HWA COLD-HARDINESS: TOWARDS DEFINING LIMITS OF RANGE EXPANSION

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Abstract

Cold temperature is probably the most important factor limiting the range of insects in temperate regions (Salt 1936 and others since then). The relationship between insects and low temperature is dynamic, making it difficult to assign specific temperatures at which an insect won't survive, or more importantly, become established in a particular region. Steinhaus considered cold to be one of several agents of noninfectious disease (Steinhaus 1962)—a useful paradigm for evaluating effects of biotic and abiotic factors on insect susceptibility to cold and changes in fitness. Table 1 lists some factors to consider when evaluating insect responses to cold stress.

The hemlock woolly adelgid (HWA), *Adelges tsugae* Annand, responds uniquely to the change of season in the progression of its life cycle. The sisten generation aestivates or rests as a first instar during summer months and resumes development in fall, which is heralded by development of their woolly coat. As temperature permits, the adelgids develop through the winter into adults. The sistens surviving overwinter to adulthood begin egg production in early spring, producing the progredien and sexuparae generation—sexuparae are a winged form that presumably don't contribute to population growth or expansion in the northeastern U.S. because they lack a required alternate host. The progredien generation in turn produces a new sisten generation in late spring that will ultimately overwinter.

Evidence of the cold–tolerance of HWA overwintering sistens has been reported in a series of publications produced by researchers at the Entomology Research Laboratory, University of Vermont (Parker et al. 1998 &1999; Skinner et al. 2003). Experiments were conducted by collecting winter-acclimated insects in the forest and exposing them to cold in a low temperature bath in the laboratory. Using this methodology, HWA survival was examined in relation to intensity and duration of cold exposure, and the geographic location and season in which collections were made. The use of HWA that had experienced a natural change of season before cold exposure enhances the usefulness of these findings for gauging responses of forest populations to winter climates.

Several critical temperatures for HWA survival have been observed. The lower lethal threshold where little or no survival occurs in mid-winter (January) is between -30 and -35° C. During the same season -25° C was identified as a transitional point where substantial mortality begins to occur. However, as spring approaches this transitional temperature increases to -15° C, which has no effect on survival during mid-winter. In more southerly locations the loss of cold-acclimation occurs earlier in the year, most likely related to earlier onset of spring. However, there is also evidence of a genetic component to variation in cold-tolerance (Butin 2003).

Table 1.—Important factors relevant to insect responses to cold.

Variables to Consider	Example
Insect stage of development	Sensitivity of overwinter vs. reproductive stages
Seasonal acclimation	Change of season increases cold tolerance
Intensity and duration of cold	Very low temperatures for short times
Genetic influences on tolerance	Genetic populations can vary in cold tolerance
Interactions with other stressors	Unhealthy trees increase sensitivity to cold
Individual vs. population responses	Few survivors expand population rapidly
Sub-lethal effects of cold exposure	Reduced reproduction and longevity of survivors

Extensive data is available on ambient temperatures and other environmental parameters for most areas threatened by HWA. Temperature is monitored in weather stations protected from sunlight and other elements and does not necessarily represent conditions in the HWA microhabitat– the tips of branches on hemlock trees. Understanding the relationship between ambient and microhabitat temperatures is necessary in order to infer geographic range limits from cold-hardiness data. We are in the second year of a project (2002-2004) to elucidate this relationship and have sites at Mt. Tom Reservation (yrs 1 & 2) Holyoke, MA and Kettletown State Forest (yr 2), Southbury, CT. We are monitoring temperature (15-min. intervals) on the north and south aspect of hemlock trees (yr 1 – 6 trees; yr 2 – 12 trees) from late December through March with probes placed on the underside of the current year's growth. In addition, ambient temperature is monitored in three weather stations per site along with observations of solarization, rainfall, leaf wetness, relative humidity and wind speed. Data taken on HWA survival will not be presented.

During the winter of 2002-2003 (yr 1) the ambient temperature at Mt. Tom Reservation never dropped below -25° C, the transitional temperature where major negative effects on HWA survival can be expected to occur (Fig. 1). On three occasions the minimum daily temperature dropped below -15° C, the point where previous data suggests reductions in survival would occur later in the season. Currently we have no way to predict when the change in acclimation that reduces cold tolerance takes place. However, there is substantial scientific background to develop meaningful research in this area.

We found only small differences between daily minimum ambient and microhabitat temperatures (Fig. 2) and 90% of differences were less then 1° C. These results suggest that minimum ambient temperature may provide insight for course delineation of HWA potential range relative to the critical threshold of -25° C and lower. In contrast, daily maximum temperature generally tracked higher in the HWA microhabitat relative to ambient (Fig. 3). The temperature increase was most pronounced on southerly aspects of trees, and when days were sunny. These data

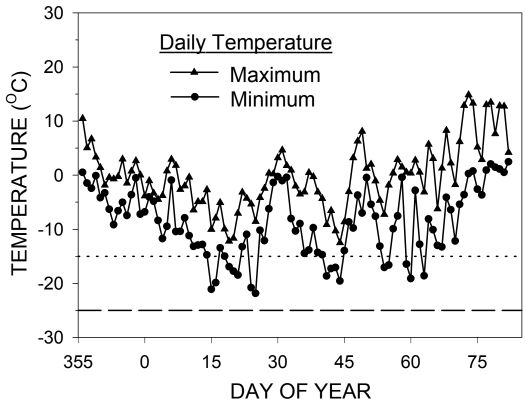

Figure 1.—The average minimum and maximum daily temperature at Mt Tom Reservation, Holyoke, MA.

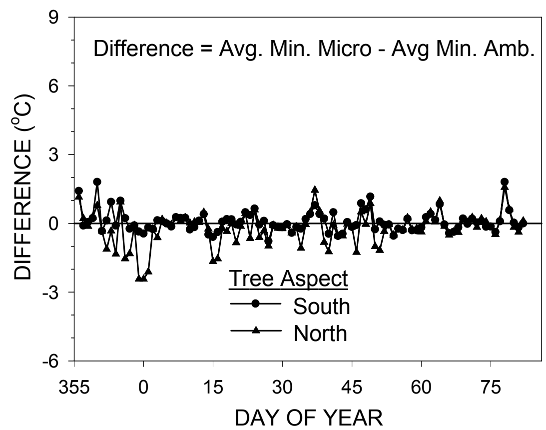

Figure 2.—Daily differences between minimum ambient (zero reference line) and minimum microhabitat temperatures on two of hemlock trees.

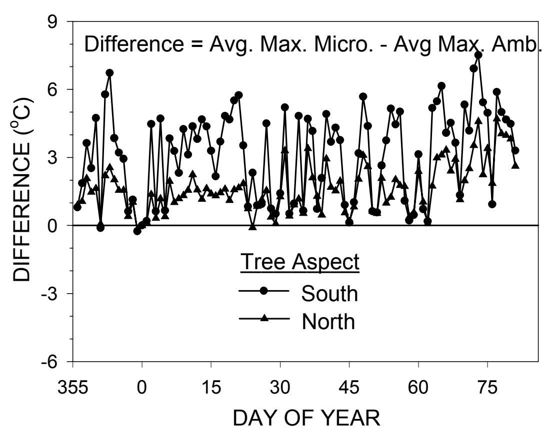

Figure 3.—Daily differences between maximum ambient (zero reference line) and maximum in HWA microhabitat temperatures on two aspects of hemlock trees.

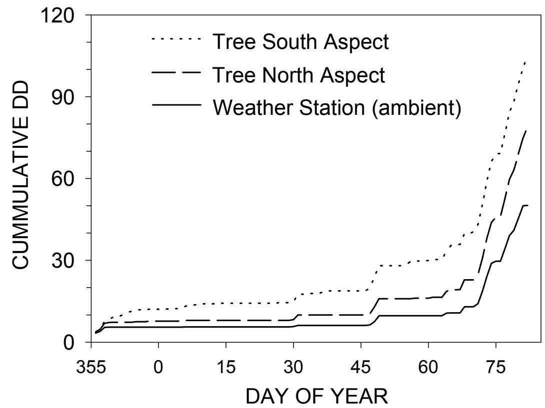

Figure 4.—Cumulative degree-days in HWA microhabitat on north and south aspects of hemlock tress and in weather stations.

indicate that HWA are experiencing more warming than ambient temperatures would indicate. The accumulation of warmth by insects is strongly associated with physiological changes and progression of development. Loss of cold-acclimation by HWA may be influenced in this way.

A degree-day model may be a useful approach for predicting changes in HWA cold-acclimation. These models are based on the accumulation of warmth above a minimum developmental threshold and a thermal constant necessary for a particular physiological event to occur. No developmental threshold is available for HWA sistens, but Salmon et al. (2002) determined the value to be 3.8° C for 2nd instars of progridien HWA. An exercise using this value to calculate degree-day accumulation finds ambient temperature a poor predictor for degree-days in the HWA microhabitat (Fig. 4). No thermal constant is available for loss of cold-acclimation by HWA, and factors such as photoperiod may also be involved.

Customarily, USDA plant hardiness zone maps (USDA 1990) are consulted for linking experimental data on HWA mortality to climatic conditions within a region. We know HWA are already established in areas corresponding to zones 5a and 5b, and experimental results suggest survival may be possible in zone 4b and potentially zone 4a. Survival in zone 3 seems unlikely. However, this course approach doesn't take advantage of the abundance of climatic data that is available, nor can it incorporate developing understanding about the effects of duration and timing of cold exposure on survival, or changes in HWA susceptibility to cold relative to season and factors mentioned in table 1. For minimum temperatures, ambient data may have utility without adjustment for microclimatic effects for predicting geographical range limits of HWA. For maximum temperatures, our data will help define the ambient and microhabitat relationship, but understanding the role warmth has for modulating HWA susceptibility to cold is essential for narrowing predictions of HWA range limits.

There are numerous practical incentives for defining potential limits of HWA range, including better allocation of resources for surveillance and management. Several avenues of investigation are needed to enhance this effort. The response of HWA to cold needs to be defined in increments smaller then 5° C, which is the precision currently available. Threshold temperatures for sisten development and thermal constants for loss of cold-acclimation are essential for predicting lethal effects of the less severe temperatures in late winter. Data are needed from early winter on microhabitat temperature and HWA survival. Research on sublethal effects of cold, genetics of HWA populations, and range expansion in colder regions would better relate individual responses to consequences for populations. Finally, a synthesis of environmental, geographical and forest cover data is essential for characterizing the risk of invasion of northern hemlock forests by hemlock woolly adelgid.

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