# Ecological Adaptations of the Mountain Pine Beetle to Cold Temperatures

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## INTRODUCTION

As forest management moves towards a framework for decision-making which is ecologically couched, the important functional role of insects and diseases in the forest ecosystem is becoming more fully recognized. This is especially true for indigenous insect species such as the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) (MPB). Although the MPB is currently a serious competitor with humans for natural resource commodities, the fact that MPB populations have been an important ecological component of western forests for millennia can not be ignored. From this, it follows that our understanding of population cycles of this insect species will be furthered if we take an ecosystem perspective and look at adaptations of the MPB to the forest ecosystem. Several components of the forest ecosystem which are important driving forces on MPB populations are the cyclic and acyclic abiotic processes of the environment. Changes in abiotic environmental processes, both long and short term, can have a drastic effect on insect populations and may require highly evolved adaptations (Tauber et al.,1986). Weather in particular is thought to be a key component of pine beetle population outbreak dynamics (Beal, 1927; 1933; Keen and Furniss, 1937; Safranyik, 1978; Terrell, 1954; Werner and Holsten, 1984; Wygant, 1942). Although weather is a broadly occurring phenomena, when expressed as the temperature regime of the phloem of host trees it becomes an effective factor useful in understanding local adaptations of pine bark beetles to their microhabitat.

The importance of temperature to MPB populations was initially recognized by Hopkins (1899). Since that time, temperature thresholds for development (Amman, 1973; Bentz et al., 1991; Powell, 1966; Reid, 1962; 1963; Reid and Gates, 1970; Safranyik and Whitney, 1985; Wygant, 1942), emergence and flight (Gray et al., 1972; McCambridge, 1971; Safranyik and Jahren, 1970; Shepherd, 1966), and the effect of general climatic regimes on population dynamics (Powell, 1969; Safranyik, 1978) have been investigated. Studies were also conducted on cold tolerance of 4th instar MPB, the principle lifestage thought to be overwintering (Somme, 1964; Wygant, 1942; Yuill, 1941). In a study which included factors such as competition and predation, Cole (1981) found winter temperature to be the most important mortality factor in MPB populations. These studies have demonstrated the importance of temperature as a driving force on MPB population dynamics. However, little research has been focused at understanding the mechanisms

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involved in the response of all MPB lifestages to low temperatures during the winter, or spring and fall which also may be influential times in the beetle life cycle.

The geographic range of the MPB encompasses elevations and latitudes that transcend a monotypic weather pattern. In the Intermountain region, MPB populations are frequently found in habitats where typically adverse conditions are the norm (e.g. high elevations). Consequently, individuals of this species are forced to tolerate a wide range of fluctuating and cold temperatures, frequently for extended time periods (Bartos and Amman, 1989; Schmid et al., 1993). What adaptations have this nondiapuasing species evolved to tolerate this type of environment? The likelihood of survival during periods of cold temperatures is a complex process dependent on several factors including the frequency and duration of exposure, and the cold-hardiness of the individuals. Since the time the original studies were conducted on MPB cold tolerances, more sophisticated and accurate techniques have become available, with a concomitant increase in knowledge of the cold-hardiness process in insects. A mechanistic understanding of cold tolerance in the MPB requires more in-depth studies of cold-hardiness of all MPB lifestages at all times of the year, in relation to the temperature regimes of their natural habitat.

Temperature is an important indicator of seasonal change used by many insect species, including the MPB, to keep their life cycle synchronized with the environmental conditions they are experiencing. Phenology is a term used to describe this process. Phenology is the set of adaptations that lead to appropriate seasonal timing of recurring events such as development, growth, reproduction, and dispersal in relation to the environment (Tauber et al., 1986). Using a phenology model developed for predicting temperature-driven MPB development, Bentz et al. (1991) hypothesized a strategy for seasonal synchrony of the MPB that allows for coincident adult emergence, an important life-history strategy for this species. Included here is a brief validation of this model, using results obtained from an intensive year-round sampling study. Also included are results from a preliminary analysis of cold-hardening capabilities of MPB lifestages, and a discussion of MPB population adaptations to low temperatures and strategies for survival.

## METHODS

Four sites, all in close proximity to current MPB infested lodgepole pine (*Pinus contorta* Douglas), were selected in July 1992 (Table 1). Although the areas were chosen to represent a range of elevations and latitudes, MPB populations levels were very low during this time in the Intermountain region, and consequently availability of possible sites was limited. At each site, five to 10 trees were baited with synthetic MPB aggregation pheromones (Pherotech Inc.). After beetle flight, colonization of baited trees was monitored, and temperature probes were placed in the phloem, 1.4 meters above the

ground on the north and south side of each successfully infested tree. Temperature probes consisted of YSI thermilinear thermistors connected via special purpose communication cable to a Campbell Scientific 21x micrologger. Phloem temperatures were measured every 15 minutes and averaged for an hour, beginning just after successful colonization and ending during beetle emergence and flight the following August. Ambient air temperatures were measured 1.4 meters above the ground, using a temperature probe which was placed in the shade. At each site, to measure below snowline temperatures, two additional probes (N and S sides) were placed on an infested tree about .5 meter above the ground. Infested bolts were used at the Togwotte site because no infested trees were available.

Table 1. Research site information.

| Site | Elevation | Latitude | Aspect | BA |
|---|---|---|---|---|
| Logan (Utah) | 2043 m | 41°56' | NE | 210 |
| Moose (Wyoming) | 2121 m | 42°45' | N | 100 |
| Ranch (Idaho) | 2061 m | 44°07' | SW | 140 |
| Galena (Idaho) | 2348 m | 43°54' | W | 170 |
| Togwotte (Wyoming) | 2927 m | 43°45' | S | 220 |

Each site was visited monthly (bimonthy during winter months), and four 100 $cm^2$ samples taken from each infested tree: two from each aspect (N/E and S/W, low and high). For each sample, the bark was removed and all individuals extracted and placed in alcohol and returned to the laboratory where larval headcaps were measured for instar determination. Parent and larval galleries in the sample space were also measured and counted. The beginning of July, four fine-mesh screen cages were placed on each infested tree (N/E and S/W, low and high), and adult emergence monitored. At each site, on each sample date, live larvae were collected from two additional infested trees (N and S aspect of the bole). Larvae were placed in petri dishes with moist filter paper, and the dishes packed in insulated coolers and shipped via overnight mail to Virginia Polytechnic Institute and State University, Blacksburg, VA for supercooling point determination. To determine supercooling points, individual larvae were slowly cooled and the sudden temperature increase associated with formation of the ice lattice in the tissue was measured using thermocouples attached to the top and bottom of each insect. Cooling was accomplished by placing the insects on a cold plate connected to a refrigerated water circulator.

## RESULTS

**MPB Microhabitat:** MPB larvae are exposed to daily fluctuations in phloem temperature which, on the south side of the tree, can be as great as 30°C on a given day (Fig. 1). This is a large amount of variation for an insect to adapt to, especially when the daily temperature fluctuates above and below the development threshold. Temperatures recorded from the north and south aspects of boles provide an indication of the temperature variation larvae within a single tree are exposed to. Daily minimum phloem temperatures on the north and south aspect of trees are generally the same, although maximum south aspect temperatures were almost always greater than maximum north aspect temperatures. Differences in temperature between north and south aspects of a single tree were reduced during winter. Werner and Holsten (1984) report one- and two-year generation *Dendroctonus rufipennis* within a single tree, with one-year beetles on the south sides of the bole where a required phloem temperature threshold for development is obtained. Although MPB in this study did not have varying voltinism in a single tree, development rate appeared to be faster and more spread out on the south side of trees.

Daily minimum phloem temperatures on the south sides of trees are typically slightly warmer (within 3.5°C) than air temperatures in the stand. However, during the winter months, minimum phloem temperatures are often colder than air temperatures (within -1.0°C) (Fig. 2). Daily maximum temperatures on the south aspect of trees are always greater than daily air temperatures, especially in the spring and summer when phloem temperatures were typically 10 to 20°C warmer than air temperatures. These observations suggest that the MPB habitat is not protected from extremes of the environment. Attempts to get a record of standing infested tree phloem temperatures below the snowline were unsuccessful. In all plots, less than .5 meter of snow consistently accumulated at the base of the temperature monitored trees. However, at the Togwotte site, below snowline temperatures were obtained in infested bolts. Below the snowline differences between maximum and minimum phloem temperatures were much reduced, and temperatures eventually equilibrated to 0°C (Fig.3).

**Adaptive Strategies:** Insects rely on a number of strategies to increase the likelihood of survival during cold periods. Diapause is typically thought to be the most common strategy. However, the MPB, like most *Dendroctonus* species, does not have a known diapause. Some insect species also attempt to avoid exposure to low temperatures through ecological or behavioral adaptations such as migration to a protected habitat and construction of insulated hibernacula. However, phloem measurements recorded in MPB infested lodgepole pine in 1992-93 indicate that MPB do not escape exposure to extreme temperatures in this host type. In fact, differences between minimum phloem and minimum air temperatures were less than ± 2.5 °C, and during winter months minimum phloem temperatures were often lower than minimum air temperatures (Fig. 2). Also, daily maximum phloem temperatures on the south side of the bole were almost always

greater than daily maximum air temperatures in the stand. Although temperatures in infested bolts below the snow appeared to be insulated from ambient air temperatures (Fig. 3), attacking adult MPB do not necessarily prefer the lower part of a bole, which would be insulated by snow, over the rest of bole. Rasmussen (1974) found that 93% of initial attacks of MPB on lodgepole pine are between 1.2 and 2.4 meters above ground level. Consequently, adaptive strategies of the MPB to low temperatures most likely focus on adjusting physiological and biochemical processes that enhance their tolerance to exposure to subzero temperatures. This can occur through some sort of dormancy and or cold-hardening strategies. Although some insect species are able to withstand the formation of ice in the extracellular body fluid (freeze tolerant species), freeze intolerant species must avoid freezing of body tissues (Salt, 1961). Freeze avoidance is accomplished through a process known as cold-hardening. In the cold-hardening process, the supercooling point refers to the temperature at which spontaneous nucleation of body water occurs and ice crystals begin to form in the insect tissue (Lee, 1989). For those species which cannot survive tissue freezing, the supercooling point represents the lower lethal temperature, although death may also result due to exposure to temperatures above the supercooling point (Lee, 1991). In preparation for winter, freeze intolerant insects decrease their supercooling point, thus increasing their cold-hardiness.

Preliminary results show MPB larvae are capable of supercooling to temperatures below -30°C in the middle of winter (Table 2). The lowest supercooling point determined was -41.5°C. The variation in individual supercooling points within a particular instar on a given day averaged 10 to 15 °C. However, there were no observable trends in variance by instar or season. At the Logan and Moose sites, individuals were able to supercool to -20°C without prior exposure to temperatures below 0°C. This suggests that polyol synthesis may be triggered above this temperature, or that MPB are able to supercool in the absence of antifreeze compounds perhaps due to nucleator activity as was found in *Ips spp.* (Gehrken, 1984). The mean supercooling points in all instars changed with season, dropping to a low in winter with higher values in the fall, spring, and summer. Mean supercooling points in the spring and fall were often much closer to minimum phloem temperatures larvae were experiencing than were mean supercooling points measured in the middle of winter (Fig. 4). In other words, larvae appear to maintain a large cushion in the middle of winter when temperatures are typically very cold, in contrast to other times of the year. Supercooling is a metabolically taxing endeavor and it is not advantageous for individuals to invest resources when it is not necessary to cold-harden to very low temperatures. This suggests that spring and fall might be the times of greatest temperature-induced mortality in the MPB, not winter as was previously believed. However, due to the large daily fluctuations in temperature during the spring and fall (Fig. 1), maintaining supercooling points so close to the actual minimum temperature in the habitat seems to be a risky strategy. One possibility is that MPB larvae are able to rapidly (e.g. within minutes) alter their cold-hardening capacity (Lee et al. 1987). If this were true, larvae would be able to track wide fluctuations in temperature, surviving the lows and taking advantage of the highs. Also, temperature thresholds for metabolism of antifreeze components may not have been met. Timing of field sampling in this study

made mortality estimates in the field difficult, so it is not known what proportion of the individuals did die due to cold temperatures during the spring and fall when supercooling points were closer to minimum temperatures experienced in the phloem.

Table 2. Supercooling points (SCP) estimated during the winter (January) of 1992-93 for four MPB lifestages at four geographic locations.

| Lowest Estimated Winter SCP | | | | |
|---|---|---|---|---|
| **Site** | **Instar I** | **Instar II** | **Instar III** | **Instar IV** |
| Moose | -34.8 | -28.7 | -41.5 | -32.1 |
| Logan | -13.9 | – | -32 | – |
| Galena | -21.2 | -35.4 | -35.2 | -35.4 |
| Ranch | – | -38.2 | -36.9 | -35.6 |

Despite the fact that south aspect temperatures were typically much warmer, there were no consistent differences in supercooling points of samples taken from N/E and S/W aspects. There were also no discernable differences in timing of larval development on the 2 aspects of the bole. However, latitude and elevation did have an effect on development. Individuals from Galena, the site at the highest elevation and furthest north latitude, were more delayed in development than those at the Logan site which is lower in elevation and furthest south in latitude. Differences in development between the two sites occurred as early as the September sample date. Colder fall temperatures at the Galena site resulted in the occurrence of instars I and II in winter samples, while instars III and IV were predominate in winter at the warmer Logan site. Although no one particular instar was found to be consistently more cold-hardy than another, supercooling points among pooled instars were significantly different ($\alpha$=.05). There were no consistent trends in variance within a particular instar on a sample date, or among sample dates. These results may be due to small sample sizes however. The range of instars found overwintering was more diverse than earlier studies had indicated (Table 2). Although Schmid et al. (1993) also found 1st and 2nd instar larvae in ponderosa pine (*Pinus ponderosa*) during the winter, it was previously thought that only the larger instars (3rd and 4th) overwintered in lodgepole pine.

Based on all samples from all collection sites, the greatest proportion of lifestages sampled during this generation (1992-93) were instar III and IV (Fig. 5). In constant temperature experiments these two instars had higher thresholds for development than

other instars (Bentz et al. 1991) which might, in part, explain their presence at higher proportions. Lower thresholds for development in the eggs, instar I, and instar II result in rapid movement through the early lifestages in late summer and fall. As individuals move into the 3rd and 4th instar, colder temperatures and higher developmental thresholds cause individuals to stay in those lifestages through winter and spring. Accordingly, colder temperatures in late summer and during the fall would result in slower development in the early instars, delaying movement into the later lifestages. This is the pattern observed at the Ranch and Galena sites, where instars I and II were also present during the winter. The adaptive significance of this is unclear at this time. Because all larval instars appear to be equally able to cold-harden, the relative temporal distribution of each lifestage may be as important for maintaining uni-voltinism as for winter survival.

**Phenology Model Validation:** Bentz et al. (1991) developed a temperature-driven phenology model for the MPB using data from constant-temperature laboratory experiments. The model is executed using hourly phloem temperatures, and includes temperature-based oviposition and recruitment. Therefore, the model can be run for consecutive years. Currently, lifestage specific mortality is expressed in a step-wise fashion using temperature thresholds based on expert opinion. See Logan et al. in this proceedings for further description of the model. Data collected in the study described here were used for a preliminary evaluation of model performance. The evaluation was performed by initiating the model with the proportion of the population in each instar on the first field sample date at a particular geographic site. Hourly phloem temperatures from the same site were used to drive the model. Model predictions were then compared to collections made in the field of observed lifestages present on each sample date. The intent of the model is not to predict numbers of individuals in each lifestage at a particular point in time. This is an unrealistic goal. Instead, the function of the model is to represent MPB population trends both within a generation and between generations.

Using data collected in 1992-93, within generation model behavior for eggs through eclosion to the teneral adult is good for all but the 3rd instar. Figure 5 includes results for a comparison of data from the Ranch site (north side). Temperature thresholds and/or development rate for instar III are inadequately represented in the model, causing development to instar IV, and subsequently pupae, to occur too rapidly. However, the model did correctly predict the presence of instar II in the winter. Behavior of the model for between generations was also encouraging. The model was initiated as before, but run continuously for 10 years, using the same year temperature file. Model predictions of lifestage timing are good, with few aberrant lifestages present at times during the year when field samples suggests they should not be. Again, problems with instar III are indicated.

The relative temporal distribution of each lifestage plays a vital role in the

continued survival of MPB populations. Synchrony of emerging adults is an important component of successful colonization of optimal, more vigorous, hosts. How the MPB, a nondiapausing, univoltine species, maintains the required synchrony is not fully known. One hypothesis is that different inherent thermal thresholds and developmental times in the lifestages help to synchronize individuals of distinct cohorts resulting in coincident adult emergence. This hypothesis was tested by Bentz et al. (1991) using the MPB phenology model. In the temperature regime used to drive the model in that study, individuals from distinct cohorts became temporally synchronous in instar III, with eventual coincident eclosion to the teneral adult stage. Phloem temperature measurements collected in the current study were used to test the same hypothesis, in the same manner. The model was initiated with three different recruitment levels of egg cohorts: (1) 100 eggs laid during 1 day; (2) 100 eggs laid over 10 days; and (3) 100 eggs laid over 20 days. Using phloem temperature measurements from the north side of trees at the Ranch site in 1992-93, the synchrony or "catch up" of the different cohorts occurred as individuals moved into the pupal stage, much later in the lifecycle than was observed by Bentz et al. (1991) using a temperature record from 1989-90. These results suggest that seasonality in the MPB is indeed mediated by inherent thermal thresholds, but that the timing is flexible and depends greatly on the temperature regime individuals are exposed to. Beck (1991) and Danilevskii (1961) reported that several species of *Agrotis* had a nondiapause dormancy important to their seasonal biology, although they failed to exhibit a consistent periodism and that some had a "moveable quiescence".

**Quantifying cold-hardiness:** From the preliminary data described here, a conceptual model for quantification of cold-hardiness in the MPB is being developed. The current model provides a mechanism for asking questions about the complex cold-hardening process in the mountain pine beetle, and upon completion will be included in our MPB phenology model for mortality prediction. The model uses daily temperature accumulation recorded in the field to predict instar specific freezing mortality at the individual supercooling point. Based on limited data, the model currently assumes that MPB are freeze intolerant and that the supercooling point is the lower lethal temperature. Sublethal and lethal effects due to freezing above the supercooling point are not yet included in the conceptual model. An outline of the model is provided in Appendix I.

## CONCLUSIONS

Recently it has become recognized that "natural" disturbances such as MPB outbreaks play an important role in healthy, functioning ecosystems. A central issue is an improved understanding of the MPB outbreak phenomena. Climate and weather play a key role in the outbreak phenomena both through direct effects such as winter mortality, and mediated through more subtle pathways such as influencing timing and maintaining

appropriate seasonality. The cold-hardening process is an essential component of the climatic adaptive strategy for this nondiapausing species. Because the MPB does not have a diapause, it must have alternative means to maintain seasonality and synchrony. This is especially true for MPB populations infesting non-stressed host trees which typically requires a mass attack to overcome host defenses. Nondiapause dormancy (quiescence) allows for a high degree of responsiveness to the immediate conditions of the environment, unlike diapause which is under the control of token stimuli occurring in advance of seasonal changes (Tauber et al., 1986). Although diapausing insect species can also cold-harden, diapause may prohibit immediate access to some of the insects metabolic machinery (e.g. inability to resynthesize glycogen from glycerol until after diapause has been broken) (Danks, 1987). Insect species typically diapause to maintain seasonality, synchrony, and survive adverse conditions (e.g. high or low temperatures, moist, dry periods or food shortages). The MPB has evolved alternative strategies. The MPB microhabitat under the bark of lodgepole pine trees is not protected from temperature extremes of the environment. In the middle of winter, daily minimum phloem temperatures were often colder than air temperatures in the stand. Preliminary results from the first year of an ongoing study indicate that in the middle of winter, all MPB larval instars are capable of cold-hardening to very low, sub-freezing temperatures which are typically colder than phloem temperatures of their habitat. Larval supercooling points in the spring and fall, however, are much closer to minimum phloem temperatures the larvae are experiencing.

An evaluation of a temperature-dependent phenology model for the MPB using field collected phloem temperatures and lifestage samples indicates that the model does a good job of predicting development in all but the third instar. Experiments designed to provide a more accurate representation of instar III development will be conducted and included in refinements to the phenology model along with mortality predictions based on seasonal cold-hardening capabilities. Further research using intensive laboratory experiments is aimed at more fully understanding the complex temperature-based mechanisms responsible for mortality and maintenance of seasonality in this ecologically important forest insect.

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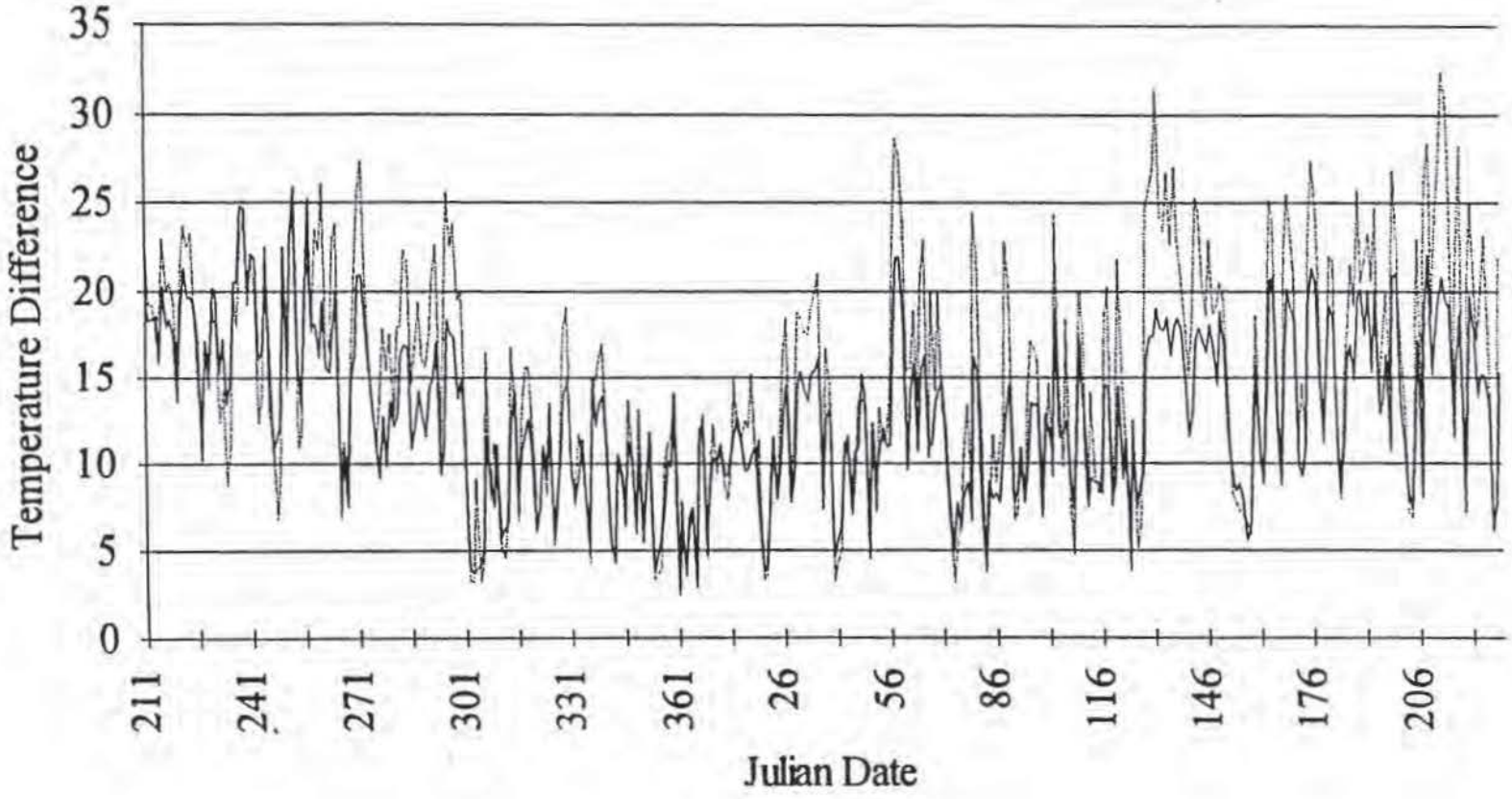



**Figure 1**. Difference between daily maximum and daily minimum phloem temperatures (°C) of four MPB infested lodgepole pines, north (solid line) and south (dashed line) bole aspect (Ranch site, 1992-93).

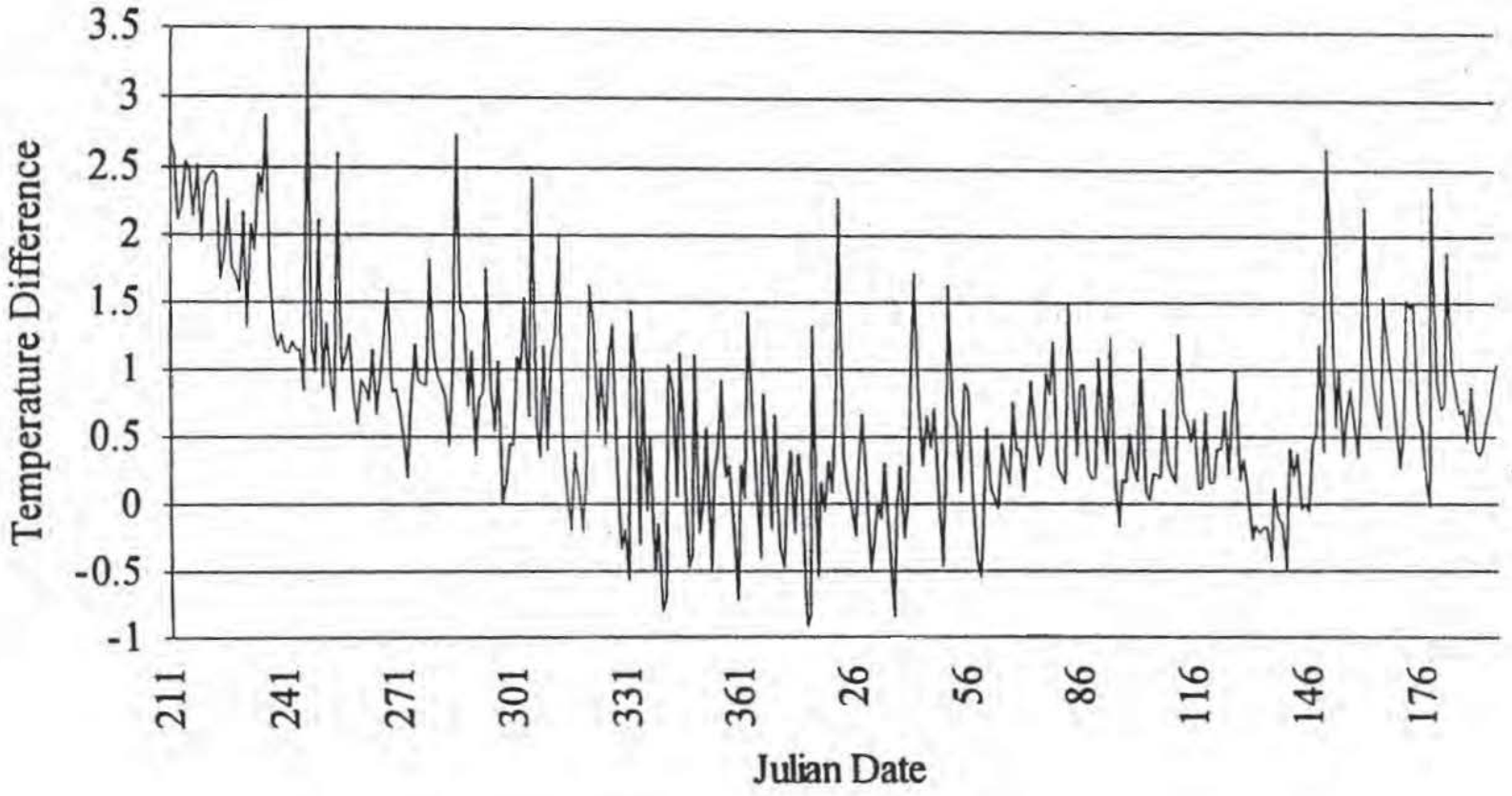



**Figure 2.** Difference between daily minimum phloem temperatures (°C) on the south side of four MPB infested lodgepole pines and daily minimum air temperatures in the stand (Ranch site, 1992-93).

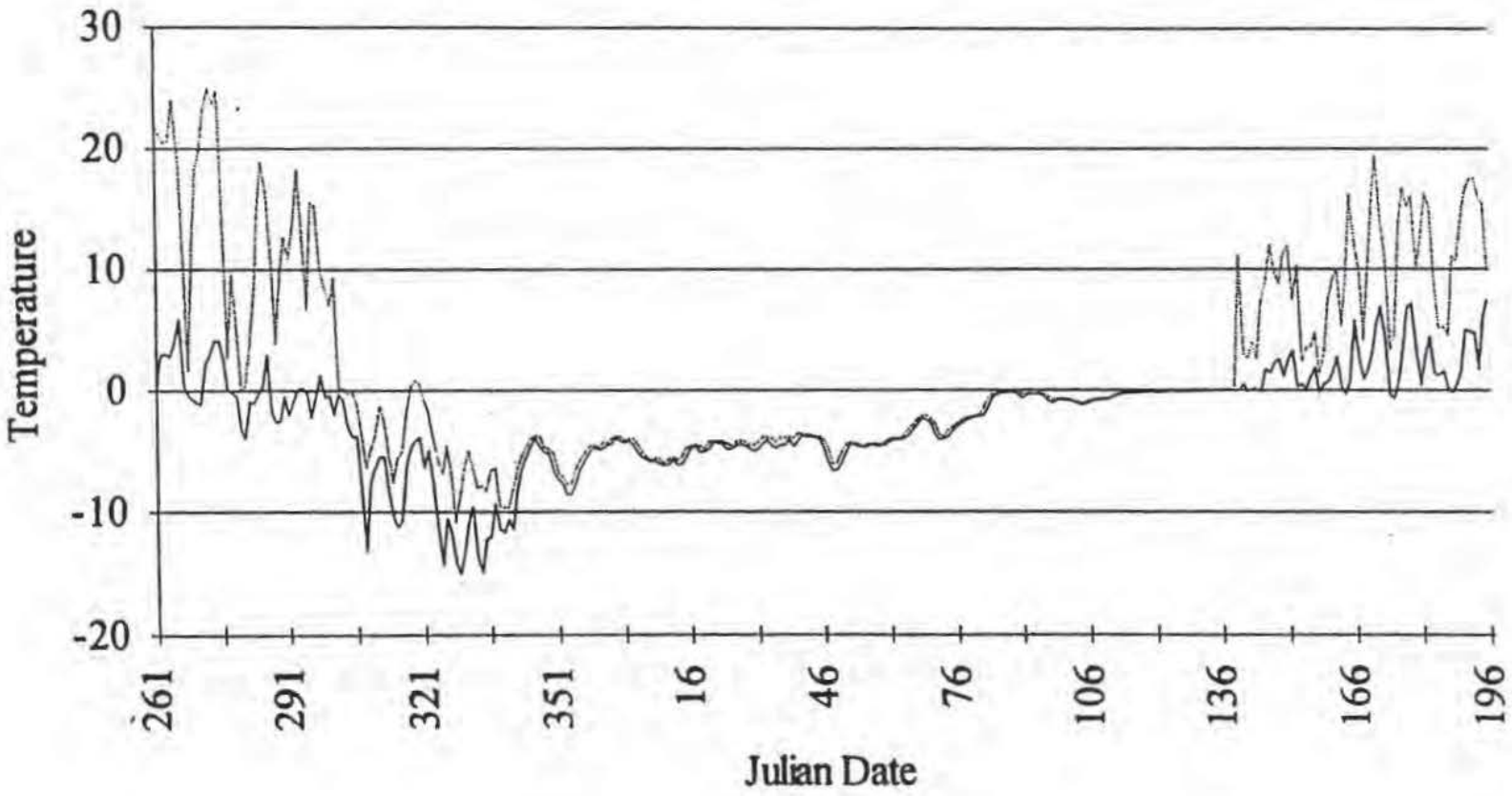



**Figure 3.** Daily maximum (dashed line) and minimum (solid line) phloem temperatures (°C) in a MPB infested bolt at the Togwotte site, 1992-93. The bolt was below the snow for a portion of the life cycle.

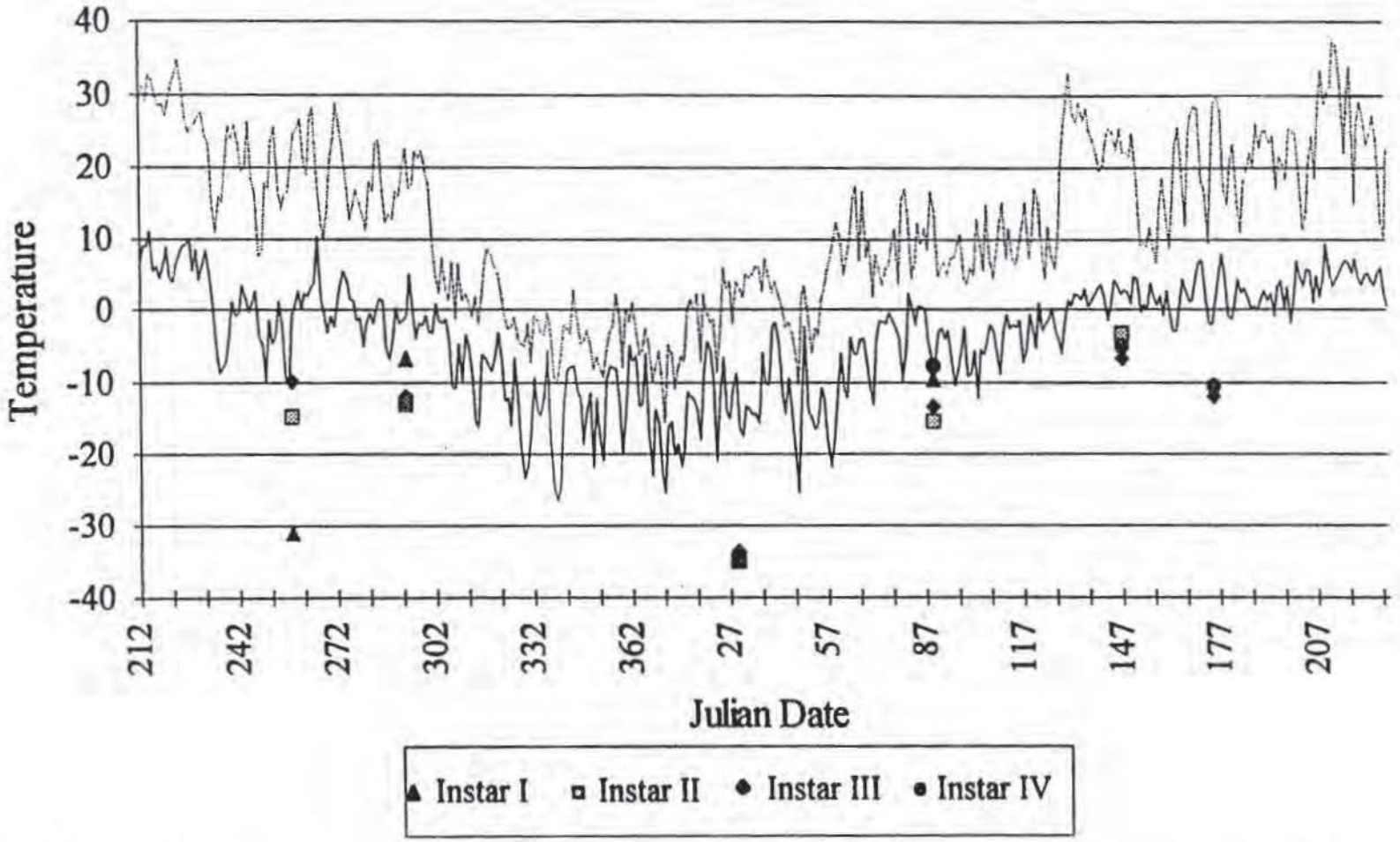
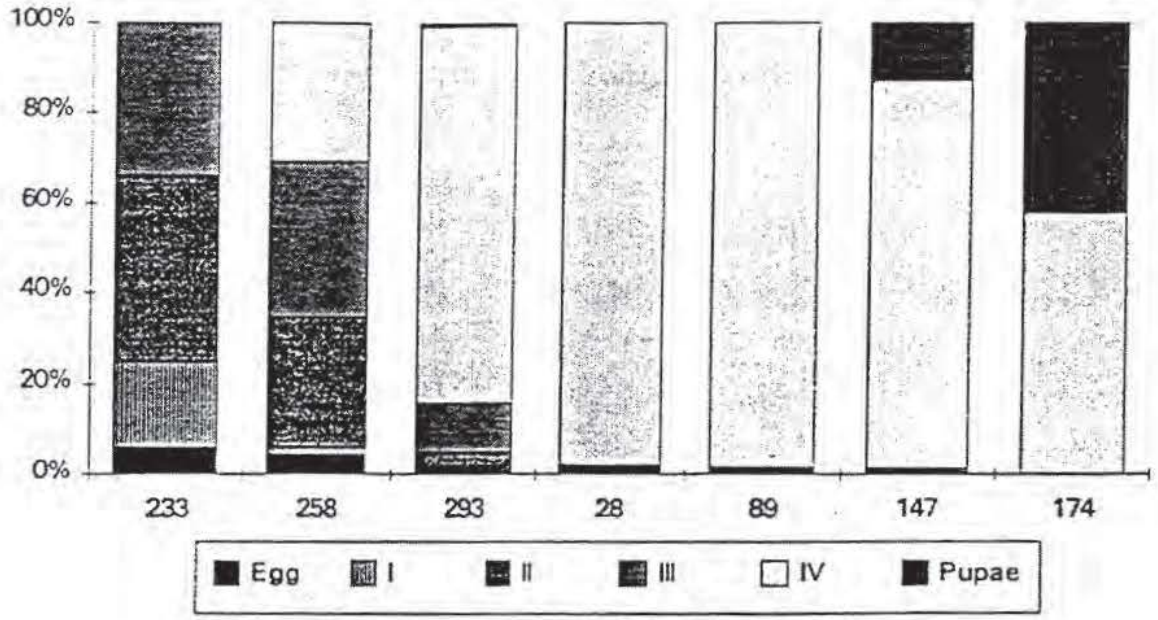



**Figure 4.** Daily maximum (dashed line) and minimum (solid line) phloem temperatures in four MPB infested lodgepole pines with mean supercooling points for each instar collected at the same site (Ranch site, 1992-93).

A.




B.

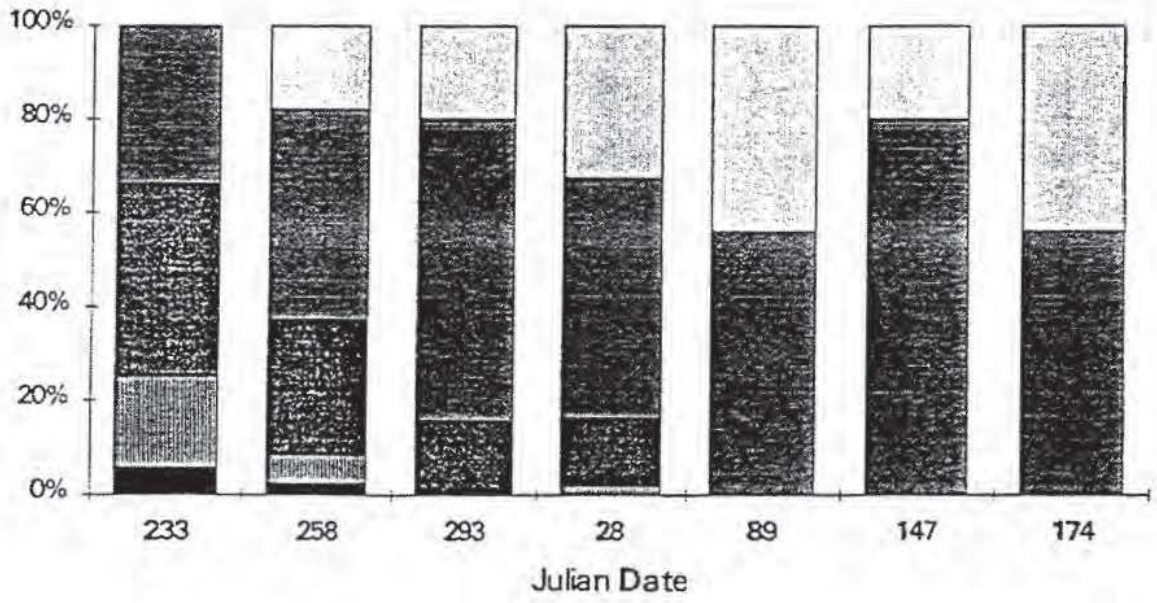



**Figure** 5. (A) Phenology model predictions using phloem temperature measurements from the Ranch site to drive the model. The model was initialized on JD 233 with population samples collected in the field. (B) Observed percent individuals in each lifestage throughout the life cycle at the Ranch site.

**Appendix 1. Conceptual model for quantification of insect cold-hardiness.**

ACC represents temperature acclimation necessary for cold-hardening:

$$ACC = f(CDD, HDD, UDD)$$

where:

CDD = cooling degree days below a temperature threshold (e.g. 0°C)
HDD = heating degree days above a temperature threshold but below UDD (e.g. 5 to 10°C)
UDD = upper heating degree days above a higher temperature threshold (e.g. 10°C)

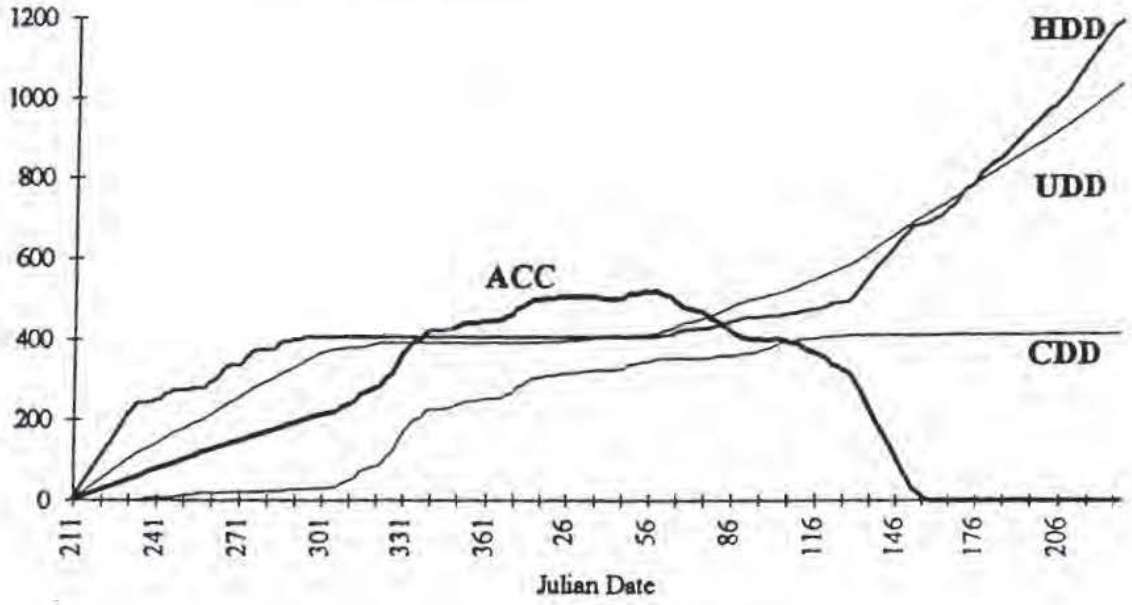



**Figure 1.** CDD, UDD, HDD, and ACC computed using phloem temperatures from the Ranch site, 1992-93.

Temperature thresholds for CDD, HDD, and UDD will change with time and increases and decreases in ACC. Determining temperature thresholds for the ACC function is an important aspect of the conceptual model. Current thresholds are based on preliminary data and values in the literature (Fig. 1).

The mean (Fig. 2) and variance (Fig. 3) for supercooling points of a particular instar are plotted as a function of ACC and curves are fit to the data. Based on a known temperature profile, the probability of freezing for each instar on a particular day may then be estimated (Fig. 4).

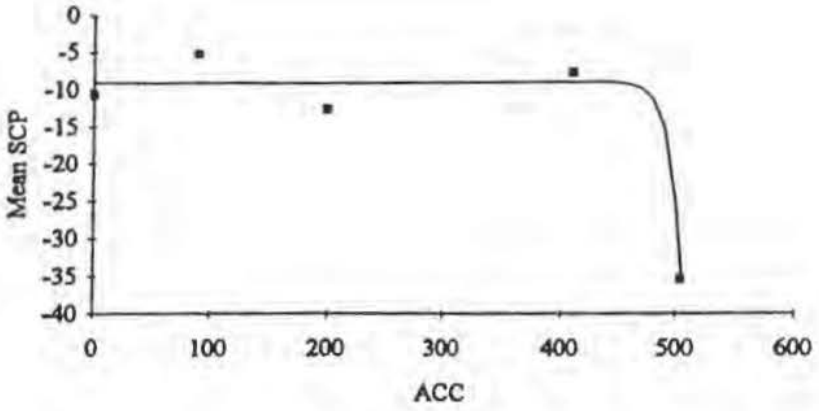



**Figure 2.** Mean supercooling points of 4th instar larvae as a function of ACC (Ranch site, 1992-93).

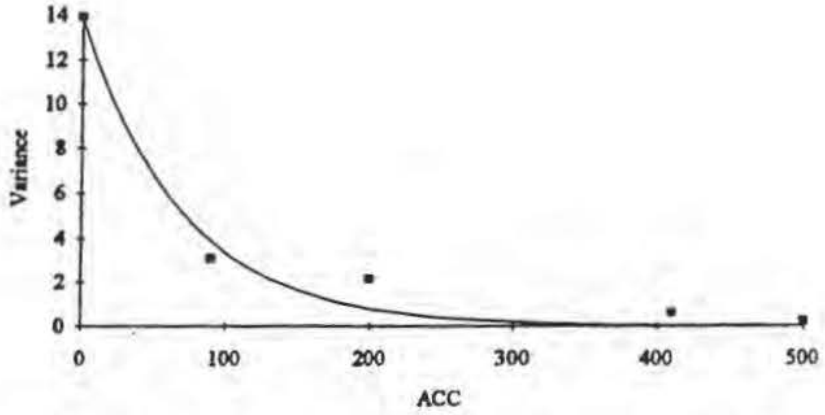



**Figure 3.** 4th instar larvae supercooling point variances as a function of ACC (Ranch site, 1992-93).

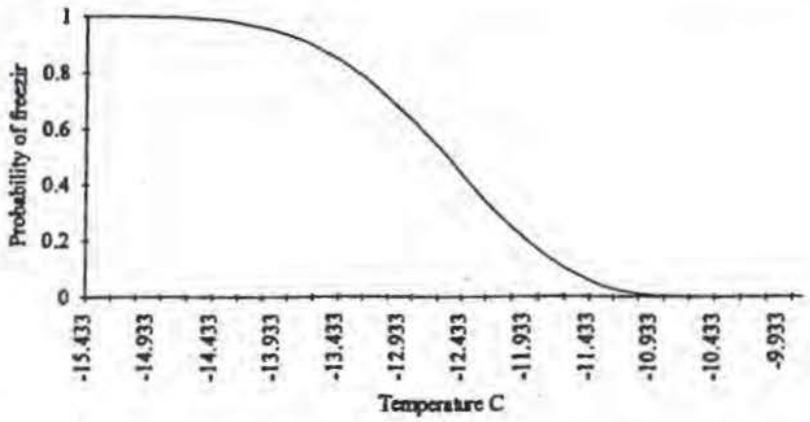



**Figure 4.** Freezing probability distribution for 4th instar larvae on a particular day (ACC=200, JD=291), given a phloem temperature regime.