

## Chapter 4

### Cold tolerance and winter mortality of bark beetles at Itasca State Park

#### 4.1 INTRODUCTION

Temperature has broad effects on the physiology and behavior of virtually all insects in all developmental stages. Temperature influences metabolic rate, flight activity, reproduction, nutrition, development, and survival. The ability to survive annual temperature minima can be a critical determinant of insect abundance. However, it is not known whether winter conditions exert significant mortality on populations of *Ips* bark beetles at Itasca State Park. In fact, surprisingly little is known about the overwintering biology of any *Ips* species. If winter conditions are a significant source of mortality for *Ips*, then it should be possible to reliably predict population abundance in the upcoming summer as a function of winter temperatures and snow cover. Such models could have high utility for management decisions. For example, controlled burning, which appears to increase the risk of bark beetle attacks (Chapter 6), could be planned to follow winters when beetle populations have been reduced by a particularly cold winter. Similarly, it might be desirable to place a priority on beetle control measures (e.g., mass-trapping or sanitation removal of winter blow downs) following mild winters when beetle populations are more likely to be high. This component of the research was designed to accomplish the following objectives: (1) measure the lower lethal temperature of the different species and life stages of *Ips*; (2) identify their overwintering sites; and (3) develop a model that incorporates knowledge of cold tolerance, overwintering sites, and microsite temperatures to predict winter mortality of *Ips* using easily measured climatic parameters (e.g., air temperature and snow depth). Appendix 6 is a related manuscript "Cold tolerance of four species of bark beetle (Coleoptera: Scolytidae) in North America" which has been submitted to Environmental Entomology. Here we summarize the components that are salient to forest management at Itasca.

#### 4.2 METHODS

**Cold tolerance.** We conducted field and laboratory studies to test the ability of beetles to survive at low temperatures. Supercooling points were measured by cooling individual insects at 0.20 °C / min and recording the temperature at which crystallization occurred (evident as an exotherm). Our studies included over 2500 measurements of supercooling points in *Ips pini*, *I. grandicollis*, and *I. perroti* of different life stages at different times during the winter and subjected to different acclimatization regimes. Because supercooling points are functionally synonymous with lower lethal temperatures for all of these species and life stages, the results provided a rather detailed characterization of cold tolerance in *Ips* spp. that inhabit Itasca State Park. These represent the first physiological measurements of cold tolerance that have been conducted for any of these species.

Logs infested by wild populations of *Ips* were collected in September 1997 and held in environmental chambers for one month at 10-15 °C under natural photoperiods. As adults emerged from logs they were introduced into screen boxes containing soil and litter and placed within the soil of a pine forest in Hanover, New Hampshire (43° 42' N, 72° 17' W). One box was removed from the soil each month for measurement of supercooling points in adults. One additional box containing 60 *I. pini* was placed in the forest at 1 m above ground where it was exposed to air temperatures without snow cover. Similar studies were conducted during the winter of 1998-99 and yielded similar results.

We tested for freeze-tolerance in association with the measurement of supercooling points. After we observed the exotherm associated with freezing, adults and immatures were warmed to ≈-22 °C and monitored for the ability to resume activity. Finally, we tested for the ability of immature *Ips* to resume activity and continue development after freezing. Logs with first instars and others with third instars and pupa were acclimated for one day at 15 °C, then one day at 8

°C, then one day at 0 °C before being exposed for seven days to -17 °C. After the -17 °C treatment, logs containing larvae were gradually warmed (1 day at 0 °C, then one day at 8 °C and one day at 15 °C before being moved to 22 °C) and placed into boxes containing a fresh log. Logs with first instars were dissected after 7 d at 22 °C to see whether early larvae had survived and resumed development. Remaining logs were examined after one month at 22 °C to see whether late larvae or pupae had completed development and begun to reproduce within the new log.

**Overwintering habitats.** In October 1998, 975 recently emerged *Ips grandicollis* and 284 *Ips pini* were introduced into litter of a 40-year-old *Pinus resinosa* forest at Colfax, Wisconsin and allowed to choose their overwintering microhabitat. To aid in locating the animals later, beetles were released within two 20-cm diameter PVC pipes that had previously been inserted into the soil with a minimum of disturbance to the soil and litter. In January and March 1999, pipes were removed with soil and litter intact and sliced into 2.5 cm and 1 cm sections respectively. Beetles within each of these depths were separated, identified, and scored as dead or alive.

**Microclimate of overwintering habitats.** In association with the studies of overwintering habitats, we collected detailed measurements of the microclimates experienced by overwintering beetles. From November 1998 through April 1999, air, litter, and soil temperatures were recorded every 30 minutes with an array of 28 thermistors spread among three 2 x 2 m sites with natural snow depth, no snow, or 2.5 cm of snow. The three climate study sites, and the studies of beetle overwintering habitat were all within 10 m of each other and within an area that was homogenous with respect to litter and soil characteristics. Snow was excluded from the no-snow site with an elevated lean-to. At the site targeted for 2.5 cm of snow, any snow in excess of 2.5 cm was carefully removed with a shovel within 24 h of deposition. Actual snow depth was recorded daily. Within each site, temperatures were recorded at the top of the litter, at the soil-litter interface ( $\approx$  2 cm below the top of the litter),

and at 1, 3, 5, and 8 cm below the soil-litter interface. Air temperature was recorded at 2 m. Some depths within some sites were measured with replicate probes. In all cases, the replicates provided very similar measurements ( $\approx$  0.5 °C) and were subsequently averaged. Prior to analyses, raw data were processed further to yield daily minimum temperatures under each combination of soil depth and snow cover. After this data reduction, our climatic measurements yielded 1834 measurements of daily minimum temperatures across a range of snow depths and throughout the soil and litter profile that constitutes the overwintering habitat for adult bark beetles.

### 4.3 RESULTS AND DISCUSSION

**Cold tolerance.** All three species of *Ips* that occur at Itasca were freeze-susceptible. No individuals of any species survived freezing. A few adults were able to move their antennae after freezing but otherwise never recovered normal movements. *I. pini* adults within a litter box exposed to New Hampshire air temperatures sustained complete mortality (100% of 60 individuals). Some immatures of *I. pini* and *I. grandicollis* survived temporarily following brief freezing but were apparently injured because they were unable to resume development. There was no survival of larvae or pupae in logs exposed to -17 °C for seven days; one month after treatment, logs contained a single fresh gallery that was excavated by one adult female and contained no eggs. In contrast, the control logs contained 13 new galleries with eggs and larvae. For all life stages of *Ips*, the supercooling point indicates the maximum cold tolerance. Under prolonged exposure to cold temperatures, some individuals die even though temperatures did not reach their supercooling point (Appendix 6), but no individuals ever survive temperatures below their supercooling point, and under most ecologically relevant climate scenarios, the supercooling point is functionally equivalent to the lower lethal temperature. Consequently, our measurements of supercooling temperatures in *Ips* provide a sound basis for evaluating the role of winter climate in the overwinter survival and population dynamics of *Ips* at Itasca State Park.

*Ips* adults were more cold tolerant than larvae or pupae (Tables 4.1-4.2). Eggs of *I. pini* had relatively high cold tolerance, with values similar to adults (mean  $\pm$  SD =  $-15.6 \pm 4.6$   $n = 7$ ). Because immatures of *Ips* have less cold tolerance than adults, and because they are obliged to spend the winter within the phloem of their host trees, where they are poorly buffered from temperature extremes, we doubt that immatures of any species of *Ips* ever survive the winter at Itasca. In all likelihood, it is only the adults who have reached overwintering sites within the litter of the forest floor that survive to reproduce the following year. In many years, winter mortality of *I. pini* immatures may be significant at Itasca. *I. pini* reach their maximum abundance in late summer, and even in September, many adults are still laying eggs. Any progeny that do not complete development pupation before the the first day when air temperatures drop below about  $-15^\circ\text{C}$ , will probably die. Consequently, the timing of the fall reproduction in *I. pini*, and the number of warm days that follow, probably has a strong impact on the abundance of *I. pini* the next year.

**Table 4.1. Lower lethal temperatures ( $^\circ\text{C}$ ) of overwintering adults of three species of *Ips* that inhabit Itasca State Park. Values are mean supercooling point  $\pm$  SD and sample size.**

Species	Lower lethal temperature
<i>I. pini</i>	$-12.6 \pm 5.7$ (496)
<i>I. grandicollis</i>	$-15.2 \pm 4.0$ (195)
<i>I. perroti</i>	$-14.4 \pm 5.0$ (32)

**Table 4.2. Lower lethal temperatures ( $^\circ\text{C}$ ) during winter of immature life stages of *Ips* bark beetles that inhabit Itasca State Park. Values are mean supercooling point  $\pm$  SD and sample size.**

	Pupae	Larvae
<i>I. pini</i> and <i>I. grandicollis</i>	$-8.3 \pm 3.4$ (176)	$-9.6 \pm 4.0$ (66)

Across all our measurements of cold tolerance during the winter months, the supercooling point of *I. pini* adults, *I. grandicollis* adults, and *I. perroti* adults averaged  $-12.6$ ,  $-15.2$ , and  $-14.4^\circ\text{C}$  (Table 4.1). There were some seasonal patterns in the supercooling point of *Ips* adults. For example, in 1997- 98, the average supercooling point of *I. pini* adults reached a minimum of about  $-16^\circ\text{C}$  during autumn, and then increased by mid-winter

to values of about  $-12^\circ\text{C}$ , and remained there throughout the spring and summer until the next autumn (Appendix 6). Adults of *I. grandicollis* and *I. perroti* also showed a tendency to have lower supercooling points in autumn than winter. Seasonal adjustments in the lower lethal temperature in *Ips* are probably an adaptive response to climatic patterns in the Great Lakes states. For insects that overwinter in the forest litter, snow cover provides a strong buffer against low temperatures. Consequently, the greatest risk of mortality from low temperatures comes from the combination of no snow and low temperatures. In Bemidji, there is a window of one month during the autumn when the probability of no snow is  $> 0.2$  and air temperatures can drop below  $-20^\circ\text{C}$  (2 November to 2 December; see climatic analyses in Appendix 6). During most years, air temperatures drop below the lower lethal temperature for *Ips* adults sometime during November (mean  $\pm$  SD of November minimum air temperature =  $-23.2 \pm 6.0$ ). Based on the same climatic criteria, there also appears to be a window of vulnerability to freezing during spring (25 March - 7 April in Bemidji), but we saw no evidence in either year of increased cold tolerance during spring. An assortment of experiments with different acclimatization regimes indicated that cold tolerance in *Ips* is unaffected by temperatures encountered during the previous hours, days, or weeks. Apparently, seasonal changes in cold tolerance are regulated by photoperiods or endogenous rhythms, and are not a direct response to changing temperatures.

**Overwintering habitats.** When allowed to choose their own overwintering microhabitats, most *I. pini* adults moved to within 1 cm of the bottom of the litter layer, which was  $\approx 2 - 3$  cm deep and comprised chiefly of pine needles (Table 4.3). In the January sample, 78% of 210 *I. pini* were beneath the litter layer, compared to only 19% of 573 *I. grandicollis*. The majority of *I. pini* had burrowed about one body length into the sandy soil below the litter layer while *I. grandicollis* almost never burrowed into the soil beneath the litter. *I. pini* were also in deeper microhabitats than *I. grandicollis* in the March samples (Table 4.3).

**Table 4.3. Overwintering microhabitats of *I. pini* and *I. grandicollis* adults in January and March 1999.**

Depth below litter surface <sup>a</sup> (cm)	<i>Ips pini</i>			<i>Ips grandicollis</i>		
	Number	% alive	% in stratum	Number	% alive	% in stratum
January 1999						
< 2 - 3 (litter)	47	55	22	465	85	81
2.5 - 5	163	82	77	108	88	19
5- 7.5	2	50	1	0	0	0
7.5 - 12	0	0	0	0	0	0
March 1999						
< 1	1	0	1	3	100	1
1 - 2	6	50	8	128	89	32
2 - 3	46	98	64	247	99	61
3 - 4	19	100	26	24	100	6
4 - 6	0	0	0	0	0	0

<sup>a</sup> Litter was ≈3 cm of pine needles

### Microclimate of overwintering habitats

We used our microclimatic data to develop an empirical mathematical model that could estimate temperatures within the overwintering habitat of *Ips* adults. We evaluated an assortment of different statistical models, but found that one relatively simple model could accurately predict soil temperature profiles using only snow depth and minimum daily air temperature.

$$Y = B_0 + B_1 \cdot Air \cdot \left( \frac{-a \cdot snow}{1 + a \cdot snow} + 1 \right) \quad \text{Eq. 4.1}$$

where:

- $Y$  = minimum daily soil temperature,
- $B_0$  = 0.60,
- $B_1$  =  $e^{-0.176} \cdot X^{-0.457}$ ,
- $a$  =  $e^{-1.07} \cdot X^{-0.470}$ ,
- $X$  = soil depth (in cm) + 1,
- $Air$  = minimum daily air temperature (°C),  
and
- $Snow$  = snow depth (in cm).

This model explained 74% of the variation in minimum daily soil temperatures. The statistical model was highly significant ( $P < 0.001$  for each parameter and the model as a whole). Estimation errors from the model averaged  $< 0.7$  °C, and seldom exceeded 2.0 °C. Models that also included minimum daily air temperatures on 1-2 d previous to the day of estimation provided only slightly better fit and were rejected in the interest of parsimony. Equation 4.1 produces estimates

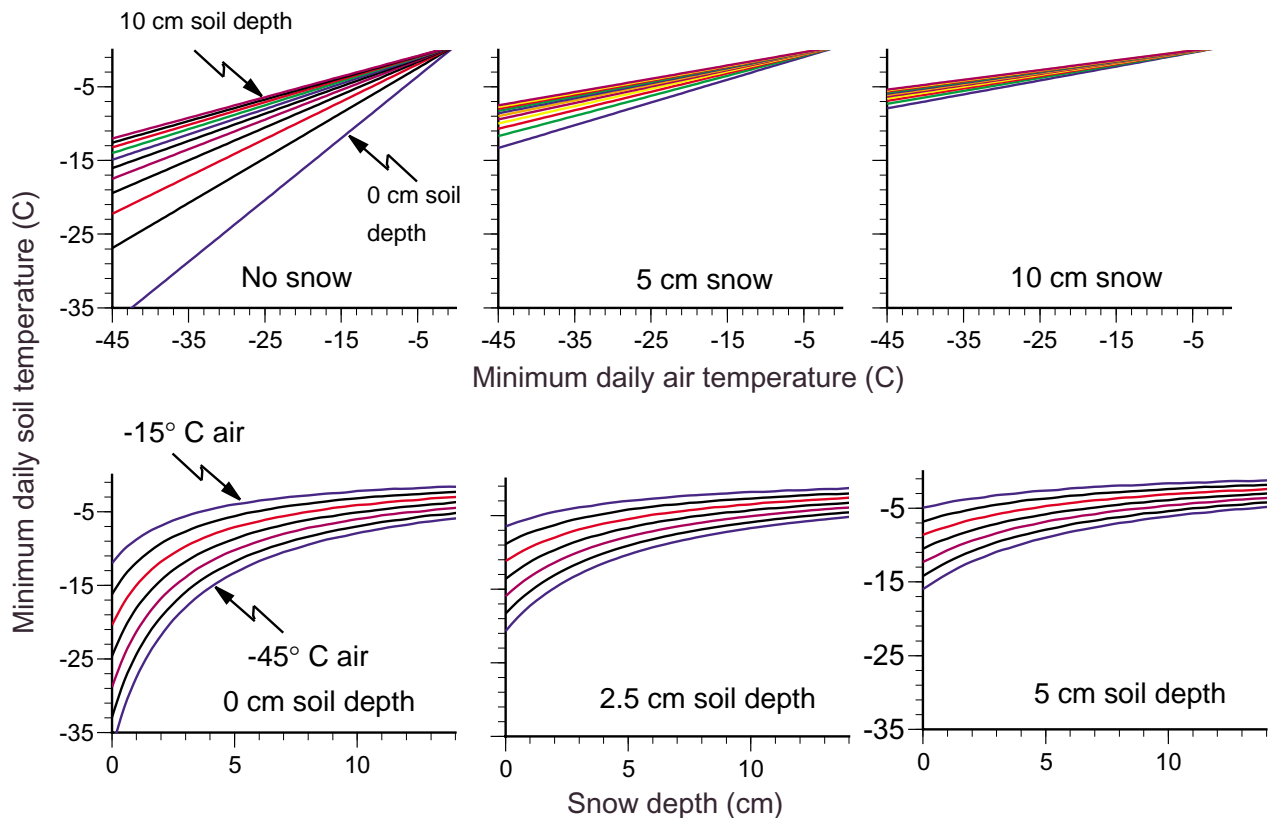
that are slightly biased with respect to day of the winter (estimates average ≈1 °C too cool in the early winter and ≈1 °C too warm in the late winter, presumably because the model does not account for the gradual loss of stored heat from the forest soil as winter progresses). This bias can be removed with models that incorporate day of the winter or cumulative cooling degree days, but the modest gain in precision did not warrant the additional complexity for our applications.

Fig. 4.1 uses equation 4.1 to depict soil temperature profiles as a function of air temperature under conditions of no snow, 5 cm of snow, and 10 cm of snow (upper panels of Fig. 4.1) and to predict soil temperature as a function of air temperature and snow depth at either 0 cm soil depth, 2.5 cm soil depth, or 5 cm soil depth (lower panels of Fig. 4.1). With no snow, minimum daily temperatures in the upper litter layer of the forest floor (0 cm soil depth) nearly match air temperatures. However, at soil depths greater than about 2 cm, microclimates are quite well buffered against the extremes of air temperature (e.g., at 2.5 cm soil depth, even with no snow, a minimum daily air temperature of -45 °C only corresponds to minimum soil temperature of -21 °C). In the upper soil, snow cover provides a strong buffer against extremes in soil temperature. With 5 cm of snow, a minimum daily air temperature of -45 °C corresponds to a minimum temperature at the top of the soil litter (0 cm soil depth) of only -13 °.

We combined our measurements of lower lethal temperatures in beetles (Table 4.1), beetle overwintering behavior (Table 4.3), and soil temperature profiles (Equation 4.1 and Fig. 4.1), to identify the conditions under which winter temperatures would exert significant mortality on bark beetle populations. A graphical analysis indicates that conditions of no snow, with minimum daily air temperatures of less than  $-25^{\circ}\text{C}$  would exert some mortality on *Ips* adults in the upper soil strata (Fig. 4.2). Air temperatures of  $-40^{\circ}\text{C}$ , with no snow cover, would produce significant mortality even among beetles as far as 3-4 cm into the forest floor.

By making a few simplifying assumptions, we are able to calculate the mortality of *I. pini* and *I. grandicollis* adults during any real or hypothetical cold weather (Fig. 4.3). For example, during a cold snap where minimum air

temperatures reach  $-35^{\circ}\text{C}$ , with no snow cover, we would expect 64% mortality among *I. pini* adults that are overwintering in the soil and 69% mortality among *I. grandicollis* adults that are overwintering in the soil. The mortality functions for *I. pini* and *I. grandicollis* ended up being quite similar (Fig. 4.3), because although *I. grandicollis* tended to be more cold tolerant (Table 4.1), this was almost exactly compensated by their tendency to overwinter at slightly shallower depths in the soil (Table 4.3). Fig. 4.3 was constructed to allow easy estimates of the expected mortality for either species under any specified combination of snow cover and minimum daily air temperature. The model uses the mean and standard deviations of lower lethal temperatures for adults (Table 4.1), the distribution of beetle overwintering depths (Table 4.3, Fig. 4.2) and equation 4.1. The



**Fig. 4.1.** Effects of air temperature and snow depth on soil temperature profiles in a red pine forest during winter. Response surfaces were calculated from Equation 4.1, which was estimated from empirical measurements of soil temperature profiles.

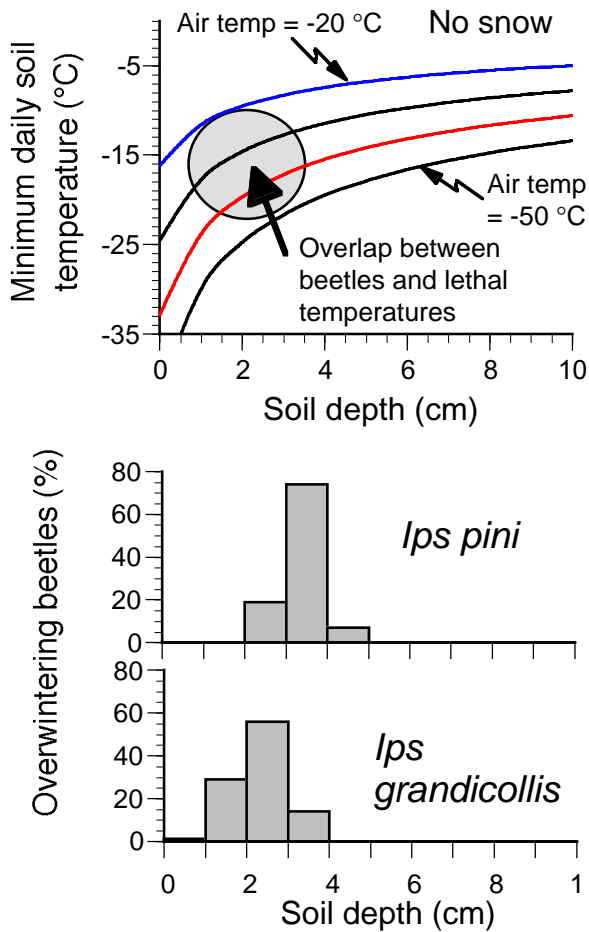


Fig. 4.2. Upper figure identifies the general combinations of soil depth and air temperature where winter soil temperatures can drop below the lower lethal temperatures for *Ips* adults (see also Figs. 4.1 and 4.3). Lower figure shows the depths at which *I. pini* and *I. grandicollis* adults overwinter (see also Table 4.3).

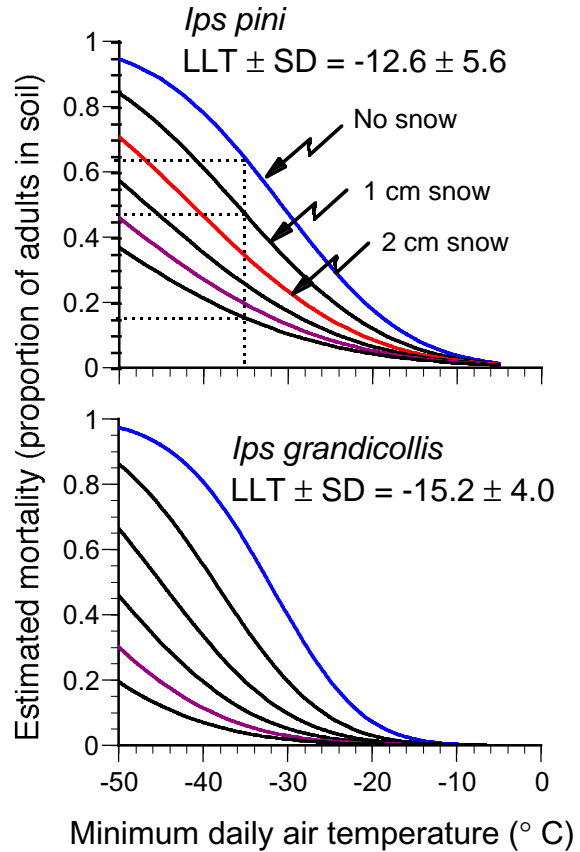
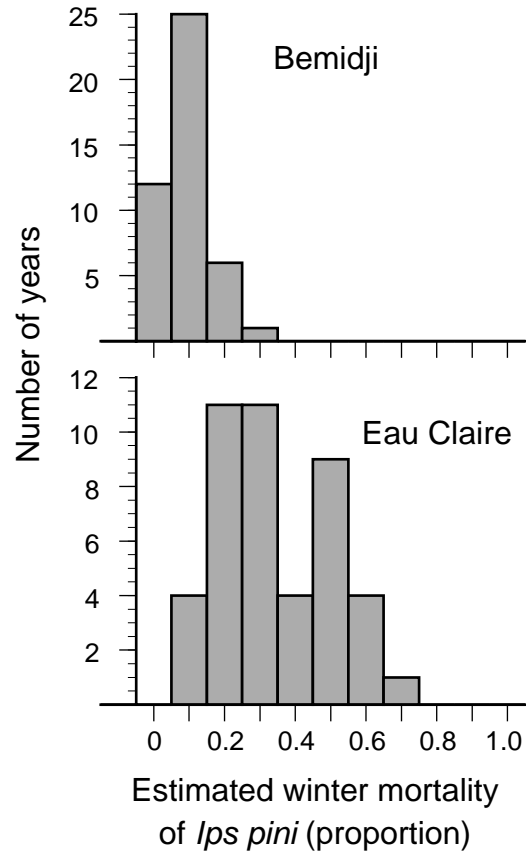


Fig. 4.3. Estimated mortality of overwintering *Ips* adults as a function of snow depth and minimum daily air temperature. Model incorporates physiological measurements of lower lethal temperatures, behavioral studies of microhabitat selection, and microclimatic measurements.

model assumes that lower lethal temperatures are normally distributed, that overwintering depth is independent of lower lethal temperature, and that lower lethal temperatures remain constant during the winter. We know that this last assumption is not strictly true (so the model tends to overestimate mortality somewhat in the autumn and underestimate mortality somewhat in mid-winter), but sensitivity analyses indicate that this bias is not very large. Other sensitivity analyses indicated that spatial variation in soil temperature profiles have negligible effects. The model implicitly ignores all life stages other than adults and any adults that have not gone into the forest soil; these assumptions are reasonable for the northern Great Lakes region, including Itasca

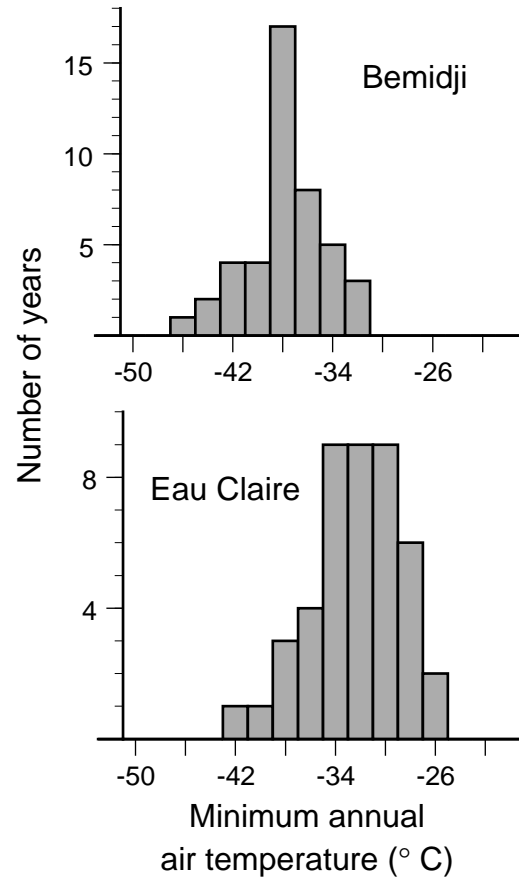
State Park, because we are quite certain that the only *Ips* that can possibly overwinter successfully are those adults that leave their host trees and go into the forest soil before winter.

To assess the historical importance of winter temperatures for *Ips* populations at Itasca State Park, we used the model summarized in Fig. 4.3 to analyze climate records from 1948-1992 recorded at the the nearby weather station in Bemidji. For comparison, we performed comparable analyses for weather records from Eau Claire, Wisconsin, near our other bark beetle study site at Colfax, Wisconsin. During each year of the weather records, we used equation 4.1 to calculate the upper soil temperatures (0.5 cm depth) for each day of the winter, identified the



**Fig. 4.4.** Frequency distribution of estimated winter mortality of *I. pini* under historical climates (1948-1992) recorded at Bemidji, MN, near Itasca State Park, and Eau Claire, WI, in west central WI.

day when upper soil temperatures were minimized, and then calculated the percent mortality of *I. pini* for that day using the functions represented by Fig. 4.3. Surprisingly, these analyses indicated that winter mortality is more significant for *Ips* populations in west central Wisconsin than in Itasca State Park (Fig. 4.4). During a 45 year record, estimated winter mortality reached a maximum of only 33% under the Bemidji climate, compared to 71% under the Eau Claire climate (Fig. 4.4). This was in spite of the fact that minimum annual air temperatures were generally colder at Bemidji (Fig. 4.5).

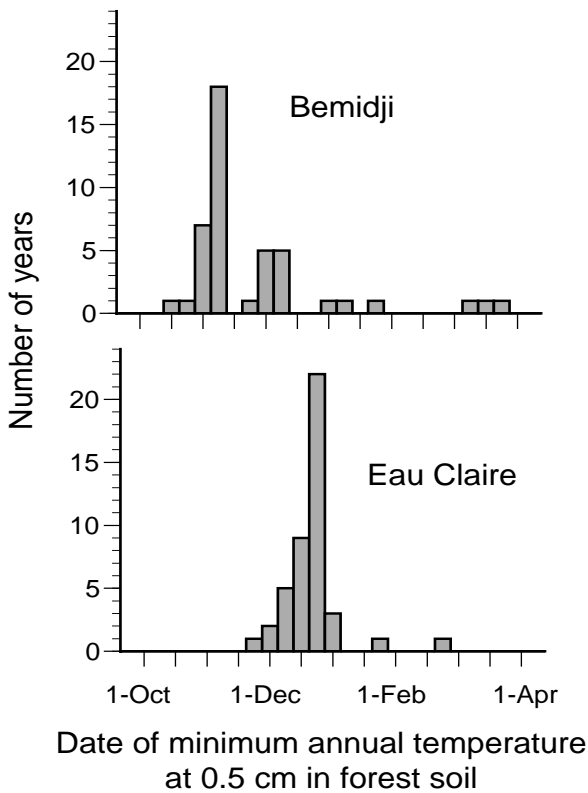


**Fig. 4.5.** Frequency distribution of minimum annual air temperatures under historical climates (1948-1992) recorded at Bemidji, MN, near Itasca State Park, and Eau Claire, WI, in west central WI.

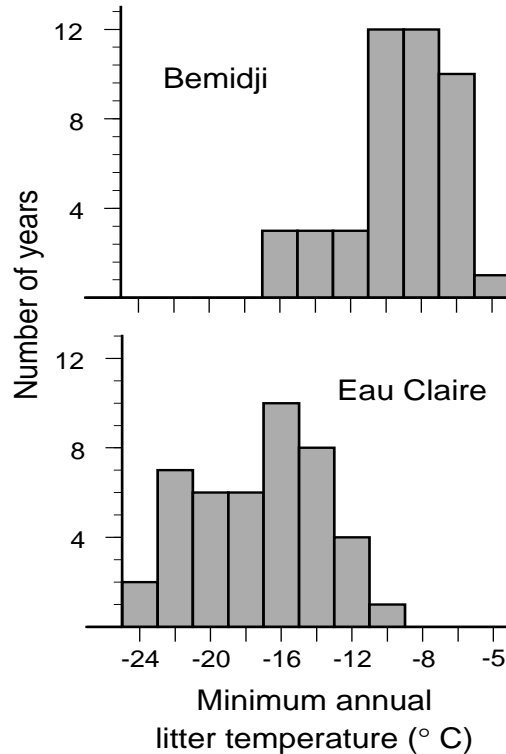
However, snows tended to be earlier in Bemidji than Eau Claire, and the minimum soil temperatures are usually reached on the coldest day when there is no snow. In Eau Claire, it has been common to have snow-free days in December while this has been rare in Bemidji. The date of coldest upper soil temperatures in Bemidji has commonly been in November, while in Eau Claire, it tends to be in December (Fig. 4.6). As a result, minimum annual temperatures in the upper soil commonly drop below  $-20^{\circ}\text{C}$  in Eau Claire and seldom drop below  $-12^{\circ}\text{C}$  in Bemidji (Fig. 4.7).

**Conclusions** Because of the generally early snowfall at Itasca, winter mortality from cold temperatures is probably only important to resident *Ips* populations in some years. Fig. 4.3 provides an easy tool for identifying those winters. Probably no immature *Ips* ever survive the winter at Itasca, so the proportion of *Ips* populations that enter the winter as immatures in host material vs. as adults in the soil litter may exert considerable effects on population dynamics in most years. Management practices that influence the depth of the litter layer may influence overwinter mortality of *Ips* adults,

because few overwintering adults burrow beyond the bottom of the litter, and the depth of the litter above them influences their microclimate. We hypothesize that prescribed burns will sometimes increase overwinter mortality of *Ips* adults because of the decreases in litter depth following fires. However, this suggestion should not be invoked as a rationale for prescribed burns without first conducting the appropriate experimental tests. We also point out that if reduced litter increases the mortality of *Ips*, it might also increase the mortality of beneficial insects such as *T. dubius* that also overwinter below the litter.



**Fig. 4.6.** Frequency distribution of the dates on which minimum annual temperatures were reached in the forest litter as calculated by Equation 4.2 under historical climates (1948-1992) recorded at Bemidji, MN, near Itasca State Park, and Eau Claire, WI, in west central WI.



**Fig. 4.7.** Frequency distribution of minimum annual temperatures at 0.5 cm depth in the forest litter, as predicted using Equation 4.2 under historical climates (1948-1992) recorded at Bemidji, MN, near Itasca State Park, and Eau Claire, WI, in west central WI. Note that the date of minimum annual temperatures in the forest litter generally come earlier in the winter at Bemidji compared to Eau Claire (Fig. 4.6)