Comparative Phenology and Cohort Survival of Beech Scale (Hemiptera: Eriococcidae) in Part of its Native Range (Caucasus Mountains, Georgia) and in an Invaded Area (Massachusetts, USA)

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Comparative phenology and cohort survival of beech scale (Hemiptera: Eriococcidae) in part of its native range (Caucasus Mountains, Georgia) and in an invaded area (Massachusetts, USA)

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Abstract

The phenology and survival of beech scale, *Cryptococcus fagisuga* Lindinger (Hemiptera: Eriococcidae), were investigated in part of its native range (Caucasus Mountains, Georgia) and in an invaded area (Massachusetts, USA). Despite nearly identical growing seasons (as measured by cumulative day-degrees), the scale was found to be bivoltine in the Caucasus Mountain region but univoltine in Massachusetts. In Georgia, scales overwintered as adults, whereas in Massachusetts, 1st instar crawlers were the overwintering stage. In Massachusetts, protective cages increased scale survival over a year-long period, but the effect was not great and was presumed to be due to exclusion of generalist predators, not specialized natural enemies. There was no effect of caging on survival in Georgia, and no support was found for the hypothesis that specialized natural enemies might exist in the scale's native range that might be imported for biological control of the pest in the United States. Rather, it appears that selection for resistance in American beech (*Fagus grandifolia* Ehrhart; Fagales: Fagaceae) may offer the best chance to restore healthy stands of American beech in North American forests.

Key Words: overwintering stage; natural enemy exclusion; beech forest; invasive insect

Resumen

Se investigó la fenología y sobrevivencia de la escama de la haya, *Cryptococcus fagisuga* Lindinger (Hemiptera: Eriococcidae), en parte en su área de distribución natural (Cáucaso Mts., en el pais de Georgia.) y en una zona invadida (Massachusetts, EE.UU.). Se encontró que la escama es bivoltina en la región de las Montañas del Cáucaso, pero univoltina en Massachusetts, a pesar de las estaciones de crecimiento casi idénticas (medido por grados días acumulados). En Georgia, la escama como adulto inverna, mientras que en Massachusetts, inverna en el estadio del primer instar (rastreadores). En Massachusetts, las jaulas protectoras aumentó la sobrevivencia de la escama durante un período de un año, pero el efecto no fue grande y se atribuyó a depredadores generalistas, no enemigos naturales especializados. No hubo efecto de las jaulas sobre la sobrevivencia en Georgia y no se encontró apoyo para la hipótesis de que podrían existir enemigos naturales especializdos en el área de distribución natural de la escama que podrían ser importados para el control biológico de la plaga en los Estados Unidos. Más bien se recomienda que la selección para la resistencia en las líneas de haya americana (*Fagus grandifolia* Ehrhart; Fagales: Fagaceae) ofrece la mejor oportunidad para restaurar la salud de los rodales de haya americana en los bosques de América del Norte.

Palabras Clave: etapa de invernación; exclusión de enemigos naturales; bosques de hayas; insectos invasivos

In North America, health and growth of American beech (*Fagus grandifolia* Ehrhart; Fagales: Fagaceae) have been degraded seriously by beech bark disease caused by the fungus *Neonectria faginata* (Lohman et al.) Castlebury & Rossman and to a lesser degree by *Neonectria ditissima* (Tul. & C. Tul.) Samuels and Rossman (= *N. galligena* [Bres.] Rossman & Samuels) (Hypocreales: Nectriaceae), whose infection of hosts is facilitated by bark cracks induced by feeding of the invasive scale *Cryptococcus fagisuga* Lindinger (Hemiptera: Eriococcidae) (Houston 1994; Castlebury et al. 2006). Beech scale was transported to North America by movement of scale-infested beech trees from Europe to Nova Scotia, which precipitated an epidemic of beech bark disease (Hewitt 1914). Although the scale has been known in parts of western Europe since 1832 (Fries 1832), analysis of genetic diversity of beech scale collections at locations from the United Kingdom to Iran (the easternmost point of the scale's known distribution) suggest that the native range (based on greatest genetic diversity) is between Bulgaria, Turkey, and the Caucasus Mountain region (Gwiazdowski et al. 2006). In that region, the scale's original host is oriental beech (*Fagus orientalis* Lipsky; Fagales: Fagaceae), from which it appears to have spread or been moved into association with *Fagus sylvatica* L. (Fagales: Fagaceae) in western Europe, likely as oriental beech was planted in western Europe.

Given this native range for beech scale, studies in Georgia in the Caucasus region were conducted from 2011 to 2013 to search for

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specialized natural enemies of beech scale. To date, no parasitoids or specialized predators have been discovered. However, previous work showed that scale density in Georgia was only about 2.5% of that in Massachusetts (an invaded area) (Van Driesche & Japoshvili 2012). The good condition of beech that we observed during our natural enemy surveys in Georgia might reflect high tree resistance to beech scale, presence of important natural enemies missing in invaded areas, or resistance in Georgian beech to local species of *Neonectria* pathogens. To determine the relative importance of natural enemies vs. tree resistance in the Caucasus region vs. New England (USA), cohort survival studies (caged or uncaged) were done in the country of Georgia and in western Massachusetts. In addition, the seasonal phenology of beech scale at these 2 locations was recorded. Here we present comparative survival of scale cohorts between the country of Georgia and Massachusetts, USA, and we compare the bivoltine seasonal phenology seen in Georgia with the univoltine pattern found in Massachusetts.

Materials and Methods

BEECH SCALE PHENOLOGY

Georgia (Caucasus Mts.)—Phenology

The phenology of life stages of beech scale was observed from Jan 2011 to Jan 2012 at 1 forested site in the Caucasus Mountains, in the country of Georgia (Gulelebi Forest, Fig. 1, 41°55ˈ31.03"N, 44°55ˈ51.79"E; 1,196 m asl). Every 2 wk, we haphazardly collected 100 woolly dots covering adult or nymphal beech scales (the number collected per tree varied because densities were low). Scales were placed in plastic tubes and taken to the laboratory, where all scales in the sample were classified to life stage. The numbers of individuals in different life stages (egg, nymph—both instars [1 + 2]—, or adult) were then determined for each date. If there were eggs in a woolly mass, they were recorded as 1 case of eggs, rather than the actual number of eggs present. The resulting data were grouped by month for presentation.

To assess the effect of local temperature on voltinism, we calculated the number of day-degrees (base 10 °C). Because temperature data were not originally collected at the site when the phenology of beech scale was studied, we substituted available temperature records for 2011 from a location known as Tianeti, which was 25 km from the study site and at a similar altitude (1,100 m). From daily maximum and minimum temperatures, cumulative day-degrees were calculated (as Max + Min / 2 – LTH) when LTH (low temperature threshold) was set at 10 °C, which is an approximation because the actual value for beech scale is unknown.

Massachusetts (USA)—Phenology

In the United States, beech scale phenology was assessed in 2013 at 1 site, Notchview Reservation (Trustees of Reservations) in Windsor, Massachusetts (42°50ˈ36"N, 73°2ˈ78"W; 650 m elevation). At the study site, samples of scale-infested bark were collected monthly, May through Nov. For each sample, several irregularly sized pieces of scale-infested bark (approximately 1 or 2 cm on a side) were collected with a knife from each of 10 beech trees. The same trees were re-sampled on each sample date. In the laboratory, pieces of bark were removed haphazardly from the sample bags and checked under a dissecting microscope. Scale body lengths were determined for the first 10 scales found for each tree (total *n* = 100 scales checked per sample date). Scale body lengths were then categorized as 1st or 2nd instar nymphs or adult females (there are no males) based on discrete jumps in body size, as no obvious morphological differences except size exist among life stages. The occurrence of eggs was not recorded in the 2013 Massachusetts phenology observations, but in a separate experiment in

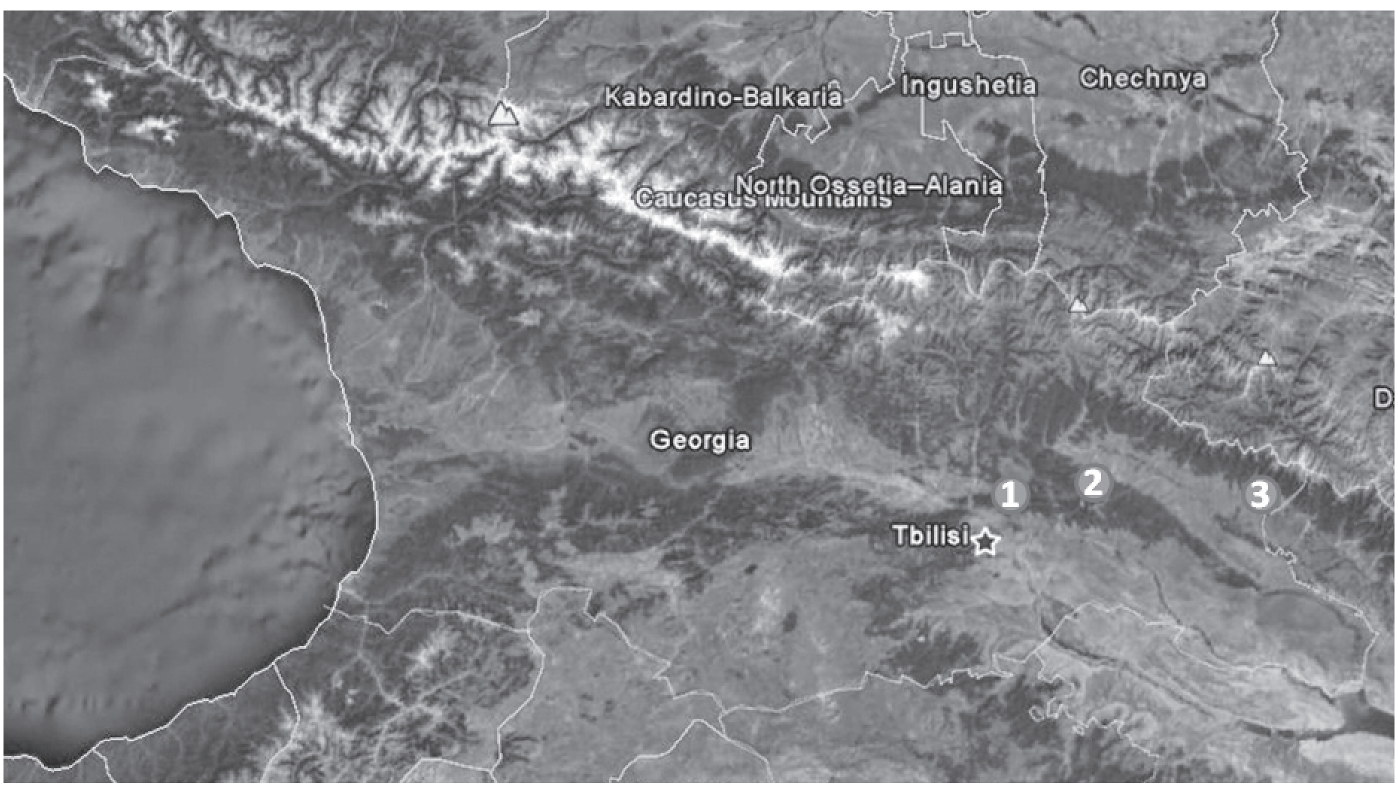

Fig. 1. Sites in Georgia where studies were conducted. Site 1 (Gulelebi Forest) was used in 2011 for the phenology observations, and sites 2 (Gombori) and 3 (Lagodekhi) were used for the cohort survival experiment in 2012.

the previous year (2012, see the scale cohort survival) at the same site, eggs were observed to occur in Sep and Oct. Temperature data from a weather station on the Windsor/Peru town line (4 km from research site, 600 m elevation) from 2013 were used to calculate day-degree values, following the same procedure as for the Georgian site.

SURVIVAL OF BEECH SCALE COHORTS UNDER FIELD CONDITIONS

Georgia (Caucasus Mts.)—Cohort Survival

This study was done in beech forests at 2 sites in Georgia: Gombori (41° 52ˈ 28.68" N, 46° 21ˈ 38.41" E) and Lagodekhi (41° 51ˈ 1.50" N, 46° 17ˈ 23.69" E). In Apr, we chose 7 trees (25–80 cm diameter at breast height) from each site, dividing each into 2 equally infested 50 cm long sections of the trunk. One part was wrapped with very fine mesh (0.1 mm) fabric, and the second section was left uncovered for further observation on scale survival over the season (Fig. 2). Numbers of surviving scales were counted on 19 Apr, 20 May, and 16 Sep in 2012 for each 100 cm^2 patch and then averaged.

Because counts were intended not to injure scales (which were recounted if they survived), counts were of the white woolly masses, which covered actual scale bodies. Dead scales could not, therefore, be distinguished until the wool disappeared or degraded.

Massachusetts (USA)—Cohort Survival

To determine the effect of caging on beech scale survival in the invaded range (Massachusetts, USA), cohorts of scales were created on beech trees in a mixed deciduous hardwood stand at Notchview Reservation (Windsor, Massachusetts) in fall of 2011 at the same site described above for phenological observations. An initial attempt to create beech scale cohorts was made on 12 Sep 2011 based on collecting ovisacs with eggs and relocating them onto other trees in the same stand on patches of clean bark. This failed to produce crawler establishment, perhaps because the bark lacked cracks, a preferred site for crawler settling. Consequently, on 25 Oct 2011, cohorts at the same stand were created by choosing patches of bark with 8 to 50 (average 19) naturally settled crawlers per patch (circles 3.5 cm in diameter).

Six such patches of settled crawlers were located on each of 10 beech trees. Three patches per tree were designated as treatment patches (i.e., exposed to natural enemies) and left uncaged, and 3 were considered control patches from which natural enemies were excluded by placing open-bottom, top-screened 3.5 mm diameter Petri dishes over the scale patches (Fig. 3a and b). The Petri dish was sealed to the bark with modeling clay and prevented from falling off by driving nails on either side of the cage and then passing a copper wire tightly over the cage from nail to nail. Caged and uncaged patches were paired at each of 3 heights, over the bottom 2 m of the trunk. Patch number and number of settled crawlers per patch were written on the tree's bark with a permanent marker to aid in recognizing each patch on subsequent examinations. Tree number (1 to 10) was written on flagging tape tied to each tree. Scales were recounted in spring (1 Jun) and fall (1 Oct) of the following year (2012), and scales were classified non-destructively in the field as nymphs or adults (based on the size of the woolly patch). Observation over this time period allowed survival of a cohort to be followed over 1 full generation of the scale. Survival to the adult stage 1 yr after choosing cohorts of settled crawlers was the measure of generational survival.

Fig. 2. Cloth wrapping used to cage beech trunk section in 2012 at Gulelebi Forest in Georgia where one part of the scale cohort survival study was conducted.

Fig. 3. (a) Example of trunk cages made from small Petri dishes (with an open bottom) that were used to isolate scale patches in Massachusetts. (b) Patches of beech scale initiated by delimiting groups (<50) of newly settled crawlers with top patch (defined by black circle marked on bark) left uncaged, whereas lower patch was caged (caged removed here) from Oct 2011 to Oct 2012 (1 scale generation) at which time scales were a mixture of adults and crawlers of the next generation; done on American beech at Notchview Reservation (property of Trustees of Reservations), Windsor, Massachusetts, USA. Note the greater number of large white woolly dots (adults of the test generation) in the bottom circle, suggesting significant mortality due to factors, like generalist predators, that were excluded by the cages.

DATA ANALYSIS

Untransformed data from the cohort survival experiments in Georgia and Massachusetts were analyzed using 1-way ANOVA in IBM SPSS 21 (IBM SPSS Statistics for Windows, Version 21.0. Released 2012. IBM Corp., Armonk, New York, USA).

Results

BEECH SCALE PHENOLOGY

Georgia (Caucasus Mts.)—Phenology

In the Gulelebi Forest of Georgia, beech scale had 2 partly overlapping generations (Fig. 4). Scales overwintered as adult females that began to oviposit in Mar, with egg laying peaking in May. Oviposition by females of the 2nd scale generation began in Jul and peaked in Aug.

Massachusetts (USA)—Phenology

In contrast to the bivoltine pattern for beech scale in Georgia, beech scale at our Massachusetts (USA) study site was univoltine and overwintered as settled 1st instars (Fig. 5). Adults were present throughout summer and fall. On 13 Sep 2011 (in the cohort study), adult scales were found to have numerous unhatched eggs in their ovisacs at the study site.

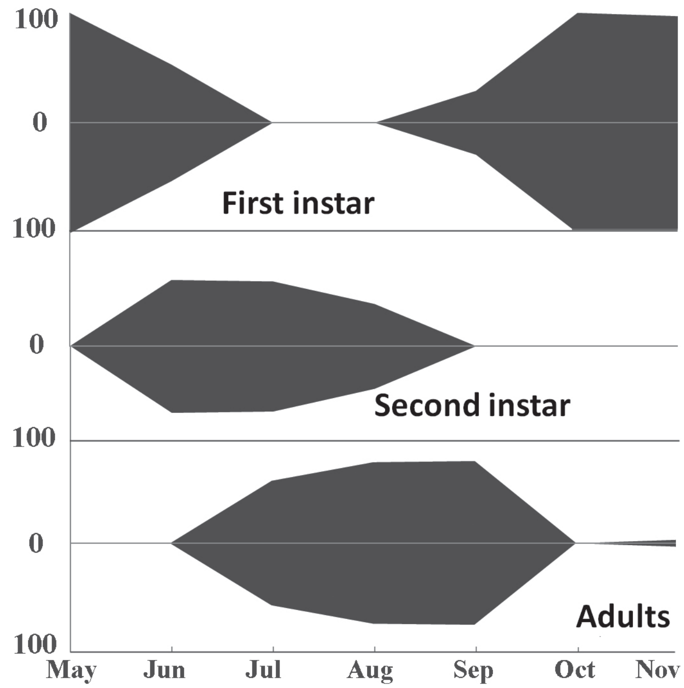

Fig. 5. Phenology of life stages of beech scale in Massachusetts (USA) (Notchview Reservation, property of Trustees of Reservations, Windsor, 2013), showing univoltine cycle, with settled crawlers being the overwintering stage.

SURVIVAL OF BEECH SCALE COHORTS UNDER FIELD CONDITIONS

Georgia (Caucasus Mts.)—Cohort Survival

For caged cohorts, counts of scales in samples increased over the season (2 generations) from 18 to 32% ($R_{0\ per\ gen.}$ = 1.09–1.15), whereas numbers in the open cohorts declined, on average, 1.1% ($R_{0\ per\ gen.}$ = 0.98–1.01); however, these changes were not statistically significant by ANOVA (Table 1). In Gombori, in the caged cohort in Apr there were initially 8.3 ± 10.1 (SD) scales per 100 cm^2, and at the last count in Sep there were 11.0 ± 10.7 (SD) scales per 100 cm^2 (Table 1). In the open (uncaged) cohorts at Gombori there were initially 8.3 ± 10.1 (SD) scales per 100 cm^2 and 8.0 ± 10.4 (SD) at the final sample date. At the 2nd site, Lagodekhi, for the caged cohorts there were initially 20.5 ± 26.9 (SD) scales per 100 cm^2 (Table 1) and at the last count there were 24.3 ± 30.3 (SD); for the open (uncaged) cohorts there were initially 20.5 ± 26.9 (SD) scales per 100 cm^2 and on the final sample date there were 20.8 ± 25.3 (SD). None of the differences between the first and last counts within treatments were statistically significant, nor were comparisons within dates between treatments (Table 1).

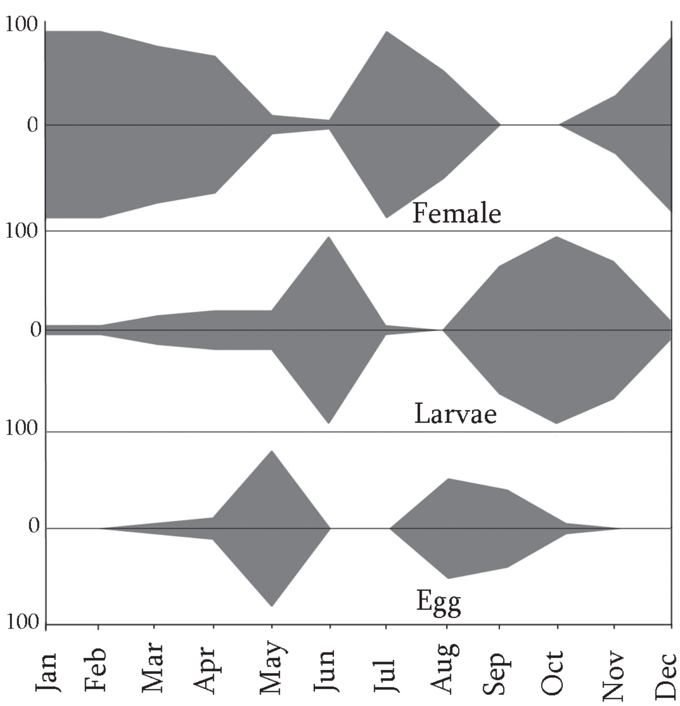

Fig. 4. Phenology of life stages of beech scale in Georgia (Gulelebi Forest, Tianeti District, 2011), showing bivoltine cycle, with adult females being the overwintering stage.

Massachusetts (USA)—Cohort Survival

The numbers of 1st instars in caged and uncaged cohorts at the beginning of the experiment (25 Oct 2011), which were selected visually to be similar in starting density, were not statistically different (Table 2) as intended. In Jun 2012, there were fewer live scales in both groups, with the uncaged group being smaller than the caged group (8.2 vs. 13.2) and with this difference between groups being significant ($F_{1, 58}$ = 8.90, P = 0.004). By the end of the generation, densities of members of the initial cohort (now all adults, with counts of their offspring excluded) had declined further in the uncaged group to 2.2 (vs. 8.1 in the caged group), which difference was also significant ($F_{1, 58}$ = 2.29, P = 0.017). Declines in density over time (sample dates) for cohorts within treatment type (caged or uncaged) were significant (caged: Tukey HSD post hoc test, $F_{2, 89}$ = 20.7, P < 0.05; uncaged: Tukey HSD post hoc test, $F_{2, 89}$ = 68.5, P < 0.001). Densities of next generation nymphs were not compared statistically as they did not represent the full reproductive output of cohorts.

In terms of percentage survival, caging raised generational survival (from 25 Oct 2011 to 1 Oct 2012) of the parental cohort from 11.6% (in the uncaged group) to 40.5% (Table 2). Survival during the period from

Table 1. Counts of beech scales (nymphs + adults) in patches (mean ± SD) on beech trees that were either caged (for natural enemy exclusion) or uncaged (permitting natural enemies access to scales) at 2 sites (Gombori and Lagodekhi) in the Republic of Georgia, 18 Sep 2011 to 21 Sep 2012. Numbers are means and standard deviations of 10 cohorts (1 per tree), each occupying an area of 100 cm^2.

	Gombori		Lagodekhi	
Date of count	Caged	Uncaged	Caged	Uncaged
19 Apr	8.3 ± 10.1aA	8.3 ± 10.1aA	20.5 ± 26.9bB	20.5 ± 26.9bB
20 May	9.4 ± 10.8aA	8.1 ± 9.7aA	23.2 ± 28.2bB	20.5 ± 24.4bB
20–21 Sep	11.0 ± 10.7aA	8.0 ± 10.4aA	24.3 ± 30.3bB	20.8 ± 25.3bB
% change in cohort from Apr to Sept	32.5%	−3.6%	18.5%	1.5%
R_0 (per gen. est.)[a]	1.15	0.98	1.09	1.01

Values with shared uppercase letters within columns are not statistically different (at $P \leq 0.05$); values with shared lowercase letters within rows and within site are not statistically different. Values were not compared across sites.
[a] $R_{0\ per\ generation}$ was estimated as the square root of the change for the whole year (two generations, assuming a constant rate of change).

Oct 2011 to Jun 2012 differed between caged and uncaged treatments by 23 percentage points (66 vs. 43%), whereas survival from spring to fall of 2012 differed between treatment groups by 35 percentage points (61 vs. 26%) (Table 2).

Population growth rates for all live scales (adults and nymphs combined) over the observation period (1 yr) were R_0 = 0.81 (caged) and 0.77 (uncaged), but these are underestimates of the generational R_0 values because substantial numbers of adults from the parental generation were still alive, particularly for the caged treatment cohort; therefore, further reproduction within the generation was still likely to occur.

Discussion

In Georgia (Caucasus Mts. region), beech scale was observed to have 2 generations annually, whereas in Massachusetts, there was only 1. This had important effects on the scale's seasonal phenology, changing the overwintering stage from adults in the country of Georgia to settled 1st instars in Massachusetts. In western Massachusetts, beech scale oviposition occurred in fall (Sep/Oct) in contrast to May and again in Aug/Sep in Georgia. However, Brown (1934) noted that a univoltine population of beech scale near Boston, Massachusetts, laid its eggs in Jun and Jul. Hawboldt (1944) also noted that beech scale in the Canadian Maritimes was univoltine. The change in voltinism between Massachusetts and the country of Georgia was not driven by differences in total seasonal heat units, as examination of temperature records from each study region showed little to no difference in cumulative day-degrees (approx. 10% more in Georgia) (Fig. 6).

In Massachusetts, caging greatly increased the percentage of 1st instars that survived to become reproductive adult females (from 11.6% for uncaged controls to 40.5% for the caged group). Cages enhanced survival in both sample periods, but the larger effect was during the summer/fall period of Jun to Oct (in 2012), rather than the preceding winter/spring period of Oct 2011 to Jun 2012. In this summer/fall period, the factor excluded or affected by cages was more likely to be natural enemies than adverse weather. This seasonality suggests that generalist natural enemies (such as the coccinellid coleopteran *Chilocorus stigma* [Say], which was observed at the study site) may have had a greater impact on beech scale survival than is generally supposed. Because the Oct 2011 to Oct 2012 period of observation covered just 1 generation, the effects of reproduction (detected as the number of nymphs in the Oct 2012 count) on this estimated or within-generation survival could be excluded. The fact that R_0 values calculated (by combining nymphs with adults in the final observation period) for the Massachusetts site were below 1.0 for both caged and uncaged cohorts suggests that this count missed some potential individuals of the new generation, which had yet to be produced by the surviving adults. Those individuals may have been present as eggs, which were not counted.

In contrast, in Georgia, changes in numbers of beech scales in marked patches over a full season (Apr to Sep) were the product of survival over 2 generations, together with 2 periods of reproduction. When averaged over both sites, caging produced an apparent slight increase in the estimated per generation rate of increase (R_0 = 1.12) that contrasted with the stable to declining growth rates of the uncaged cohorts ($R_{0\ per\ gen.}$ = 0.995). However, these differences were not statistically significant. Therefore, all populations were essentially at R_0 = 1.

In conclusion, our study suggests that natural enemies may have had a modest effect on scale survival in Massachusetts but none in Georgia. No parasitoids of beech scale were observed in our surveys in Georgia, and earlier studies of beech scale mortality in Europe and North America detected only generalist predators such as coccinellids and chamaemyiid flies (Schwenke 1972; Baylac 1980, 1986). We

Table 2. Survival of caged versus uncaged cohorts of beech scale (*Cryptococcus fagisuga*) over a 1 yr period (25 Oct 2011 to 1 Oct 2012) at Notchview Reservation (TORR), Windsor, Massachusetts (USA), part of the North American invaded range, spanning 1 full generation (settled crawlers at initiation; adults with eggs or new 1st instars at termination) (mean ±SD, n = 30).

	Number in cohort (adults, nymphs)		Survival between sample dates **(survival over entire year)**	
Date of count	Caged	Uncaged	Caged	Uncaged
25 Oct 2011	20.0 ± 9.1aA	19.0 ± 7.2aA	—	—
1 June 2012	13.2 ± 6.4aB	8.2 ± 5.7bB	66%	43%
1 Oct 2012 (Adults, P_0)	8.1 ± 4.8aC	2.2 ± 3.0bC	61% **(40.5%)**	26% **(11.6%)**
1 Oct 2012 (Nymphs, F_1)[a]	8.1 ± 9.7	12.4 ± 10.2		
R_0 (per gen. est.)[a]	0.81	0.77		

Values with shared uppercase letters within columns are not statistically different (at $P \leq 0.05$); values with shared lowercase letters within rows are not statistically different.
[a]Not compared statistically.

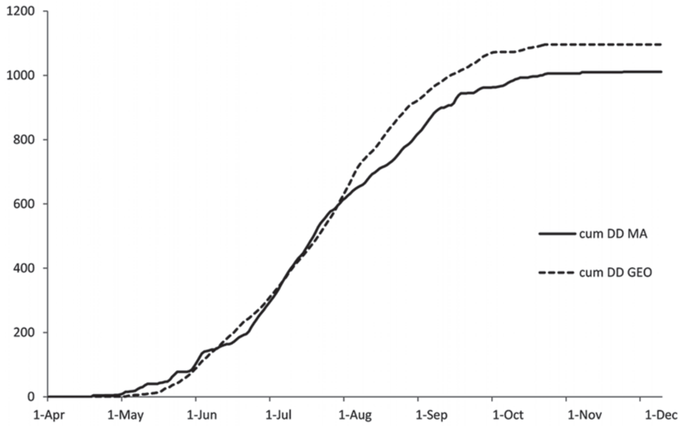

Fig. 6. Comparative cumulative day-degrees for Tianeti in the country of Georgia (cum DD GEO) and Windsor, Massachusetts, USA (cum DD MA), each in the years in which phenological observations on beech scale were made at the 2 locations.

found no evidence suggesting potential for classical biological control of beech scale in North America via importation of natural enemies from Georgia. Rather, silvicultural preservation and expansion of the fraction of the American beech population possessing natural resistance (e.g., Koch et al. 2010) to beech bark disease seems to be a more promising tool for restoration of American beech in forest stands.

Acknowledgments

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