were re-

Table 1. Mean ± SE duration of development in days, and number of individuals entering each stage of *S. pyrioides* on 'Delaware Valley White' azalea cuttings[a]

Temp, °C	Egg	Instar					Total nymphal	Total
		1	2	3	4	5		
15	43.8 ± 0.9 (208)	11.2 ± 0.3 (113)	9.2 ± 0.2 (46)	7.8 ± 0.2 (43)	10.0 ± 0.4 (41)	15.4 ± 0.9 (41)	53.6 ± 1.1 (36)	97.4 ± 0.5 (36)
18	26.3 ± 0.3 (—)[b]	5.9 ± 0.3 (64)	4.9 ± 0.1 (49)	4.5 ± 0.1 (47)	5.2 ± 0.1 (46)	8.3 ± 0.2 (42)	28.8 ± 0.2 (39)	55.1 ± 0.4 (39)
21	23.0 ± 0.2 (265)	4.8 ± 0.1 (200)	3.6 ± 0.1 (140)	3.8 ± 0.1 (128)	4.4 ± 0.1 (124)	6.9 ± 0.1 (122)	23.6 ± 0.1 (119)	46.5 ± 0.2 (119)
24	13.6 ± 0.1 (—)[b]	2.8 ± 0.5 (81)	3.0 ± 0.1 (69)	2.0 ± 0.1 (64)	2.7 ± 0.1 (62)	4.2 ± 0.1 (58)	14.8 ± 0.1 (57)	28.3 ± 0.1 (57)
27	12.0 ± 0.1 (230)	2.4 ± 0.1 (118)	2.1 ± 0.1 (76)	2.2 ± 0.1 (72)	2.4 ± 0.1 (70)	3.7 ± 0.1 (67)	12.9 ± 0.1 (64)	24.9 ± 0.1 (64)
30	11.4 ± 0.1 (330)	2.0 ± 0.1 (165)	1.7 ± 0.1 (136)	1.9 ± 0.1 (130)	2.1 ± 0.1 (128)	2.6 ± 0.1 (121)	10.4 ± 0.1 (117)	21.7 ± 0.1 (117)

[a] Values in parentheses are numbers of individuals entering each stage.
[b] Data not obtained.

corded as intact, hatched, or as having had a parasitoid emerge. Parasitoid emergence is detectable because the adult parasitoids chew their way through the operculum of the azalea lace bug egg, leaving a circular emergence hole. The content of intact eggs was not determined. Voucher specimens of azalea lace bugs and parasitoids were deposited in the Entomology Department Insect Museum at the Georgia Station.

Results

Controlled Temperature Studies. Successful development occurred at all temperatures except 33°C (Table 1). Although nymphs attempted to emerge from 62 of the 231 eggs maintained at 33°C, only one individual completed eclosion, dying shortly thereafter. Adverse effects of high temperatures on development of *S. pyrioides* eggs are apparent in the decreasing rate at which percentage development per day increases at temperatures above 24°C. Such high temperatures are typical of summers in this region. Duration of development from oviposition to ecdysis to the adult stage ranged from 21.7 d at 30°C to 97.4 d at 15°C. About half of the total developmental period was spent in the egg stage. Time required for the development of the third instar was the least, whereas fifth instars required the longest time. These findings are consistent with data reported by Neal & Douglass (1988).

Time required for development of males and females did not differ significantly ($P > 0.05$) at any temperature or for any developmental stage except for time required by the egg stage at 21°C. At that temperature, 46 eggs that developed as males required an average of 23.8 d to hatch, whereas 73 females required 22.5 d ($t = 3.04$, df = 118, $P < 0.05$). Female/male sex ratio averaged 2:1 among all temperatures tested.

Survivorship was lowest at 15°C. Greatest mortality was incurred by the egg at those temperatures at which egg survivorship was examined, and by the first instar (Table 1). Although great care was taken in transferring newly enclosed nymphs, some of this loss may be attributed to handling mortality.

Linear Development Model. Regression equations for the reciprocal of developmental times on temperature for each life stage, and values for T_o and K (Table 2) may be used to predict activity of *S. pyrioides* during a given season. When data from Neal & Douglass (1988) for azalea lace bug development at the two temperatures within the linear range measured in their study (20.6 and 26.1°C) are included in the analysis, threshold temperatures and thermal unit requirements differ only slightly from the values given in Table 2. For example, T_o for egg and complete development become 10.3 and 11.1°C, respectively. Mean thermal unit requirements for the

Table 2. Linear thermal unit models, threshold temperatures (T_o), and mean thermal unit requirement (K) for development of each stage of *S. pyrioides*

Developmental stage	Equation and r^2[a]	T_o, °C	K, DD
Egg	$Y = 0.0047t - 0.048$ $r^2 = 0.88$	10.2	213.1
Instars			
First	$Y = 0.0309t - 0.400$ $r^2 = 0.73$	12.9	31.9
Second	$Y = 0.0350t - 0.442$ $r^2 = 0.56$	12.6	28.8
Third	$Y = 0.0292t - 0.299$ $r^2 = 0.49$	10.2	35.9
Fourth	$Y = 0.0308t - 0.380$ $r^2 = 0.45$	12.3	33.2
Fifth	$Y = 0.0239t - 0.330$ $r^2 = 0.67$	13.8	39.5
Total nymphal	$Y = 0.0054t - 0.066$ $r^2 = 0.95$	12.2	179.2
Complete	$Y = 0.0025t - 0.028$ $r^2 = 0.95$	11.2	394.0

[a] Y, reciprocal of mean development times; t, temperature; r^2, coefficient of correlation.

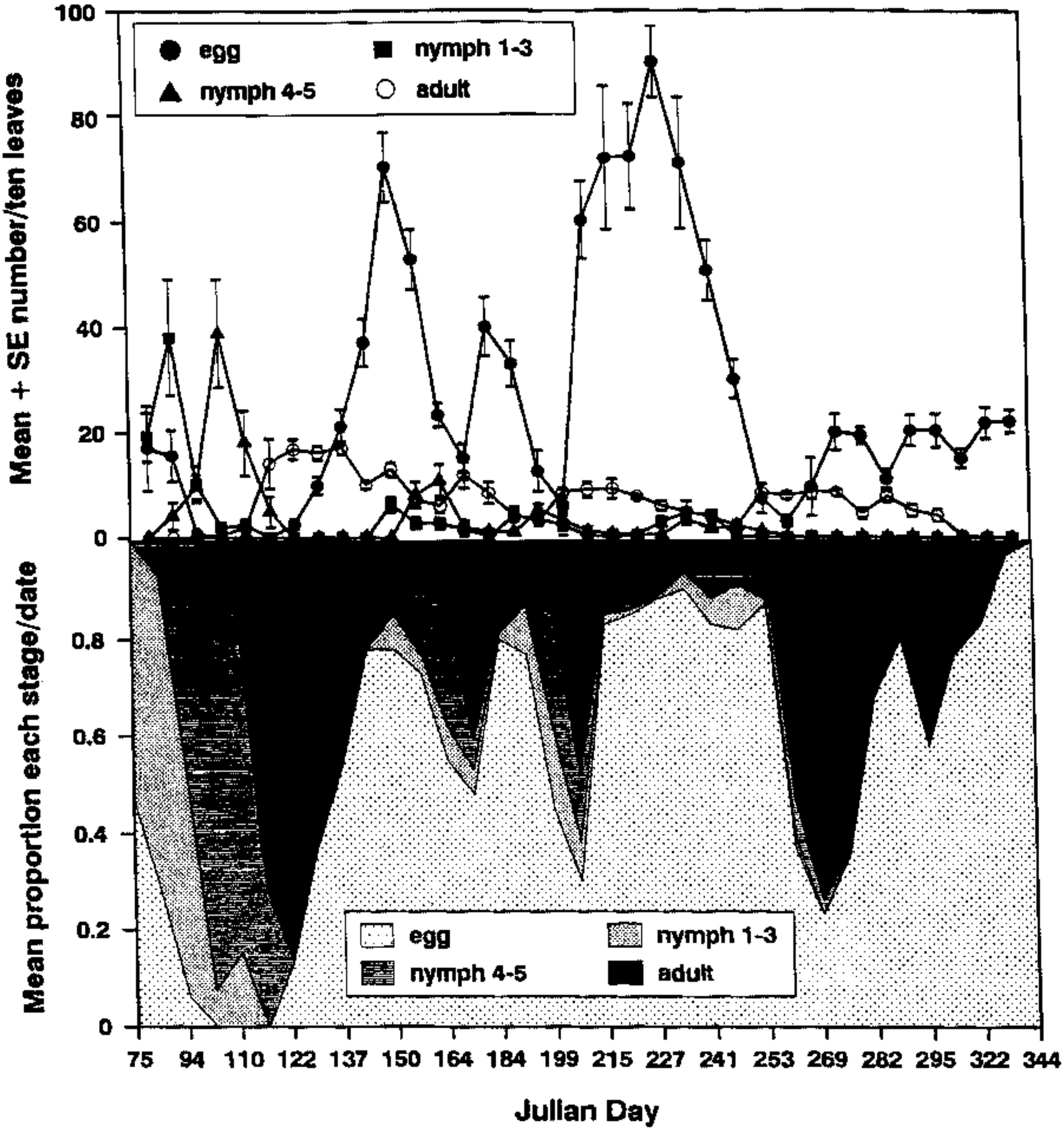

Fig. 1. Seasonal occurrence of immature and adult azalea lace bugs in the landscape at Griffin, Ga., 1989.

development of the egg stage and for complete development using these thresholds become 211.1 and 398.4 DD, respectively.

Field Phenology Studies of *S. pyrioides*. Intact eggs, nymphs, males, and females collected at site 1 during 1989 totaled 5,892, 1,360, 405, and 1,050, respectively. Numbers of individuals collected in those respective categories at site 1 during 1990 were 3,032, 738, 84, and 262. The ratio of females/males among all individuals collected was 2.7:1. This sex ratio was higher than that observed in the laboratory developmental studies, but was again female biased. Four generations of azalea lace bug occurred in central Georgia (Fig. 1 and 2), consistent with the voltinism reported in Maryland (Neal & Douglass 1988). Two to three generations were reported to occur in the New England states (Bailey 1951).

About 50% of the overwintered eggs had hatched by mid-March (day of year or Julian day 75) in 1989 and 1990. Development of the first generation was largely completed by late April (Julian day 120). Adult lace bugs were thereafter present throughout the season, contributing

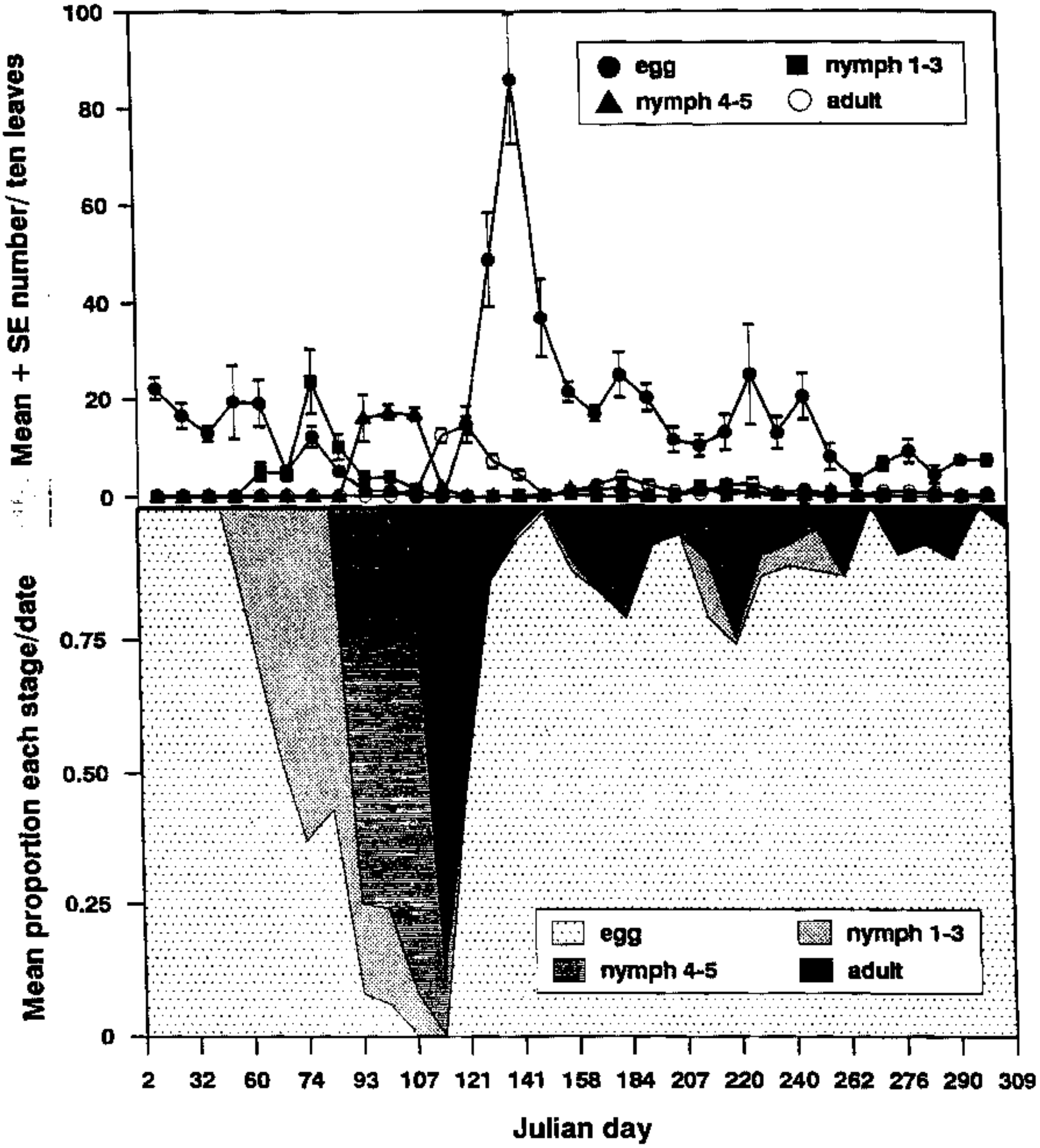

Fig. 2. Seasonal occurrence of immature and adult azalea lace bugs in the landscape at Griffin, Ga., 1990.

eggs to the population. Subsequent generations were, therefore, less well defined than the first. However, when the data are presented graphically as the proportion of individuals in each age category of total individuals observed on a particular date (Fig. 1 and 2), the progressive development of each generation becomes apparent.

Development of the fourth generation was particularly prolonged. This may be at least partially explained by our earlier observation that azalea lace bug is adversely affected by the high temperatures typical of that time period. Adults of the final generation matured by the end of September (Julian day 273) and were occasionally still found in December (Julian day 335). Eggs deposited during October or later overwintered.

Degree-day accumulations through 30 September for 1989 and 1990 at Griffin, Ga., were compared with the physiological time required to complete a generation: 394 DD for develop-

Table 3. Predicted versus observed dates of occurrence of *S. pyrioides* population events during the first generation

Event	Predicted/observed Julian day of occurrence[a]	
	1989	1990
1	74/ 75	72/ 74
2	102/104	107/107
3	117/116	119/114

[a] Event 1, emergence from overwintering eggs, 213 DD above 10.2°C, event 2, development of first generation from egg to third instar, 301 DD above 11.2°C; event 3, maturation of first generation, 394 DD above 11.2°C.

ment and an additional 75-DD preoviposition period (estimated from data presented by Neal & Douglass 1988). During 1989 and 1990, 2,090.8 and 2,208.4 DD above 11.2°C had accumulated, respectively. Thermal unit requirements predict development of four generations as was observed in the landscape (Fig. 1 and 2). When degree-day accumulations for Griffin were initiated on 1 December of the previous year, using the determined base temperatures (Table 2) and an upper limit of 31°C, the predicted date of occurrence for selected first-generation population events compared closely with the observed timing of occurrence in the landscape (Table 3, Fig. 1 and 2). Maturation of subsequent generations is less closely predicted.

During 1989, the second, third, and fourth generations were predicted to mature by Julian days 172, 207, and 243, respectively. Based on observed population trends apparent in Fig. 1, maturation of the second and third generations was closely predicted. That of the fourth generation, however, was delayed in comparison with the predicted value. During 1990, the second, third, and fourth generations were predicted to mature on Julian days 169, 203, and 237, respectively. Again, late-season events observed in the landscape were delayed in comparison with predictions. The phenological status of late-season populations may be less closely predicted because generations overlap subsequent to the development of the first generation. Additionally, the adverse effects of higher temperatures on development may limit the use of the present model to predict late-season activity. It is prediction of events in the first generation, however, that is of greatest importance in azalea lace bug management efforts.

Field Phenology Studies of Parasitism. The eggs of *S. pyrioides* revealed the presence of a parasitoid when collected in Tift, Spalding, and Clarke counties, which range from southern to northern Georgia, respectively. To our knowledge, parasitism of the eggs of *S. pyrioides* has not been previously reported. Sites 2, 3, and 4 were initially heavily infested with azalea lace bugs. For unknown reasons, the population at site 4 declined drastically during the season. The parasitoids collected from sites 2 and 3 were subsequently identified as belonging to *Anagrus* (Haliday) (Hymenoptera: Mymaridae), a genus that attacks the egg stage of the azalea lace bug. *Anagrus* parasitoids develop in the eggs of various insect species, primarily Homoptera, Hemiptera, and Lepidoptera (Peck 1963, Huber 1986). *Anagrus takeyanus* reduced overwintering egg populations of *S. takeyai* by an estimated 35% in Connecticut (Dunbar 1974).

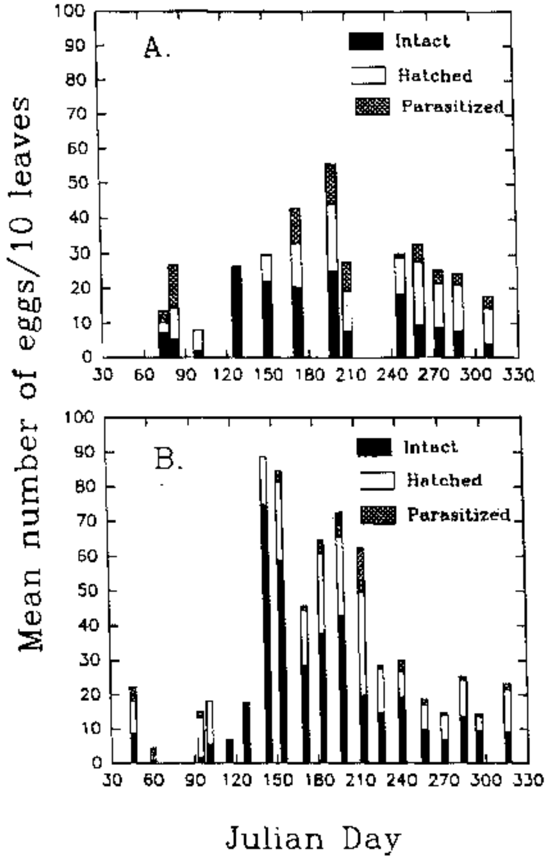

Fig. 3. Activity of the egg parasitoid *Anagrus* sp. (A) At site 2, Spalding County. (B) At site 3, Clarke County.

Leaves collected throughout the 1990 season contained large numbers of eggs but relatively few nymphs and adults. This may have been a consequence of parasitism. Parasitism of eggs varied by date and location (Fig. 3) and ranged from 3.3 to 48.8%. Typically, uneclosed eggs are present throughout the season as females from several overlapping generations oviposit (Fig. 1 and 2). Overlapping phenology of susceptible host stages and parasitoids makes it difficult to relate percentage parasitism to generational parasitism (Van Driesche 1983, Van Driesche et al. 1991).

When parasitism in this study was measured as the ratio of eggs from which parasitoids had emerged to the total unhatched, hatched, and parasitized eggs, the greatest mortality from parasitoids occurred in the overwintered eggs at both sites 2 and 3 (Fig. 3). Midseason peaks in eggs from which parasitoids had emerged suggest another period of increased activity.

Discussion

The predictive model presented here permits forecasting azalea lace bug phenology in the landscape. Ability to predict development of early-season populations of azalea lace bug allows optimal focus of control measures aimed at this pest. Such predictive tools facilitate monitoring pest activity and reduce unnecessary insecticide applications. Degree-days can be used to determine when to concentrate sampling efforts to identify a stage vulnerable to control efforts, resulting in further reduction in costs and damage from those pests. Although the azalea lace bug was apparently introduced into this country largely without natural enemies, the previously reported association of a predaceous mirid (Henry et al. 1986, Neal et al. 1991) and the present report of parasitism underscore the need for consideration of natural enemies in the development of decision-making guidelines.

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