Influence of Temperature on Development of Hemlock Woolly Adelgid (Homoptera: Adelgidae) Progrediens[1]

Scott M. Salom,[2] Alexei A. Sharov, Warren T. Mays and David R. Gray[3]

Department of Entomology, Virginia Polytechnic & State University, 216 Price Hall, Blacksburg, VA 24061-0319; Canadian Forestry Service, Atlantic Forestry Centre P. O. Box 4000, Fredericton, N.B. E3B 5P7 Canada

J. Entomol. Sci. 37(2): 166-176 (April 2002)

Abstract There are three generations of hemlock woolly adelgid, *Adelges tsugae* Annand, that develop on the secondary host *Tsuga* spp. Two of these generations, the progrediens and sexupara, are present concurrently in the spring. Sistens are present from early summer until the following spring. Constant temperature studies were conducted to quantify the influence of temperature on hemlock woolly adelgid progrediens development and to develop a degree-day model. Progrediens development in the field also was sampled to test the accuracy of the model. Hemlock woolly adelgid progrediens developed at temperatures ranging from 4 to 22°C. Duration of first-instar progrediens was less dependent on temperature than in the other nymphal stages and may have been a result of the difficulty in determining the median point of settled first-instar nymphs and the inability to distinguish progrediens from sexuparae at this stage. Duration of development from second stadium to adult was highly dependent on temperature. Using this range of progrediens stages, it was determined that the low temperature threshold was 3.9°C and requires 222 degree-days to reach the adult stage. The number of degree-days needed to complete development in the field ranged from 110 to 123% of degree-days required to complete development in the laboratory.

Key Words Adelgidae, *Tsuga* spp., temperature, development, degree-days, development rate

The hemlock woolly adelgid, *Adelges tsugae* Annand (Homoptera: Adelgidae), is an introduced pest of two hemlock species in the eastern U.S.: eastern hemlock, *Tsuga canadensis* (L.), and Carolina hemlock, *T. caroliniana* Engelm. For 30 years following its inadvertent introduction into Richmond, VA, hemlock woolly adelgid spread slowly and was considered an occasional pest of ornamental hemlocks. However, in the mid-1980's, its rate of spread increased, and within a few years the insect was established along the eastern seaboard from Virginia to Connecticut (Souto et al. 1996). With the spread came a coincident increase in hemlock woolly adelgid population density. The densities reached levels high enough to kill trees within a few years. Subsequently, large numbers of hemlock trees began dying throughout the range of hemlock woolly adelgid. Hemlock woolly adelgid continues to spread south, west, and north within the range of eastern hemlock at a rate of 16 to 24 km per year,

[1]Received 25 June 2001; accepted for publication 06 August 2001.

[2]To whom offprint requests are to be addresses (email: salom@vt.edu).

[3]Canadian Forestry Service.

but this rate is highly variable (Suoto et al. 1996). Currently, the range extends to Massachusetts in the north, eastern West Virginia in the west, and western North Carolina in the south (USDA Forest Service 2000).

Pesticides are available and effective against the hemlock woolly adelgid on ornamentals (McClure 1991, 1995, Steward and Horner 1994), but are not practical for use in the forest. Hemlocks are often associated with riparian habitats that are sensitive and often off limits to traditional insecticides. Additionally, the scattered location of hemlocks in the forest, their inaccessible canopy that is often below the canopy of more shade intolerant dominant tree species, and the high cost of individual tree treatments, makes this pest an unsuitable candidate for chemical control options in the forest. Efforts are now focused on identifying, evaluating, and releasing host-specific predators of hemlock woolly adelgid collected in Japan (Cheah and McClure 1996, 1998), China (Montgomery et al. 2000) and western North America (Zilahi-Balogh et al. 2000).

Efforts to quantify the phenology of hemlock woolly adelgid lifestages mirror similar efforts currently being carried out with its predators *Pseudoscymnus tsugae* Sasaji & McClure (Coleoptera: Coccinellidae) (Cheah and McClure 2000) and *Laricobius nigrinus* (Coleoptera: Derodontidae) (Zilhai-Balogh et al., unpub.). Comparing phenologies and more specifically degree-day requirements between predators and their prey help determine the suitability of predators as biological control agents.

The life history of hemlock woolly adelgid was first studied in Connecticut (McClure 1987) and subsequently in Virginia (Gray and Salom 1996). Two apterous stages complete development on hemlock: progrediens, from March/April to June, and sistens, from June until the following March/April. A winged lifestage, sexupara, develops simultaneously with progrediens. Sexupara adults fly in search of spruce, *Picea* spp., on which to oviposit (McClure 1989). Sexupara produce progeny called sexuales, which have not been observed to successfully complete development on spruce in North America.

The life history of progrediens has been studied extensively in the field (McClure 1987, 1991, Gray and Salom 1996). Progrediens stages largely overlap. Eggs can be found in woolly ovisacs from March through May. Each of four nymphal stages can be found between April and May. Adults can begin ovipositing in May. Little has been done to quantify the effects of temperature on progrediens development. Gray and Salom (1996) monitored temperature at sample sites, but no attempt was made to relate development to temperature, in part because field sampling was too infrequent (2 to 3 wk intervals) for the relatively short progrediens developmental period. It was necessary to conduct lab and field studies that measured development more frequently. This paper reports on a study in which we evaluated the effect of different constant temperatures on progrediens development, developed a degree-day model, and then tested the model with data collected from the field.

Materials and Methods

Laboratory study. In a preliminary study of progrediens development at different constant temperatures (12, 17, 22, 27, and 32°C), we observed that progrediens did not complete development at 27 and 32°C, indicating that the high temperature threshold for development was >22°C and <27°C. In addition, it did not appear that the low temperature threshold was approached at 12°C. Therefore, we designed a developmental rate study using the constant temperatures of 4, 8, 12, 14.5, 17, 19.5, and 22°C.

Populations of hemlock woolly adelgid have been maintained continuously on seedlings in our laboratory by infesting 2-yr-old hemlock seedlings with infested hemlock twigs. The infested twigs were attached to seedlings when progrediens and sexupara crawlers began to emerge from sistens ovisacs in early spring. This technique works well, yet we have found that it takes about 1 yr for seedlings to become heavily infested. The seedlings used in this study had been infested for 1 yr. Five infested seedlings were placed in each chamber held at one of the constant temperatures and at 70% RH. One chamber was used for each temperature. The chambers were Percival® models I-30BLL and I-35LL (both ± 0.5°C). Hobo® (Onset Computer Corp., Bourne, MA) temperature and RH data recorders were used in each chamber. They were tested against mercury thermometers prior to their use, where readings from both were determined to be virtually identical. Temperature data were collected at 15 min intervals throughout the duration of the experiment. The seedlings were sampled weekly at 4 and 8°C and twice/wk at 12 to 22°C. A higher frequency of sampling was required at the higher temperatures to account for shorter developmental time of the progredients. When approximately 50% of crawlers settled as first instars, data collection on lifestage duration commenced. This starting point was based on weighted means from the frequency distribution of sistens eggs, crawlers, first-instar progrediens and sexupara, and second-instar progrediens present.

Progrediens and sexupara develop simultaneously on *Tsuga* spp. Both life forms are indistinguishable until they molt to the second stadium (McClure 1989). Therefore, measures of first instars included both life forms. Life forms of second and third instars were distinguished by the presence of a suture between the pro- and meso-thoracic dorsal plate for sexupara, not present on progrediens (McClure 1989). Fourth instars were easily distinguished with the presence of wing buds found only on sexupara.

Hemlock woolly adelgid colonizes the base of needles at densities sometimes as high as two to three per needle, making it virtually impossible to follow individuals through complete development. Individual marking of these minute insects is not possible. Because they are on live plants it would also be very difficult to record their developmental stage with a microscope. Therefore, we decided to destructively sample the seedlings and obtain progrediens stage frequency distributions for each sample period (Gray and Salom 1996). Twigs from each of the five seedlings per temperature were removed every sample period, and the nymphal stage of the first 30 progrediens encountered from the twigs of each seedling was recorded, resulting in five subsamples per temperature for each sample period.

Field study. Progrediens development in the field was observed in two second-growth hemlock woolly adelgid-infested hemlock stands located 10 to 22 km west of Blacksburg, VA, in the New River Ranger District of the Jefferson and Washington National Forest. The Poverty Hollow plot was located on a southeast facing slope, where understory hemlock trees were a small component of a predominately white oak, *Quercus alba* L., forest. A second plot, at Craig Creek, was located on a south-facing slope, where the hemlock was a similarly small component of a predominately white pine, *Pinus strobus* L. forest. The elevation at both plots was approximately 640 m.

In each plot, two 25-cm twig samples infested with hemlock woolly adelgid were clipped twice per week from the lower crown of three randomly chosen trees. The sample trees were healthy, yet infested with hemlock woolly adelgid. It was clear that the infestation cycle was in its early stage at both sites, as the trees did not yet show any signs of decline from adelgid feeding. The density of adelgids on twigs was quite variable, ranging from <1 to 7 per cm. This is typical when trees first become infested. The twigs sampled were branch tips of previous years' growth. Samples were taken from the same trees at each subsequent visit. Sampling commenced on 22 March 1999, when eggs were being oviposited by sistens adults, and continued until 14 June 1999, when progrediens were no longer present. The twigs were transported to the laboratory and stored at 3°C for no longer than 4 d. At this time, the developmental stages of the first 50 individuals encountered on a twig sample, starting from the distal end, were recorded.

Because some eggs continue to be oviposited as older eggs hatch, we attempted to estimate the date when 50% of the crawlers had settled as first-instar progrediens, using a frequency distribution analysis of the different lifestages described above in the laboratory study. The date at both plots was determined to be 23 April.

Temperature was recorded in both plots every 15 min for the duration of the study using HOBO® Pro Recorders (Onset Computer Corp., Bourne, MA) calibrated and verified with mercury thermometers. One recorder was hung from a lower branch of one of the sample trees in each plot. The sample trees were no farther than 25 m apart from each other. Mean temperatures for each day were determined by averaging all 96 temperature readings taken.

Data analysis. Analysis of cumulative numbers (or proportion) of individuals that enter a particular stage is a commonly-used method for studying insect phenology (Régnière 1984, Sharov 1993, Allen et al. 1995, Davis et al. 1996). These cumulative curves are modeled with either the logistic (Allen et al. 1995) or Weibull (Wagner et al. 1984, Casagrande et al. 1987) functions. In this study we used the logistic function because it is simpler than the Weibull function and gave the same estimates of the median time for entering a particular stage. For each sampling date *t*, we determined the cumulative proportion $p_i(t)$ of the hemlock woolly adelgid population that had reached a specific stage i by this date. Developmental stages were $i = 1$ for settled first-instar progrediens, i = 2-4 for second- to fourth-instar progrediens, and $i = 5$ for adults. Functions $p_i(t)$ were approximated by logistic equations, $x_i(t) = [1 + \exp(-a_i(x - b_i))]^{-1}$, where a_i is the slope and b_i is the median point, using a non-linear regression method (least square estimation). Equations were developed for each temperature. Thus, stage frequencies at various temperatures were not compared directly. Instead we compared median times for stage change that were estimated from the logistic model. The duration (days) of the i-th stage T_i was calculated as a distance, $T_i = b_{1+1} - b_i$ between median points of logistic curves for stage i and the following stage $i + 1$ (Fig. 1). The rate of development was then estimated as $1/T_i$ day.$^{-1}$

A linear regression of developmental rate vs temperature was used to estimate the low temperature developmental threshold and the number of degree-days needed for hemlock woolly adelgid progrediens to complete development. Degree-days are based on the concept of a "thermal constant" first described by Sanderson and Durham (1910), and can be calculated from the equation: DD = 1/b, where b is the slope of the regression equation of developmental rate vs. temperature (Shelford 1927).

We averaged development rates for five plants in each chamber and estimated non-linear regressions using these averages. The degree-day model developed from lab studies was compared to field data. The model was tested by summing, at 15 min

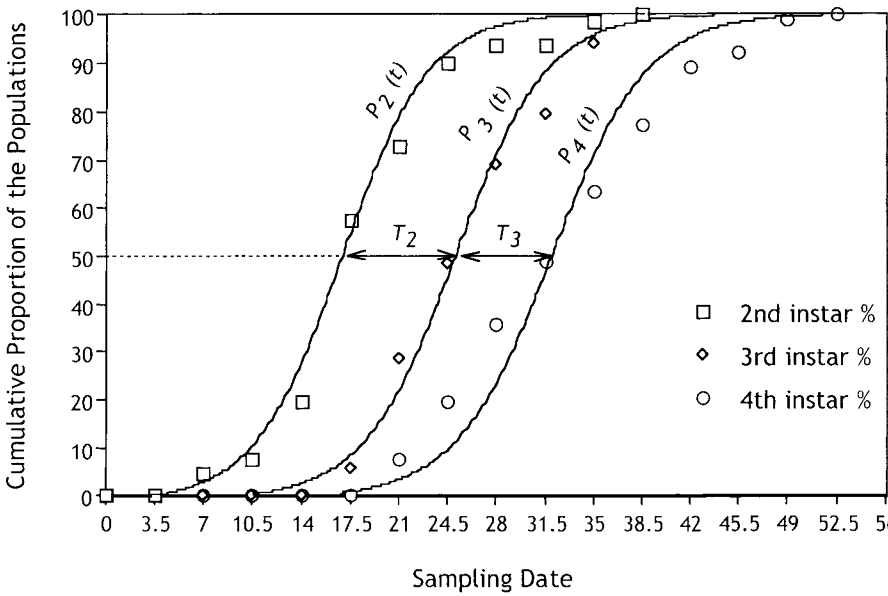

Fig. 1. Cumulative distributions of development for three hemlock woolly adelgid progrediens instars at 17°C, with a demonstration of how median developmental times were calculated for each instar.

intervals, the number of degree-days above the low temperature threshold at each plot, as recorded by our temperature recorders. Degree-days were summed from the time that 50% of first instars had settled until 50% of fourth instars had molted to adult. The number of degree-days accumulated in the field was compared to the number of degree-days estimated from the laboratory experiment.

Results

Laboratory study (first instars to adult). Hemlock woolly adelgid progrediens completed development from settled first instars to adults at all temperatures from 4 to 22°C. A significant positive linear relationship (R^2 = 0.9602; $F_{1,5}$ = 120.54; P = 0.0001) was observed between developmental rate and temperature (Fig. 2A). The low temperature threshold was −3.8°C, and the number of degree-days required for development from first instars to adults was 1250. Developmental rate dropped expectedly as temperature decreased to 8°C, yet did not drop further at 4°C.

The developmental time for hemlock woolly adelgid progrediens ranged from 147 d at 4°C to 52 d at 22°C (Table 1). The first instars had similar developmental times at 4 and 8°C, and although developmental times were significantly different for second instars, at the same temperatures, the differences were not nearly as great as at higher temperatures. Developmental time did decrease significantly at higher temperatures, yet not to the same extent as subsequent instars (second to fourth) (Table 1). For example, developmental time dropped from 53 to 41 d between 4 and 22°C for first instars and from 56 to 5 d between 4 and 22°C for second instars. As a result, we

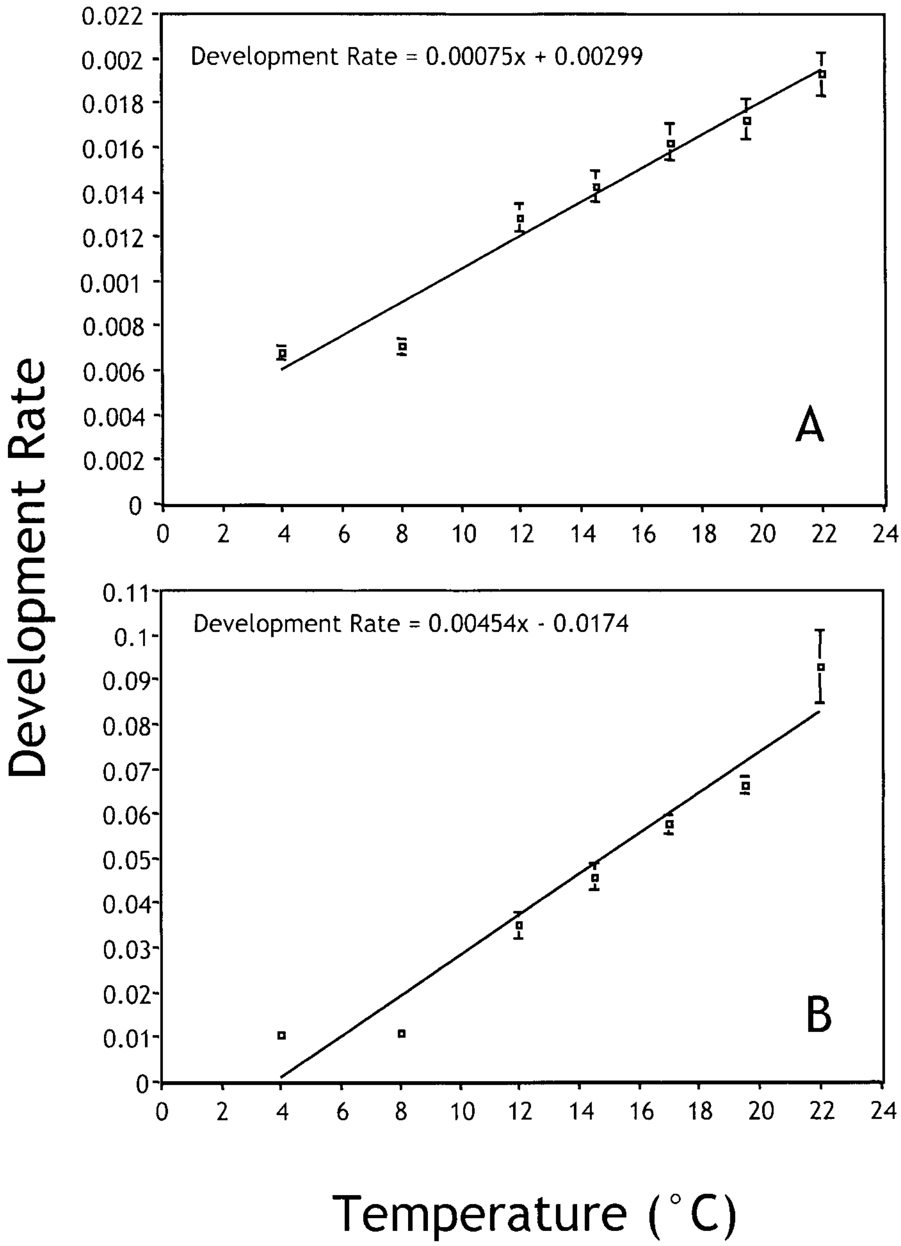

Fig. 2. Hemlock woolly adelgid progrediens development rate at constant temperatures for (A) first-instar to adult and (B) second-instar to adult.

Table 1. Mean values of developmental time estimates (days) of HWA progrediens nymphs in the lab under constant temperatures*

Temperature (°C)	1st instar to adult (S.E.M.)	2nd instar to adult (S.E.M.)	Duration of 1st instar (S.E.M.)	Duration of 2nd instar (S.E.M.)	Duration of 3rd instar (S.E.M.)	Duration of 4th instar (S.E.M.)
4	147.28 (0.49)	94.04 (1.16)	53.24 (1.12) a**	55.47 (1.41) a	24.75 (1.28) a	13.69 (1.28) ab
8	141.61 (1.25)	90.99 (2.35)	50.62 (1.26) ab	46.33 (1.59) b	27.42 (0.87) a	17.14 (1.08) a
12	77.69 (1.00)	28.71 (1.33)	48.99 (0.51) b	7.49 (0.46) c	8.92 (0.42) b	11.55 (1.23) bc
14.5	70.08 (0.99)	22.02 (0.99)	48.06 (0.38) b	4.69 (0.34) c	7.43 (0.73) bc	10.19 (1.06) bc
17	61.51 (0.31)	17.38 (0.39)	44.12 (0.42) c	4.98 (0.51) c	4.54 (0.56) cd	8.57 (0.30) c
19.5	57.88 (0.35)	15.08 (0.20)	42.80 (0.41) c	3.84 (0.77) c	4.01 (0.60) d	7.23 (0.31) cd
22	51.71 (1.25)	10.85 (0.41)	40.87 (0.50) c	5.26 (0.33) c	1.90 (0.13) d	3.69 (0.30) d

* Means based on median values from 5 replicates calculated using a logistic model with least squared estimation.
** Values within column followed by different letters are significantly different (Tukey-Kramer HSD; $P \leq 0.05$).

decided to analyze the development rate of a narrower range of lifestages. In addition to evaluating the range between first-instar progrediens and adults, we evaluated the range between second-instar progrediens and adults.

Laboratory study (second-instar progrediens to adult). A significant positive linear relationship was observed between developmental rate and temperature (R^2 = 0.9429; $F_{1,5}$ = 85.56; P = 0.0003) (Fig. 2B). The low temperature threshold at which development would cease was 3.9°C. The number of degree-days required for development from second-instar progrediens to adults was 222.

Field study (first-instar progrediens to adult). Temperatures at Craig Creek and Poverty Hollow were similar during the sample period. The mean daily minimum and maximum temperature at Craig Creek was 6.8°C (range = 5.4 to 9.4°C) and 22.6°C (range = 16.0 to 30.7°C), respectively. At Poverty Hollow, the mean daily minimum and maximum temperature was 6.7°C (range = 5.0 to 10.6°C) and 22.8°C (range = 14.9 to 31.5°C), respectively.

Mean duration of progrediens development did not differ significantly between sites (Table 2), averaging 44.8 d at Poverty Hollow and 46.5 days at Craig Creek. The number of degree days needed to complete development in the field was only from 64 (Poverty Hollow) to 68% (Craig Creek) of the number of degree-days required to complete development in the laboratory (Table 2). No differences were found between either field site.

Field study (second-instar nymph to adult). Mean duration of progrediens development from second-instar nymphs to adults did not differ significantly among sites (Table 2), averaging 17.5 d at Poverty Hollow and 19.4 d at Craig Creek. The number of degree days needed to complete development in the field ranged from 110 (Pov-

Table 2. Mean duration and degree-day accumulation of field developing hemlock woolly adelgid progrediens using laboratory-derived linear regression equations

Life-stages	Location	Mean duration (d ± S.D.)*	Degree-day accumulation	Proportion to linear models (±S.D.)†
First-instar-Adult	Poverty Hollow	44.77 ± 1.33 a**	828.18	0.641 ± 0.022 a
	Craig Creek	46.50 ± 1.73 a	893.90	0.677 ± 0.038 a
Second-instar-Adult	Poverty Hollow	17.47 ± 0.35 a	241.99	1.096 ± 0.061 a
	Craig Creek	19.40 ± 2.34 a	264.34	1.230 ± 0.172 a

* Mean values calculated from median estimates of logistic equations for each tree.

** Numbers in columns, for each life stage measure, followed by different letters are significantly different (ANOVA; $P \leq 0.05$).

† See Figures 2A and 2B for equations calculated for first-instar to adult, and second-instar to adult lifestages, respectively.

erty Hollow) to 123% (Craig Creek) of degree-days required to complete development in the laboratory (Table 2). No differences were found between either field site.

Discussion

This paper reports the first effort to quantify the effect of temperature on hemlock woolly adelgid development. Evaluation of the laboratory data showed that first-instar development was not affected by temperature nearly as much as was development in the other instars. This may have been due to the difficulty in accurately estimating the median date when a sampled population of progrediens entered first stadium. The problem associated with this is due to the many overlapping stages (progrediens eggs, crawlers, first, and second instars) that are present on a twig sample at any one time (McClure 1987, Gray and Salom 1996). In addition, indistinguishable first-instar sexuparae were likely counted with first-instar progrediens. Thus, it is not surprising that the degree-day model of hemlock woolly adelgid development in the laboratory for first instars to adults did not work well for predicting phenology in the field.

When the range of life stages used to create a degree-day model was narrowed to second-instar progrediens to adult, the model's prediction of progrediens development in the field improved considerably. This indicates, in part, greater accuracy in determining occurrence of the median point for second-instars and in counting only progrediens, which can be distinguished from sexuparae at this and later stages (McClure 1989).

The estimate for low temperature developmental threshold differed drastically depending on the range of progrediens stages sampled. For the range of first-instars progrediens to adult, the estimate was −3.8°C and for the range of second-instars progrediens to adult, the estimate was a 3.9°C. We believe the latter estimate is more realistic than the former one. Gilbert and Raworth (1996) provide data from 36 studies where both the development thresholds and emergence dates were known. They showed that the developmental thresholds are roughly equal to the lowest daily average field temperatures to which the insects are exposed. The 3.9°C threshold we calculated is close to our lowest daily average temperature of 5°C that was observed at Poverty Hollow.

From our preliminary experiments, we know that progrediens will not complete development at a constant temperature of 27°C, yet will at 22°C. This was not addressed further in this study and more research is needed to more precisely estimate the high temperature development threshold.

At this time we cannot explain why we were unable to detect any difference in development time of progrediens between 4 and 8°C. If we remove the 4°C development data from the second instar to adult model, the low temperature development threshold increases from 3.9 to 6.0°C. Despite this change, the model predictions closely approximate data at normal temperatures (from 12 to 22°C). It is clear, however, that further work is also needed to more precisely estimate the low temperature development threshold.

Eastern hemlock is generally restricted to regions with cool humid climates (Burns and Honkala 1990). Insects associated with these trees would need to be similarly adapted. McClure (1996) suggested that this insect is highly adapted to northern climates and high elevation settings. This was further supported by Parker et al. (1998) when they demonstrated from cold hardy tests that hemlock woolly adelgid sistens could survive temperatures as low as −30°C for 24 h and could likely survive the winters in southern Maine, Vermont and New Hampshire. Thus, it should not be surprising that temperature range for progrediens development is shifted toward the cooler end of the spectrum for insects living in a temperate climate. Another introduced adelgid, balsam woolly adelgid, *Adelges piceae* (Ratzeburg), is found throughout the range of *Abies* spp., which extends further north than *Tsuga* spp. (Hain 1988). Despite their presence in a more northerly climate than currently occupied by hemlock woolly adelgid, *A. piceae* neosistens eggs appear to be adapted to slightly warmer temperatures than hemlock woolly adelgid progrediens nymphs, with a low developmental threshold between 5 and 7°C and a high developmental threshold of approximately 30°C (Amman 1968). Other evidence that both these adelgid species are cold adapted is that they both have life stages that go dormant in the summer, apparently to avoid heat and water stress.

The data reported in this paper provide a basis for future efforts that should focus on the development of degree-day models for progrediens eggs, crawlers, and settled first instars. However, even without these data, prediction of progrediens development to adult can now be accurately made starting with the median occurrence of second-instar progrediens. Once progrediens oviposit, it is less than 2 wks before sistens crawlers settle as first instars and then go into aestivation (Gray and Salom 1996). At that time, treatment either by chemicals or by release of predators is not suitable or effective until sistens break diapause.

Acknowledgments

We thank Q. McClellan for developing the procedure for infesting hemlock seedlings, and K. S. Shields, M. McClure and G. Zilahi-Balogh and two anonymous reviewers for reviewing earlier versions of this manuscript. Funding for this research was provided by USDA Forest Service, Forest Health Technology Enterprise Team Cooperative Agreement #42-787 to SMS and DRG.

References Cited

Allen, J. C., Y. Yang and J. L. Knapp. 1995. Temperature effects on development and fecundity of the citrus rust mite (Acari: Eriophyidae). Environ Entomol. 24: 996-1004.

Amman, G. D. 1968. Effects of temperature and humidity on development and hatching of eggs of *Adelges piceae.* Ann. Entomol. Soc. Amer. 61: 1606-1611.

Burns, R. M. and B. H. Honkala (eds). 1990. Silvics of North America. Vol. 1, Conifers. USDA For. Serv. Agric. Handbook 654.

Casagrande, R. A., P. A. Logan and W. E. Wallner. 1987. Phenological model for gypsy moth, *Lymantria dispar* (Lepidoptera: Lymantriidae), larvae and pupae. Environ. Entomol. 16: 556-562.

Cheah, A. S-J. and M. S. McClure. 1996. Exotic natural enemies of *Adelges tsugae* and their prospect for biological control, Pp. 103-112. *In* Salom, S. M., T. C. Tigner and R. C. Reardon [eds.], Proceedings of the first hemlock woolly adelgid review. USDA For. Serv. FHTET 96-10.

1998. Life history and development and *Pseudoscymnus tsugae* (Coleoptera: Coccinellidae), a new predator of the hemlock woolly adelgid (Homoptera: Adelgidae). Environ. Entomol. 27: 1531-1536.

2000. Seasonal synchrony of life cycles between the exotic predator, *Pseudoscymnus tsugae* (Coleoptera: Coccinellidae) and its prey, the hemlock woolly adelgid *Adelges tsugae* (Homoptera: Adelgidae). Agric. and For. Entomol. 2: 241-251.

Davis, P. M., N. Brenes and L. L. Allee. 1996. Temperature dependent models to predict regional differences in corn rootworm (Coleoptera: Chrysomelidae) phenology. Environ Entomol. 25: 767-775.

Gilbert, N. and D. A. Raworth. 1996. Insects and temperature - a general theory. Can. Entomol. 128: 1-13.

Gray, D. R. and S. M. Salom. 1996. Biology of the hemlock woolly adelgid in the southern Appalachians, Pp. 26-35. *In* S. M. Salom, T. C. Tigner and R. C. Reardon [eds.], Proceedings of the First Hemlock Woolly Adelgid Review. USDA For. Serv. FHTET 96-10.

Hain, F. P. 1988. The balsam woolly adelgid in North America, Pp. 87-109. *In* A. A. Berryman [ed.], Dynamics of Forest Insect Populations. Plenum Publishing Co., New York.

McClure, M. S. 1987. Biology and control of hemlock woolly adelgid. Conn. Agric. Exp. Sta. Bull. No. 851.

1989. Evidence of a polymorphic life cycle in the hemlock woolly adelgid, *Adelges tsugae* (Homoptera: Adelgidae). Ann. Entomol. Soc. Am. 82: 50-54.

1991. Pesticides will protect ornamentals from hemlock woolly adelgid. Frontiers of Plant Sci. 44: 1-3.

1995. Managing hemlock woolly adelgid in ornamental landscapes. Conn. Ag. Exp. Sta., Bull. No 925.

1996. Biology of *Adelges tsugae* and its potential for spread in the northeastern United States, Pp. 16-25. *In* S. M. Salom, T. C. Tigner and R. C. Reardon [eds.], Proceedings of the First Hemlock Woolly Adelgid Review. USDA For. Serv. FHTET 96-10.

Montgomery, M. E., D. Yao and H. Wang. 2000. Chinese Coccinellidae for biological control of the hemlock woolly adelgid: description of native habitat, Pp. 97-102. *In* K. A. McManus, K. S. Shields and D. R. Souto [eds.], Proc. of Symposium on Sustainable Management of Hemlock Ecosystems in Eastern North America. USDA For. Serv. Gen Tech. Rept. NE-267.

Parker, B. L., M. Skinner, S. Gouli, T. Ashikaga and H. B. Teillon. 1998. Survival of hemlock woolly adelgid (Homoptera: Adelgidae) at low temperatures. For. Sci. 44: 414-420.

Régnière, J. 1984. A method for describing and using variability in development rates for the simulation of insect phenology. Can. Entomol. 116: 1367-1376.

Sanderson, E. D. and N. H. Durham. 1910. The relation of temperature to growth of insects. J. Econ. Entomol. 3: 113-139.

Sharov, A. A. 1993. Biology and population dynamics of the common pine sawfly *Diprion pini* L. in the USSR, Pp. 409-429. *In* M. R. Wagner and K. Raffa [eds.], Sawfly Adaptations to Woody Plants. Academic Press, San Diego.

Shelford, V. E. 1927. An experimental investigation of the relations of codling moth to weather and climate. Il. Nat. Hist. Surv. 16: 311-440.

Souto, D., T. Luther and B. Chianese. 1996. Past and current status of hemlock woolly adelgid in eastern and Carolina hemlock stands, Pp. 9-15. *In* Salom, S. M., T. C. Tigner and R. C. Reardon [eds.], Proceedings of the First Hemlock Woolly Adelgid Review. USDA For. Serv. FHTET 96-10.

Steward V. B. and T. A. Horner. 1994. Control of hemlock woolly adelgid using soil injections of systemic insecticides. J. Aboric. 20: 287-288.

USDA Forest Service. 2000. Hemlock woolly adelgid distribution. (http://www.fs.fed.us/na/morgantown/fhp/hwa/hwa11201.jpg).

Wagner, T. L., H.-I. Wu, P. J. H. Sharpe and R. N. Coulson. 1984. Modeling distributions of insect development time: a literature review and application of the Weibull function. Ann. Entomol. Soc. Amer. 77: 475-487.

Zilahi-Balogh, G. M. G., S. M. Salom and L. T. Kok. 2000. Host suitability and preference of *Laricobius nigrinus* (Coleoptera: Derodontidae): a predator of *Adelges tsugae* Annand (Homoptera: Adelgidae), Pp. 110. *In* K. A. McManus, K. S. Shields and D. R. Souto [eds.], Proc. of Symposium on Sustainable Management of Hemlock Ecosystems in Eastern North America. USDA For. Serv. Gen Tech. Rept. NE-267.

Zilahi-Balogh, G. M. G., S. M. Salom and L. T. Kok. 2001. Development and reproductive biology of *Laricobius nigrinus* Fender (Coleoptera: Derodontidae), a potential biological control agent of the hemlock woolly adelgid, *Adelges tsugae* (Homoptera: Adelgidae). Biocontrol. In Press.