Phenology of the Hemlock Woolly Adelgid (Hemiptera: Adelgidae) in Northern Georgia[1]

Shimat V. Joseph[2], Albert E. Mayfield III[3], Mark J. Dalusky[4], Christopher Asaro[5] and C. Wayne Berisford[4]

Department of Entomology, University of Georgia, College of Agricultural and Environmental Sciences, 413 Biological Sciences Building, Athens, Georgia 30602

J. Entomol. Sci. 46(4): 315-324 (October 2011)

Abstract Understanding the seasonal phenology of an insect pest in a specific geographic region is essential for optimizing the timing of management actions or research activities. We examined the phenology of hemlock woolly adelgid, *Adelges tsugae* Annand, near the southern limit of the range of eastern hemlock, *Tsuga canadensis* (L.) Carriere, in the Appalachians of northern Georgia, where adelgid phenology has not been previously reported. *Adelges tsugae*-infested hemlock trees were visited at various sites from 2004 - 2007. Two hemlock twigs were collected from each of 3 hemlock trees per site, except during the final 3 months of sampling when 1 twig was collected from each of 3 trees per site. Progrediens adults initiated oviposition by midMay, 2 - 4 weeks earlier than has been reported for more northern parts of the adelgid range. Sistens eggs were present until late-June (2006) or early-July (2004 - 2005). After aestivation, sistens nymphs resumed development by early October. Sistens adults were first found in early January and were present until midMay. Progrediens eggs were noted as early as February (2005 - 2007), were abundant in March and April, and persisted until midMay. Progrediens crawlers were present by early March and occurred throughout the next 2 - 3 months. Progrediens adults were found between midMay and late June. This information may be used to help optimize release of biological control agents to insure proper synchronization with adelgid life stages and to aid in collection of food for predator rearing facilities.

Key Words hemlock woolly adelgid, *Adelges tsugae*, northern Georgia, phenology

The hemlock woolly adelgid, *Adelges tsugae* Annand, is the most serious pest of eastern (*Tsuga canadensis* (L.) Carriere) and Carolina (*T. caroliniana* Engelmann) hemlock and threatens the sustainability of these species in eastern North America. The insect was introduced into Virginia from Japan prior to the mid1950s (Havill et al. 2006) and is now distributed from northern Georgia to southern Maine (USDA Forest Service 2011). *Adelges tsugae* is endemic to western North America where it occurs on western (*Tsuga heterophylla* (Raf.) Sarg.) and mountain (*Tsuga mertensiana* (Bong.) Carr.) hemlock, is not known as a damaging forest pest, and has coevolved with a number of natural enemies (Kohler et al. 2008). As an introduced pest in the

[1]Received 19 April 2011; accepted for publication 11 July 2011.
[2]Address inquiries (email: shimatbug@gmail.com). Current Address: Alson H. Smith, Jr. Agricultural Research and Extension Center, 595 Laurel Grove Road, Winchester, Virginia 22602.
[3]USDA Forest Service, 200 W.T. Weaver Blvd., Asheville, North Carolina 28804.
[4]Department of Entomology, University of Georgia, Athens, Georgia 30602.
[5]Virginia Department of Forestry, 900 Natural Resources Drive, Suite 800, Charlottesville, Virginia 22901.

eastern U.S., however, *A. tsugae* causes decline and mortality of hemlocks over a period of 2 - 12 years, infests all age classes of its host, and causes severe ecological, economic, and aesthetic damage in hemlock-dominated forests, riparian areas and other landscapes (Ward et al. 2004).

In eastern North America, *A. tsugae* has a polymorphic life cycle that includes 2 annual wingless parthenogenic generations (sistens and progrediens) and a winged generation (sexuparae) (McClure 1989). In Connecticut (McClure 1987), adults of the sistens generation oviposit beginning in midFebruary and continue to lay eggs for about 16 wk. Eggs are laid within a spherical, cottony ovisac that covers the adult. These eggs may develop into wingless progrediens or winged sexuparae apparently driven by adelgid density and host nutritional status. In both progrediens and sexuparae, mobile first-instars (crawlers) hatch in late March and June, and the insect develops through 4 nymphal instars, maturing in June. Adult progrediens remain attached to hemlock, produce a cottony ovisac similar to (but smaller than) that of the sistens generation, and lay eggs in June and July. Sistens crawlers hatch from these eggs within a few days, settle onto new growth, begin to feed, and enter summer aestivation. Sistens nymphs break aestivation in early October and progress through 4 instars before maturing to adults by February. The migratory sexuparae either die or lay eggs of a sexual generation on spruce (*Picea* spp.), but completion of this sexual generation has not been observed on any native or common exotic *Picea* spp. in North America. Some adelgids never produce the winged form, and the proportion of sexuparae in the population is highest on heavily-infested trees (McClure 1987, 1989, 1991).

The phenology of *A. tsugae* varies with geographic location and associated climate. For example, in British Columbia, the sistens generation may reach maturity in late October and early November (Zilahi-Balogh et al. 2003), 2 - 3 mo earlier than that reported in Virginia (January-February) (Gray and Salom 1996) and Connecticut (Feb.) (McClure 1989). Sexuparae were not observed by Zilahi-Balogh et al. (2003) in British Columbia despite adelgid densities similar to those observed in eastern populations where sexuparae were produced. In Virginia, progrediens adults and sistens eggs appear earlier (late May-early June) (Gray and Salom 1996, Mausel et al. 2008) than in British Columbia (midlate June) (Zilahi-Balogh et al. 2003) and Connecticut (June-July) (McClure 1989). In recent years, *A. tsugae* has begun to reach the southern extent of the contiguous range of eastern hemlock in northern Georgia, where phenological data on the pest have not been reported.

Knowledge of *A. tsugae* phenology in a given region is very useful to land managers and researchers who wish to choose the best timing for various management actions including (1) the release of biological control agents for proper synchronization with adelgid life stages, (2) monitoring of adelgid populations densities, adelgid fecundity and predator establishment, and (3) collection of appropriate adelgid life stages for use as food in predator rearing facilities. In this paper we present the phenology of the hemlock woolly adelgid near the southern extent of its North American range in northern Georgia.

Materials and Methods

Life stages of *A. tsugae* were monitored by collecting infested branch tips of eastern hemlock from several sites in northern Georgia on a weekly basis from April 2004 to June 2007. In 2004 - 2005, samples were consistently collected from the same 3 sites (Sites 1 - 3, Fig. 1, Table 1) on each sampling date throughout the year. In

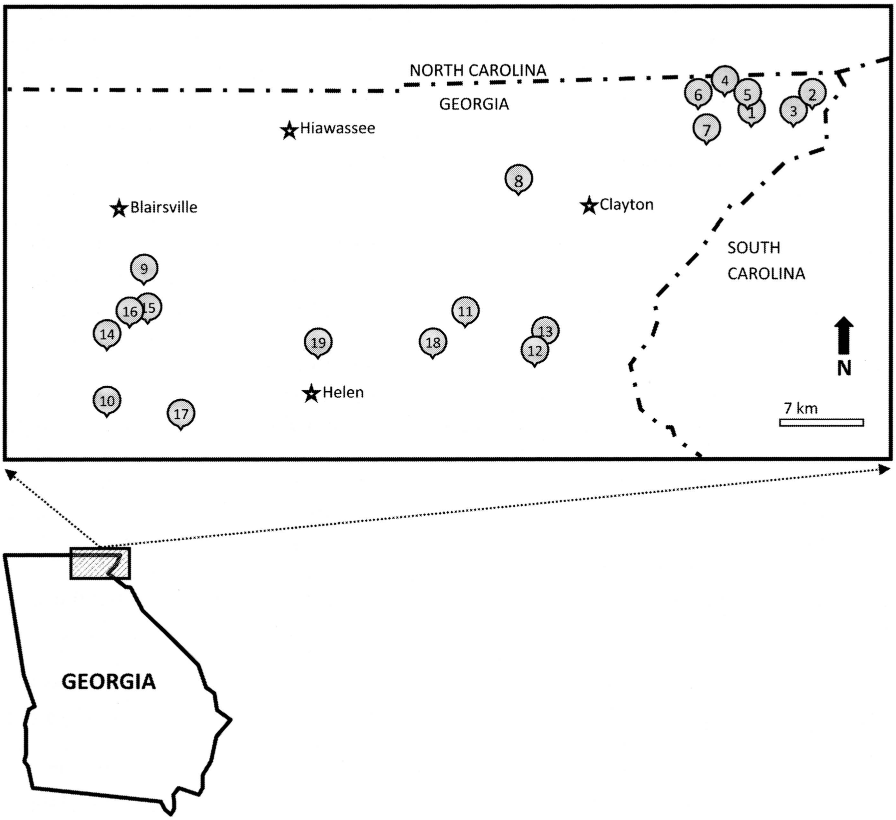

Fig. 1. Sample locations for hemlock woolly adelgid phenology data in 2004 - 2005 (sites 1 - 3) and 2006 - 2007 (sites 1, and 4 - 19) in northern Georgia, USA. Stars indicate local towns.

2006 - 2007, samples were collected from 2 sites per sampling date. In 2006 - 2007, the primary purpose of the data collection was to monitor presence of *A. tsugae* life stages across a range of sites and determine the best timing for release of biological control predators from a management standpoint. The 2 sites visited per sampling date varied throughout the year and included 17 sites (sites 1 and 4 - 19, Fig. 1, Table 1). Thus, the data summaries for 2006 - 2007 should be viewed as an average representation of *A. tsugae* phenology for northern Georgia, rather than a continuous record of phenology data from one or more sites. In all years, 2 twigs were collected from each of 3 hemlock trees per site, totaling 6 samples per site. Collections were reduced to 3 samples per site (1 twig from each of 3 trees) for the period, 21 March 2007 - 14 June 2007. Sample trees were ≥ 3.6 m tall, ≥ 5 cm in diam at breast height (DBH), lacked notable decline symptoms and exhibited new growth. Sample twigs varied in length but were typically 10 cm long, comprised of the most recent growth flush, and were infested with *A. tsugae*. Twigs were collected from 3 - 6 m high in the crown using a pole pruner. Collected twigs were returned to the laboratory, and number of adults,

Table 1. Sample locations for hemlock woolly adelgid phenology data in 2004 - 2005 (sites 1 - 3) and 2006 - 2007 (sites 1, and 4 - 19) in northern Georgia, USA. Latitude and longitude values are estimated from maps and are approximate.

Site #	Site Name	Latitude (N)	Longitude (W)
1	Overflow Creek	34.9522	–83.2111
2	Burrells Ford Rd	34.9680	–83.1388
3	Laurel Creek	34.9519	–83.1602
4	Billingsley Creek	34.9787	–83.2438
5	Holcomb Tributary	34.9670	–83.2159
6	Addie Branch	34.9704	–83.2719
7	Sarah's Creek	34.9368	–83.2661
8	Timpson Falls	34.8872	–83.4846
9	Sosebee Cove	34.8037	–83.9328
10	Dockery Lake	34.6783	–83.9745
11	Crow Creek	34.7633	–83.5502
12	Panther Creek	34.7265	–83.4675
13	Bear Gap	34.7347	–83.4561
14	Lake Winfield Scott	34.7392	–83.9736
15	Vogel	34.7664	–83.9256
16	Wolf Pen Gap	34.7631	–83.9465
17	Turners Corner	34.6651	–83.8855
18	Soque River	34.7326	–83.5881
19	Uncoi	34.7342	–83.7246

eggs and nymphs of the sistens and progrediens generations were counted per twig. Because the goal of the sampling was to determine adelgid life stages suitable for predators, the sexuparae generation was not evaluated. Adelgid densities were standardized by dividing the number of adelgids in each life stage by the length of the sample twig. The relative abundance of each life stage on a given sample date was calculated by dividing the number adelgids in each life stage by the total number of adelgids in all life stages. We derived egg density by totaling adelgid eggs and dividing by number of ovisacs regardless of their maturity, which will likely yield a very conservative estimate of eggs per ovisac. This approach also was applied for eggs per cm twig data as well. Adelgid phenology was examined for each site and year by plotting adelgid density and relative abundance over time. Mean density and abundance of all northern Georgia sites for each sample date were calculated and summarized in composite graphs (all sites) by calendar year.

Records of mean monthly temperature (°C) over a 30-yr period were collected for northern Georgia and other locations from which *A. tsugae* phenology has been previously reported. Temperature data for 1980 - 2010 for locations near the present study (northern Georgia), and for locations near previous phenological studies in Connecticut and Virginia (McClure 1987, Gray and Salom 1996) were obtained from a climate model designed by Prism Climate Group, OR State Univ. (Daly et al. 2008, Prism Climate Group 2010). In Georgia these sites were: Overflow Creek, Clayton (Latitude: 34.952; Longitude: -83.211), Dockery Lake, Dahlonega (Latitude: 34.678, Longitude: -83.974) and Soque River, Clarkesville (Latitude: 34.732, Longitude: -83.588); in Connecticut: Connecticut Nature Conservancy (Latitude: 41.28, Longitude: -72.88), Gillette Castle State Park (Latitude: 41.425, Longitude: -72.429) and Montgomery Pinetum (Latitude: 41.055, Longitude: -73.598) (McClure 1987); in Virginia: Stoney Creek, Bedford Co. (Latitude: 37.467, Longitude: -79.558) and Craig Co. (Latitude: 37.532, Longitude: -80.176) (Gray and Salom 1996). Average temperature data for 1971 - 2000 from locations near previous phenology study sites in British Columbia (Zilahi-Balogh et al. 2003) were obtained from the International Weather Station (Latitude: 48°38′50 N, Longitude: 123°25′33 W), Victoria, British Columbia. All temperature data were averaged by state and plotted in Fig. 2.

Results and Discussion

Sistens generation. In Georgia, progrediens adults initiated egg-laying by midMay and continued until the first week of July in 2004 and 2005 (Figs. 3A and 3I). However, in 2006 all the sistens eggs laid by progrediens adults had hatched by late June (Fig. 4A). Progrediens oviposited 1 - 28 sistens eggs per ovisac through midMay to late June or early July (Fig. 5). Egg production peaked by late May or early June in all sampling years (Figs. 3 and 4). In Virginia, progrediens ovisacs were not reported until early June and were present until early July (Gray and Salom 1996, Mausel et al. 2008); whereas, in Connecticut, progrediens adults were first reported by late May and were present until late June, and sistens eggs were found from early June to late July (McClure 1987). In the Pacific Northwest, appearance of progrediens ovisacs was not obvious until mid to late-June and they were present up to midJuly (Zilahi-Balogh et al. 2003). Thus, initiation of the progrediens generation in northern Georgia is 2 - 4 wk

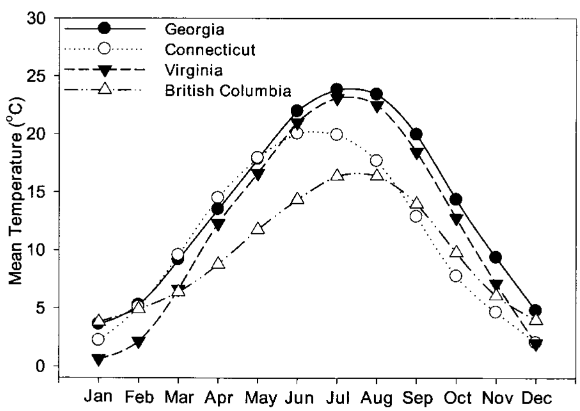

Fig. 2. Mean monthly temperature (°C) from 1980 - 2010 at various study sites of northern GA, CT and VA, and from 1971 - 2000 at Victoria, BC.

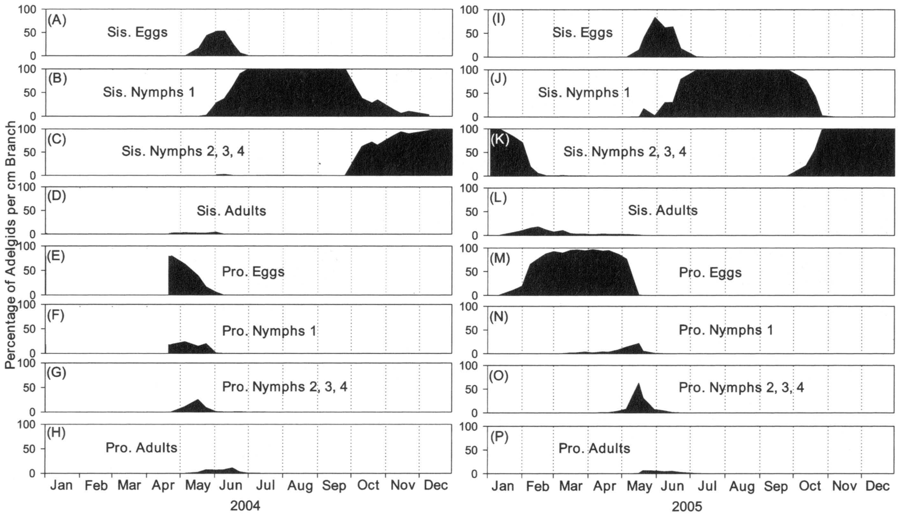

Fig. 3. Phenology of hemlock woolly adelgid in (A-H) 2004 and (I-P) 2005 in northern Georgia. The abbreviations: pro. = progrediens; sis. = sistens.

earlier as compared with their development in the aforementioned more northern locations. This accelerated development is likely due to the earlier onset of warmer conditions in the spring (Fig. 2). Environmental conditions, especially seasonal temperature, have a significant effect on development, survival, and spread of hemlock woolly adelgid in the eastern U.S. (Evans and Gregoire 2007). Trotter and Shields (2009) demonstrated that adelgid survival was significantly reduced when latitude increased and minimum temperature decreased.

Upon hatching, the mobile first-instar nymphs (sistens crawlers) immediately settled at the needle base, transformed into an immobile form, and aestivated for the remainder of the summer. Emergence of crawlers occurred 1 - 2 wk after initiation of egg laying (Figs. 3B, 3J, 4B, and 4J). Similarly, in the Pacific Northwest and the northeastern range of hemlock, first-instar nymphs undergo aestivation the entire summer (Gray and Salom 1996, Mausel et al. 2008, McClure 1987, Zilahi-Balogh et al. 2003).

During 2004, 2005, and 2006 in Georgia, aestivating nymphs resumed development (becoming second instars) between late-September and early October (Figs. 3C, 3K, and 4C). Similarly, growth of first-instar nymphs was observed by late September in Connecticut and the Pacific Northwest (McClure 1987, Zilahi-Balogh et al. 2003), and by early to midOctober in Virginia (Gray and Salom 1996, Mausel et al. 2008). Sistens adults were found as early as the first week of January in Georgia in 2007 (Fig. 4L), were abundant through late winter and early spring, and persisted until May (Figs. 3D, 3L, 4D, and 4L). In Virginia, sistens adults were initially observed by early to midJanuary, were abundant by the third week of February and were observed until early April (Gray and Salom 1996, Mausel et al. 2008). In Connecticut, sistens adults appeared about the same time as in Virginia, peaked the second week of February and were present until late March (McClure 1987). Our results in 2005 and 2006 showed that adults were found between midJanuary and midMay with peak occurrence in February and March (Figs. 3L and 4D). However, in Pacific Northwest, appearance

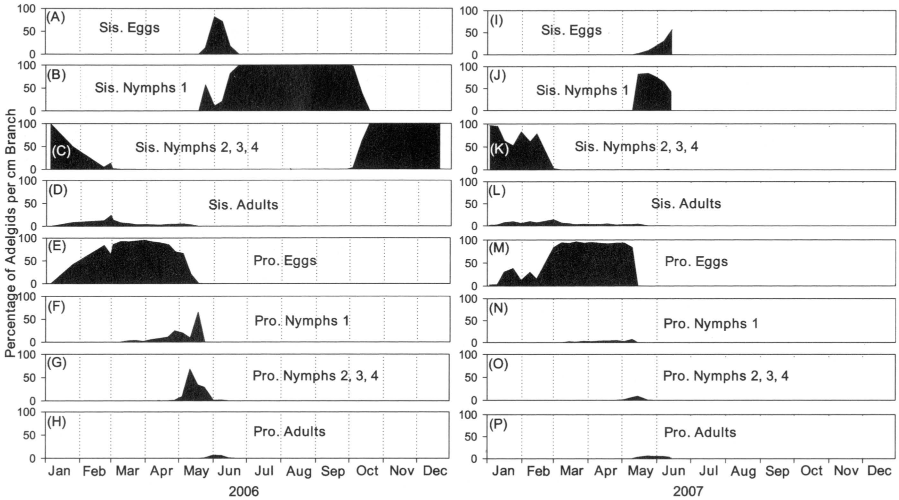

Fig. 4. Phenology of hemlock woolly adelgid in (A-H) 2006 and (I-P) 2007 in northern Georgia. The abbreviations: pro. = progrediens; sis. = sistens.

of sistens adults was reported in hemlock trees as early as late October, but their densities peaked in April (Zilahi-Balogh et al. 2003).

Progrediens generation. Progrediens egg density approached approx. 1 egg per cm branch by early February in 2005, 2006, and 2007 (Figs. 3M, 4E and 4M). Thereafter, egg densities increased and peaked at 60 - 120 eggs per cm by late March to early April in 2005 and 2006. In 2007, however, peak egg densities were seen as early as midMarch. Sistens fecundity was low during early January through February then dramatically increased after early or midMarch until midMay (12 - 62 eggs per ovisac) when their fecundity declined (Fig. 5). Sistens adults completed oviposition by the second week of May in 2005, 2006 and 2007; however, oviposition was extended until June 9 in 2004. Similarly, in Virginia and Connecticut sistens started producing progrediens eggs by the second week of February (Gray and Salom 1996, Mausel et al. 2008, McClure 1987). Egg production reached the peak during the third week of March then declined by midMay in Virginia (Mausel et al. 2008), but in Connecticut the highest egg density was observed during early April and no eggs were reported after first week of June (McClure 1987). In the Pacific Northwest, sistens adults laid eggs about the same time as in eastern regions, i.e., between early February and June (Zilahi-Balogh et al. 2003).

In Georgia, emergence of progrediens crawlers began by early March in 2005, 2006 and 2007, and continued for 2 - 3 months (Figs. 3N, 4F and 4N). Once crawlers settle at the base of the needles by inserting their proboscis, they transform into black-bodied nymphs with white fringes (McClure 1987, 1989). All crawlers had molted to second instars by early June in 2004 and 2005. However in 2006 and 2007, crawlers molted to second instar nymphs by midMay (Figs. 3G, 3O, 4G and 4O). In Virginia, progrediens crawler emergence did not begin until early April and their density peaked by late April then declined by the second week of May (Gray and Salom 1996, Mausel et al. 2008). Crawlers were not detected until early May in Connecticut and disappeared by midJune (McClure 1987). Similarly, crawlers were reported from early May

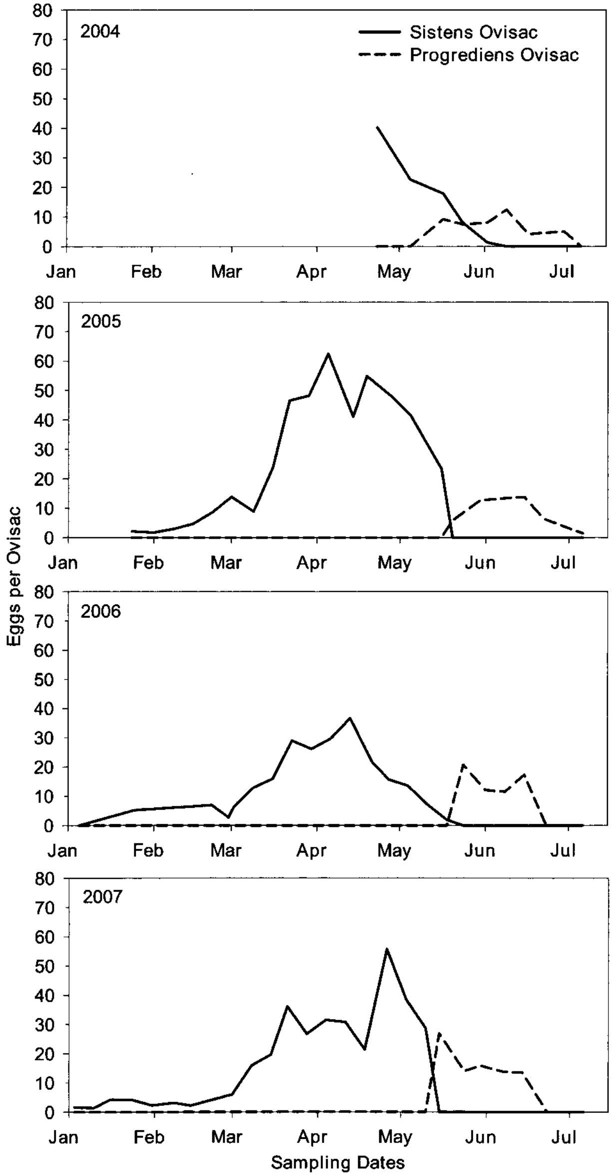

Fig. 5. Fecundity of hemlock woolly adelgid from 2004 - 2007.

to early June in the Pacific Northwest. In all years, second and higher-instar nymphs were observed between midApril and midJune in Georgia (Figs. 3 and 4). Progrediens adults were found between midMay and late June (Figs. 3H, 3P, 4H, and 4P). In Virginia, progrediens adults occurred from late May to early June (Gray and Salom 1996, Mausel et al. 2008). Progrediens adults were found from late May to late June in Connecticut (McClure 1987); whereas, in the Pacific Northwest, they are present between midJune and midJuly (Zilahi-Balogh et al. 2003). Thus, presence of adult progrediens in Georgia began and ended about 1 month earlier than in the Pacific Northwest, and began earlier but ended later or at about the same time as in Virginia and Connecticut.

The predatory beetle, *Laricobius nigrinus* Fender (Coleoptera: Derodontidae), naturally occurs in the Pacific Northwest where its phenology is synchronized with *A. tsugae* (Zilahi-Balogh et al. 2003). After multiple mating, a female beetle oviposits in *A. tsugae* ovisacs (Zilahi-Balogh et al. 2003). Zilahi-Balogh et al. (2002) observed that time of *L. nigrinus* egg hatch was in synchrony with the oviposition of *A. tsugae*; thus, the larva actively consumed *A. tsugae* eggs. It has been shown that larval density of *L. nigrinus* increased with increased availability of adelgid ovisacs in a field insectary (Mausel et al. 2008). This predator is being widely released throughout the entire eastern range of hemlock (Mausel et al. 2008, 2010). The delayed development of the progrediens generation in the Pacific Northwest and northern states relative to northern Georgia may provide *L. nigrinus* more opportunities to find food and oviposition sites.

Researchers in the southeastern range of hemlock often have been uncertain about the best time to release *L. nigrinus* into the forest. In 2006 and 2007, sites were approx. between 366 m and 732 m suggesting that natural adelgid infestations at both the extreme elevations (below 366 m or above 732 m) were not determined in this study. Adelgids in North Georgia occur from 200 m to 1070 m in elevation. Our results suggest that initial release of *L. nigrinus* could be made by last week of February or first week of March and subsequent releases in the following weeks would increase their likelihood of finding sistens ovisacs for oviposition and progrediens nymphs as food (Fig. 5). The ideal strategy would be to track progrediens eggs by elevation to determine where to release first which means starting at low elevation sites and progressing to high elevation sites. Furthermore, at some point in midMay to June switch to sites where sistens eggs are in sufficient numbers which means releasing on low elevation sites once again and following these eggs as they develop with altitude possibly even to very high elevation (approx. 1036 m) in July where adelgid eggs are likely to still be present in northern Georgia. It is possible to manipulate *L. nigrinus* adults to get egg production over 15 - 16 wks in the rearing laboratory. Sleeve cage data have supported that eggs released in July were viable and were successfully developed to late-instar larvae (Dalusky, unpubl. data). In addition, the adults released from the oviposition colony at this time of year (midJune) still have eggs which were undoubtedly laid.

Moreover, another imported predatory beetle, *Sasajiscymnus tsugae* (Sasaji & McClure) (Coleoptera: Coccinellidae), has been widely released in eastern range of hemlock and has been shown to be synchronized with adelgid life stages in Connecticut (Cheah and McClure 2000). *Sasajiscymnus tsugae* are active during late spring to summer; therefore, spring months might be best period for its release. Also, predatory rearing facilities could use these data as a guide to determine the specific adelgid life stages present in the field. However, the exact adelgid life stage present in a specific location should be determined by hemlock branch sampling.

Acknowledgments

The authors thank L. Barnes and other workers at the biological control laboratory, Athens, GA for providing technical assistance, J. L. Hanula for comments on this manuscript, and James

Vose and the USDA Forest Service, Southern Research Station RWU 4353 for providing funding for this project.

References Cited

Cheah, C. A. S.-J. and M. S. McClure. 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. For. Entomol. 2: 241-251.

Daly, C., M. Halbleib, J. I. Smith, W. P. Gibson, M. K. Doggett, G. H. Taylor, J. Curtis and P. A. Pasteris. 2008. Physiographically-sensitive mapping of temperature and precipitation across the conterminous United States. Int. J. Climatol. 28: 2031-2064.

Evans, A. M. and T. G. Gregoire. 2007. A geographically variable model of hemlock woolly adelgid spread. Biol. Invasions 9: 368-382.

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.), Proc. First Hemlock Woolly Adelgid Review. U.S. Depart. Agric. Forest Serv., FHTET 96-10, Washington, DC.

Havill, N. P., M. E. Montgomery, G. Yu, S. Shiyake and A. Caccone. 2006. Mitochondrial DNA from hemlock woolly adelgid (Hemiptera: Adelgidae) suggests cryptic speciation and pinpoints the source of the introduction to eastern North America. Ann. Entomol. Soc. Am. 99: 195-203.

Kohler, G. R., V. L. Stiefel, K. F. Wallin and D. W. Ross. 2008. Predators associated with the hemlock woolly adelgid (Hemiptera: Adelgidae) in the Pacific Northwest. Environ. Entomol. 37: 1477-1487.

Mausel, D. L., S. M. Salom, L. T. Kok and J. G. Fidgen. 2008. Propagation, synchrony, and impact of introduced and native *Laricobius* spp. (Coleoptera: Derodontidae) on hemlock woolly adelgid in Virginia. Environ. Entomol. 37: 1498-1507.

Mausel, D. L., S. M. Salom, L. T. Kok and G. A. Davis. 2010. Establishment of the hemlock woolly adelgid predator, *Laricobius nigrinus* (Coleoptera: Derodontidae), in the eastern United States. Environ. Entomol. 39: 440-448.

McClure, M. S. 1987. Biology and control of hemlock woolly adelgid. Connecticut Agric. Exp. Sta., Bull. 851, New Haven. 9 p.

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

McClure, M. S. 1991. Density-dependent feedback and and population cycles in *Adelges tsugae* (Homoptera: Adelgidae) on *Tsuga canadensis*. Environ. Entomol. 20: 258-264.

Prism Climate Group. 2010. Oregon State Univ., Corvallis. http://www.prism.oregonstate.edu/index.phtml.

Trotter, R.T. and K. S. Shields. 2009. Variation in winter survival of the invasive hemlock woolly adelgid (Hemiptera: Adelgidae) across the eastern United States. Environ. Entomol. 38: 577-587.

USDA Forest Service. 2011. Counties with established HWA populations 2010. Updated 1 Feb 2011 and accessed 6 Feb 2011 at http://na.fs.fed.us/fhp/hwa/maps/2010.pdf.

Ward, J. S., M. E. Montgomery, C. A. S.-J. Cheah, B. P. Onken and R. S. Cowles. 2004. Eastern hemlock forests: Guidelines to minimize the impacts of hemlock woolly adelgid. USDA Forest Serv., Northeastern Area, State & Private Forestry, Morgantown, WV, NA-TP-03-04. 27 p.

Zilahi-Balogh, G. M. G., L.T. Kok and S. M. Salom. 2002. Host specificity of *Laricobius nigrinus* Fender (Coleoptera: Derodontidae), a potential biological control agent of the hemlock woolly adelgid, *Adelges tsugae* Annand (Hemiptera: Adelgidae). BioControl 24: 192-198.

Zilahi-Balogh, G. M. G., L. M. Humble, A. B. Lamb, S. M. Salom and L. T. Kok. 2003. Seasonal abundance and synchrony between *Laricobius nigrinus* (Coleoptera: Derodontidae) and its prey, the hemlock woolly adelgid (Hemiptera: Adelgidae). Can. Entomol. 135: 103-115.