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Forecasting
mountain pine beetle-overwintering mortality
in a variable environment

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Abstract

A landscape-scale ecophysiological model of mountain pine beetle (MPB) overwintering mortality was developed, validated and communicated. The model was field-validated in Alberta during the winters of 2006-07 and 2007-08. Key model assumptions were tested experimentally during the winter of 2007-08. The model was operationalized for forecasting in Alberta in early 2008 and key outputs (maps and time-series) communicated to the public through a new Natural Resources Canada website.

The model describes daily overwintering mortality in the above-snow component of the MPB population. Field and lab tests suggest the model should perform reasonably well during winters characterized by at least one severe cold snap. In 2006-07 the overwintering mortality rate across Alberta was predicted to be 79%, in close agreement with the observed survival rate of 81%. The model suggested that most of the mortality occurred in a single pulse late November 2006, when temperatures across the province dropped suddenly to a winter low between -32°C and -38°C. The following year, in 2007-08, a higher level of mortality was predicted and observed, largely a result of the severe cold snap of late January 2008, when temperatures dropped to a winter low between -35°C and -47°C. In both winters, mortality was predicted and observed to be much higher in northern than in southern Alberta.

Despite the overall predictive power of the model, there is substantial unexplained variation in observed mortality. Model performance in relatively mild conditions also remains to be tested. These are two issues that require further research.

Putting these observations in context, a retrospective analysis of historical beetle winter weather in Alberta (1951-2008) indicates that the last two winters represent a temporary reversion back to "normal" (i.e., 1980s-style) winter climatic conditions. A return in the coming years to a positive warming trend in winter temperatures would pose a risk of increased potential of outbreaks and eastward range expansion.

Keywords: overwintering mortality, cold tolerance, supercooling, climatic suitability, process-based simulation, model validation

Résumé

Un modèle écophysiologique sur le terrain concernant la mortalité hivernale du dendroctone du pin ponderosa (DPP) a été élaboré, validé et communiqué. Le modèle a été validé sur le terrain en Alberta pendant les hivers 2006-2007 et 2007-2008. Les hypothèses clés du modèle ont été mises à l'essai pendant l'hiver 2007-2008. Le modèle a permis de procéder à des prédictions en Alberta au début de 2008 et les résultats clés (cartes et mesures chronologiques) ont été publiés sur un nouveau site de Ressources naturelles Canada.

Le modèle décrit la mortalité hivernale quotidienne de la population de DDP qui ne se trouve pas ensevelie sous la neige. Les essais effectués sur le terrain et en laboratoire semblent indiquer que le modèle devrait fonctionner assez bien pendant les hivers où l'on connaît au moins un coup de froid important. En 2006-2007, un taux de mortalité hivernale à la grandeur de l'Alberta de 79 % était prévu, en accord étroit avec le taux de survie observé de 81 %. Le modèle indiquait que la majeure partie de la mortalité s'est produite en une seule occasion à la fin de novembre 2006 alors que les températures à la grandeur de la province ont chuté soudainement pour se situer entre - 32 °C et - 38 °C. Ces températures ont été les plus basses enregistrées cet hiver-là. L'année suivante, en 2007-2008, un niveau de mortalité plus élevé était prévu et observé principalement en raison d'un coup de froid intense à la fin de janvier 2008, alors que les températures ont chuté pour se situer entre - 35 °C et - 47 °C. De nouveau, ces températures ont été les plus basses enregistrées cet hiver-là. Dans les deux cas, la mortalité prévue et observée était beaucoup élevée dans le nord que dans le sud de l'Alberta.

Malgré l'efficacité prédictive en global du modèle, il existe des variations importantes inexpliquées dans le taux de mortalité observé. De plus, le rendement du modèle dans des conditions climatiques relativement douces est à mettre à l'essai. Ces deux éléments nécessitent de plus amples recherches.

En mettant ces observations en contexte, une analyse rétrospective des conditions hivernales auxquelles a été exposé le DDP en Alberta (1951-2008) indique que les derniers hivers marquent un retour temporaire à des conditions climatiques hivernales « normales » (c.-à-d. comme celles connues dans les années 1980). Au cours des prochaines années, un retour à des hivers moins froids donnerait lieu à la possibilité accrue d'infestations et de progression vers l'est.

Mots clés : mortalité hivernale, tolérance au froid, surfusion, conditions climatiques favorables, simulation fondée sur les processus, validation du modèle

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1 Introduction

Climatic fluctuations are known to be a critical factor in the risk of mountain pine beetle (MPB) outbreaks (Carroll et al. 2004). In particular, overwintering mortality caused by cold exposure is one of the key factors in the population dynamics of MPB (Yuill 1941, Reid 1963, Amman 1973, Safranyik 1978, Cole 1981). In the past, very simple heuristics have been used to predict the impact of cold temperatures on MPB overwintering survival (Safranyik et al. 1999). A fixed threshold of -40C, for example, is often cited as the minimum temperature required to kill a large proportion of MPB. However, this simple heuristic does not consider the differential effect of temperatures in the shoulder seasons of autumn and spring, when beetles are known to be less cold tolerant. Also, it does not consider the temporary effect a warming *chinook* might have on a short-term loss of cold-tolerance. Finally, it does not consider the fact that the different life stages have different levels of cold tolerance, such that different areas with different climates and beetle phenologies could have different levels of cold tolerance.

In order to predict the landscape-wide impact of daily air temperature fluctuations it is therefore necessary to couple a realistic daily-scale meteorological model with a realistic model of mountain pine beetle cold tolerance physiology. This was seen as a critical component to MPB management in Alberta because of Alberta's historically volatile winter climate. Predicting short-term changes in MPB risk in real-time that are caused by rapid changes in climatic suitability would allow pest managers to dynamically re-allocate control efforts to those areas likely to exhibit very high overwintering survival.

Bentz & Mullins (1999) developed a conceptual model of MPB overwintering survival based on supercooling point (SCP) estimation, where MPB cold tolerance varies daily as a function of daily fluctuations in air and tree phloem temperatures. The model was implemented mathematically by J. Régnière (Laurentian Forestry Centre, Quebec) in 2006 and published as Régnière & Bentz (2007). This model described MPB overwintering survival as exhibited by MPB in the southern Rocky Mountains of the U.S. during the early 1990s. The purpose of this project was to test this model for use in the northern Rocky Mountains of Canada, and to move quickly toward development of an operational tool that provincial pest managers, especially those in Alberta Sustainable Resource Development, could use with confidence.

2 Material and Methods

2.1 Model Development

The MPB physiological model of Régnière & Bentz (2007) was integrated into the landscape-scale weather simulator BioSIM (Régnière 1996) in order to generate inter-provincial scale simulations of mountain pine beetle overwintering survival. The model was set up to run in real-time using daily weather data from British Columbia and Alberta as supplied online by Environment Canada. The weather databases were assembled by R. St-Amant (Laurentian Forestry Centre, Quebec) and simulations executed by B. Cooke (Northern Forestry Centre (NoFC), Edmonton). Simulations are run weekly and results uploaded to a Natural Resources Canada/Canadian Forest Service website developed by the NoFC communications group (J. Samoil, J. Golinowski, J. Elofson) in Edmonton.

2.2 Field Validation

Because cold weather can never be counted on, this study was originally designed to focus on laboratory testing of model assumptions vis à vis MPB cold tolerance ecophysiology. However, the winters of 2006-07 and 2007-08 produced cold snaps that were so cold that, post-cold, very few MPB were available for experimental testing. To have two severe winterkill events in

successive years like this is somewhat unusual, or, more precisely, uncharacteristic of MPB in BC (although this is precisely what led to the collapse of the Tweedsmuir outbreak in the mid 1980s in BC (Safranyik & Linton 1991)). The subsequent shortage of MPB prevented us from doing a complete laboratory test, however it provided a major opportunity to field-validate the model's predictions.

2.2.1   *Field validation, winter 2006-07*

A detailed description of this work is available in last year's Mountain Pine Beetle Initiative progress report (available through Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre mountain pine beetle office). Briefly, predictions from MPB/BioSIM were validated by comparing predicted and observed levels of mortality in the winter of 2006-07 in two networks of plots (Fig. 1). The two samples were taken as follows.

Sample #1

The Canadian Forest Service (CFS) conducted detailed mortality assessments in five regional locations, based on large samples of more than 1000 larvae. Sample times for each region varied from early February to late March (Table I). Eight 4-inch diameter circular disk samples were taken from each of ten trees in each of three stands, yielding 240 sample disks per sample region. Sample disks were chosen carefully by scanning a tree for characteristic adult entrance holes (evidenced by pitch tubes and/or sawdust), and chiseling above the entrance hole and left and right around the vertical adult gallery, in search of lateral larval galleries. The sample disk was taken a few centimetres directly above the spot where lateral larval galleries were observed, centred on the vertical adult gallery. Adult galleries that did not exhibit lateral larval galleries – a phenomenon which was encountered with surprising frequency – were rejected for larval sampling. Sample disks, approximately 2-3 cm thick and containing intact phloem and xylem, were obtained using a four-inch hole-saw and two-inch chisel. These were taken at both knee-to-waist-height and breast-to-shoulder-height, and at right angles from one another, in order to ensure that larvae in each disk came from independent adult galleries/sibling groups. Sample disks were placed in zippered plastic bags in a cooler on ice and transported back to the lab in Edmonton, where intact larvae were carefully removed from disk phloem, placed in individual Eppendorf tubes, warmed gradually to room temperature, and checked periodically three times a day for a week to determine survivorship. Non-intact larvae and larval remains were discarded. Eggs were ignored and not counted (due to their small size, susceptibility to human manipulation, and non-responsiveness to probing). Larval state (for the intact larvae) was recorded as either (i) responsive to probing, and clearly alive, (ii) dead with a normal cream colour (possibly slightly translucent), or (iii) dead and brownish, likely the result of resinosis poisoning. Survival was computed on the basis of the intact larvae whose state in the field could easily be inferred. Larval head capsule widths were measured in order to determine the frequency distribution of the various instars. Neither pupae nor adults were encountered in this sample.

Sample #2

During the first two weeks of May 2007, Alberta Sustainable Resource Development (ASRD) conducted a large-scale, rapid assessment of egg, larval, pupal and adult mortality in 1429 trees from 146 sites distributed across the province. Four 4-inch disk samples were taken from each tree, two from the north side and two from the south side. Samples were taken at breast-height whenever possible. Because of the unselective (i.e., unbiased) manner in which sample disks were chosen, many of these individual disks contained neither MPB nor entrance holes to a primary gallery. Subsequently, so that the survival parameters be defined (i.e., have a non-zero denominator), individual sample disk data were bulked among trees by site, and any sites that yielded neither MPB nor entrances holes were excluded from further analysis. Of the 146 sites sampled, 23 were excluded in this way, yielding 123 sites total for analysis. Survivorship at each

of the 123 sites was estimated as the ratio of living beetles to the total number of beetles sampled (eggs, larvae, pupae, adults). The various larval instars were not distinguished in this sample, although an index of phenology could be computed as the ratio of pupae + adults to eggs + larvae. The higher this ratio, the more advanced the phenology.

The spatial distribution of samples #1 (n=5 plots) and #2 (n=123 plots) are mapped in Fig. 1, along with key geographical features referred to in this paper, including elevations, region names, and weather station locations.
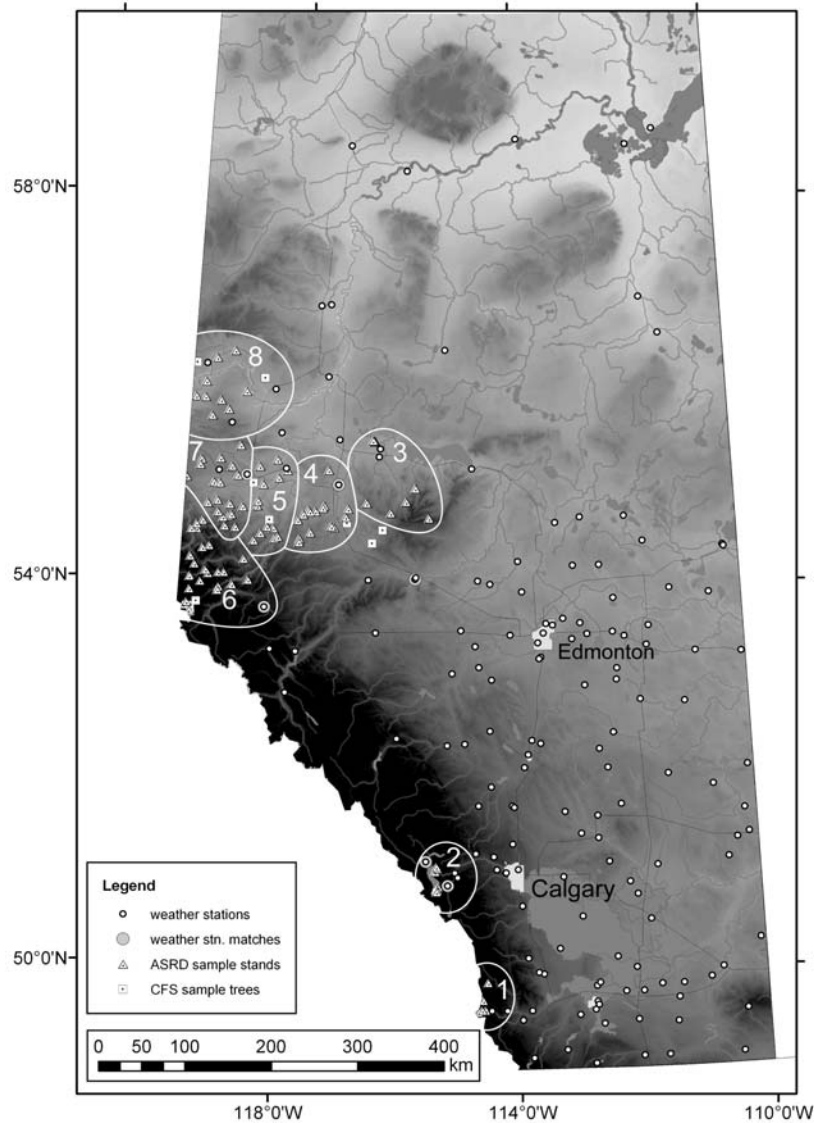
Figure 1. Sample locations and weather stations across regions of Alberta, winter 2006-07. Dark shading indicates higher elevation. Squares are locations of plots where MPB mortality was estimated by CFS (sample #1). These represent the simulation points described in Fig. 3. Triangles are plots measured by ASRD (sample #2). Clustering into eight numbered regions: (1) Crowsnest Pass, (2) Banff, (3) Swan Hills, (4) Valleyview, (5) Grande Prairie/Smoky R., (6) Willmore, (7) Grande Prairie/Wapiti R., (8) Peace River, these represent the simulation points described in the results section. White dots are Environment Canada weather stations with daily data during the winter of 2006-07. Grey circles are weather stations providing the closest match to the CFS simulation points.

2.2.2   Field validation, winter 2007-08

At the time of writing, full field validation is ongoing, in close co-operation with ASRD. This will be based on a survey of approximately 500 trees from across northern and southern Alberta. For now, what follows is a description of the partial validation methods for which results are complete.

An evaluation of mountain pine beetle winter mortality was done twice in Edmonton (24 Jan, 2008 and 01 Feb, 2008) and once in the Crowsnest Pass area (12 Feb, 2008). Bark disks containing mountain pine beetle larvae were extracted from the tree using a 4 inch hole saw and a 2-inch wide chisel. The larvae contained in the disk were removed and placed on a weighing boat sitting on a wet filter paper inside a Petri dish sealed with parafilm. Once a day for a period of 5 days, the larvae resting at room temperature were monitored for movement by gently probing the body with tweezers.

2.3   Laboratory Testing

Despite the winterkill-caused shortage of beetles during the months of Nov 2007-Mar 2008 and Feb-Mar 2008, we were able to do some laboratory testing while MPB were alive in large numbers through Oct 2007-Jan 2008.

2.3.1   MPB source and temperature measurement

Bolts from the lower 90 cm of eighteen lodgepole pines infested with mountain pine beetles were taken from the Grande Prairie region (N 54º49.778, W 119º31.317) and brought to Edmonton in late October. Wax was spread on both ends of the bolts to prevent humidity loss. Each bolt was left standing in an open space outside the Northern Forestry Centre. Four bolts were selected for phloem temperature measurement. Temperature probes of 30 gauge type E thermocouple connected to 20 gauge type E thermocouples were placed at four different heights (10 cm, 30 cm, 60 cm and 85 cm) along each bolt. For each thermocouple, about 1 cm of a temperature sensor was inserted in the phloem by making a small hole horizontally with an ice pick under the bark. The sensor was pushed in the hole and fixed with tape. On two bolts, the thermocouples were facing north while on the other two bolts, they were facing south. Two additional thermocouples were placed in a solar radiation shield to measure air temperature. All temperatures were recorded with Campbell Scientific 21X dataloggers. Temperatures were acquired on an hourly basis.

2.3.2   Cooling device and supercooling point (SCP) estimation

The cooling device consisted of a two-stage Peltier block connected to a copper heat sink via an epoxy. The whole device was embedded in a thick styrofoam box with a lid for insulation. The heat sink was constantly supplied with antifreeze (ethylene glycol) pumped by a Brinkmann RC20 which progressively cooled the antifreeze from 0ºC to -20ºC. The Peltier block was powered by a 14V DC power supply regulated by a Campbell Scientific CR1000 datalogger. The regulation of the cooling rate was achieved by fixing a type E thermocouple to the cold side of the Peltier block, which informed the datalogger of the surface temperature of the plate and compared it with a moving target temperature going from 0ºC to -55ºC at a rate of 0.5º per minute. The datalogger then analyzed the plate temperature and signaled the power supply via a solid state relay / time circuit chip to match the temperature of the plate to the target temperature. A maximum of five electrical pulses per second of around 12.5V were sent to the cooling plate to match the desired temperature.

Every day, larvae were extracted from the bolts and their supercooling points (SCP) were estimated by placing the larva on a type E thermocouple (CHCO-002, from Omega). A small chamber (slightly larger than the larva) made of plasticine held the larva in place and provided a good contact between the larvae and the thermocouple (thermocouple not touching the plasticine).

The cooling plate cooled down in a linear fashion at a rate of 0.5ºC per minute starting at 0ºC. This rate of cooling was chosen as a reasonable approximation to the temperature drop associated with a severe arctic cold air outbreak, where air temperatures could drop from -10°C to -40°C in a single hour. The temperature controller that we designed is capable of producing variable rates of cooling.

Larval SCP was estimated as the temperature at which a sudden spike in temperature occurred in response to water crystallization (i.e., freezing), typically in association with perforation of the internal tissues, and subsequent larval death (Fig. 2). Head capsule widths of all frozen larvae were measured for instar determination.
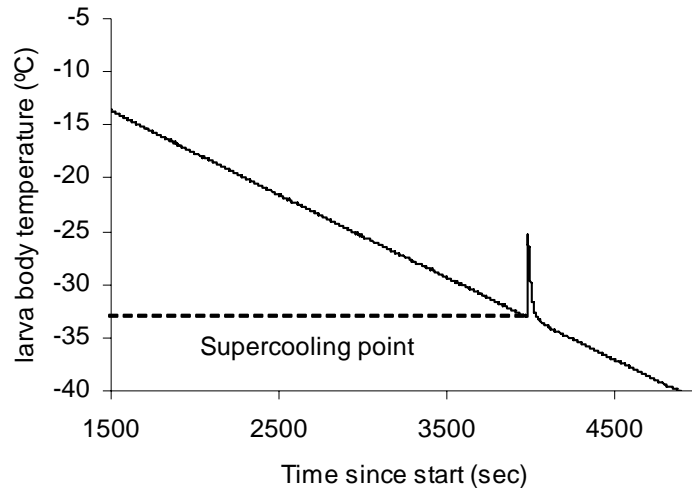
Figure 2. Example of SCP estimation for a slowly cooled MPB larva (-0.5°C/min).

2.3.3   *Additional measurements and experimentation*

Four additional effects we needed to quantify were:

1. phloem temperatures above and below snow

2. phloem temperatures on north versus south facing sides of bolts

3. phloem temperatures along different heights of bolts above snow

4. whether dead and living larvae produced similar SCP temperature spikes

2.4   **Technology Development and Transfer**

Operationalization of MPB/BioSIM required that we automate the procedure for weather database updates.

Model results were transferred directly to the provinces of Alberta and BC, and to the media and the public through the creation of a new Natural Resources Canada website, hosted at the Northern Forestry Centre in Edmonton.

3 Results and Discussion

3.1 Field Validation

3.1.1 Field validation, winter 2006-07

The rate of overwintering survival was predicted to vary tremendously across the study area, from extremely high survival (100% in some areas) in south-western British Columbia to extremely low survival (0% in some areas) in north-eastern Alberta (Fig. 3). In general, survival was predicted to be much lower in Alberta than in British Columbia, and within both provinces, much lower in the north than in the south. Additional patterning was predicted to occur at finer spatial scales, as a result of air mass dynamics interacting with topography.
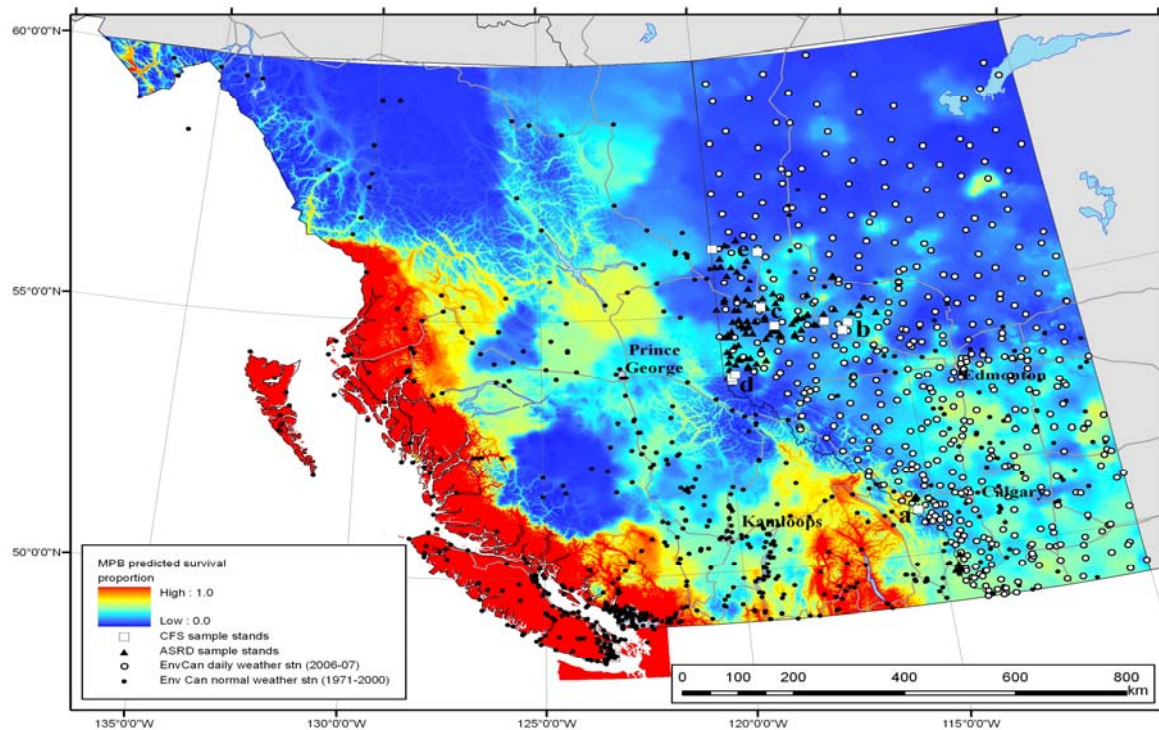
Figure 3. Predicted winter survival across British Columbia and Alberta. Mountain pine beetle survival simulated at high resolution and interpolated using regression with elevation as a spatial drift variable. Labels (a)-(e) are the five regions sampled by CFS (sample #1): (a) Banff/Bow Valley, (b) Fox Creek, (c) Grande Prairie, (d) Willmore, (e) Peace River.

The validation plots, all in Alberta, fell into two distinct groups, with low survival expected in the northern group of plots and high survival expected in the southern group of plots. The correlation between log observed and log simulated survival was nearly significant ($r = 0.83$; $p = 0.08$; inset Fig. 4). The survival values observed in three of the five regions in this set of measurements were very low but non-zero. However, predicted survival in the southernmost region was an order of magnitude higher than observed in the three northernmost regions (Willmore, Grande Prairie, Peace River).

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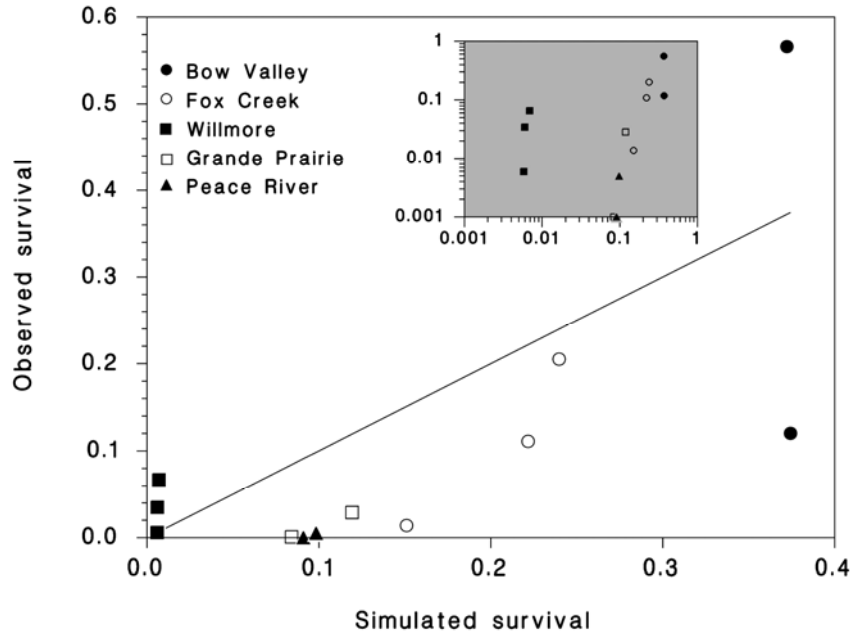
Figure 4. Observed vs. simulated survival in CFS sample #1.

Spring 2007 survey data supplied by ASRD were used to calculate survival values. Overall, average simulated survival $(0.21 \pm 0.01$ SEM$)$ was slightly but significantly different from the observed average (0.19 ± 0.02), as tested by the Mann-Whitney median test $(W = 13213, p = 0.0004)$. The distribution (Fig. 5) was very non-normal and quite different between the two.

Figure 5. ASRD spring 2007 survey data set: aspatial comparison to predictions.

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Although observed mortality was far more variable than simulated mortality, the two were somewhat closely related (Fig. 6). The observed winter minimum temperature had a sharply regional spatial structure to it (far colder in the North), so there were two ways to look at the dataset: regionally and temperature-wise. The spatial patterns (by location cluster) of observed and simulated winter mortality were somewhat similar, but the correlation was weak ($r = 0.42$, $p = 0.31$)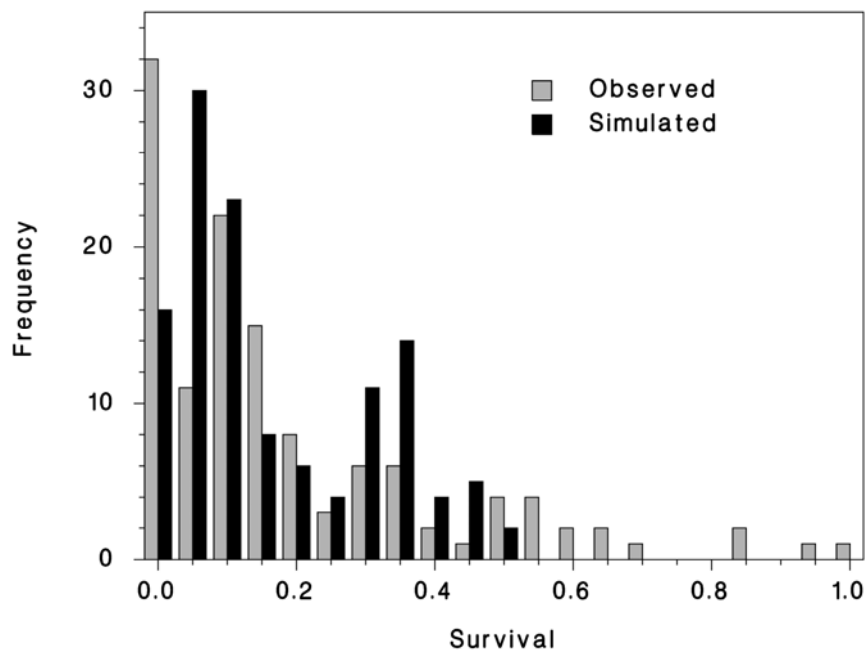 (Fig. 6A). The North-South differentiation is consistent with observations. The model output shows a very strong relationship between winter's extreme minimum temperature and survival (Fig. 6B). Observations are not inconsistent with this relationship, but measurements of survival at individual locations are far more variable than expected from model output.
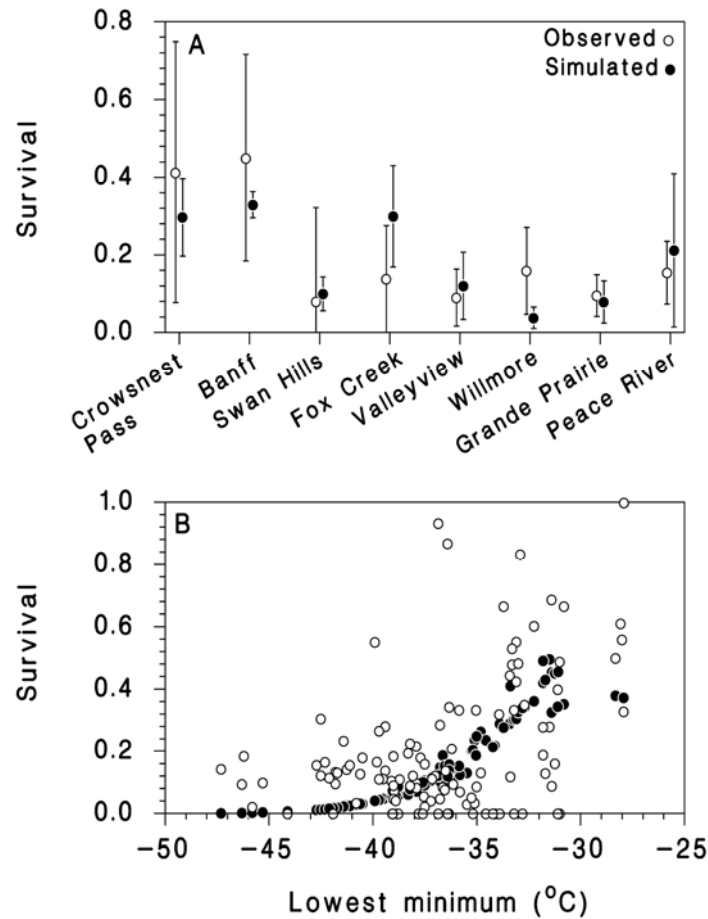
Figure 6. Spatial analysis of ASRD observed MPB survival vs. predictions. Panel A averages the 123 data points among eight regions (shown in Fig. 1) and highlights the match between observed and predicted regional means. Panel B presents the raw data point-wise and highlights the mismatch in terms of individual site-level variability, despite the fit of the mean observed to the predicted.

Figures 7-11 help to further characterize the pattern of MPB winter mortality during the winter of 2006-07, and to put it in some historical context. The captions are self-explanatory. In summary, the level of predicted and observed mortality in 2006-07 was fairly high (at least compared to BC, where mortality is often lower than 80%). This was not just due to the level of cold, but the fact that it occurred in late November, prior to mid-winter, when larvae achieve maximum cold tolerance.
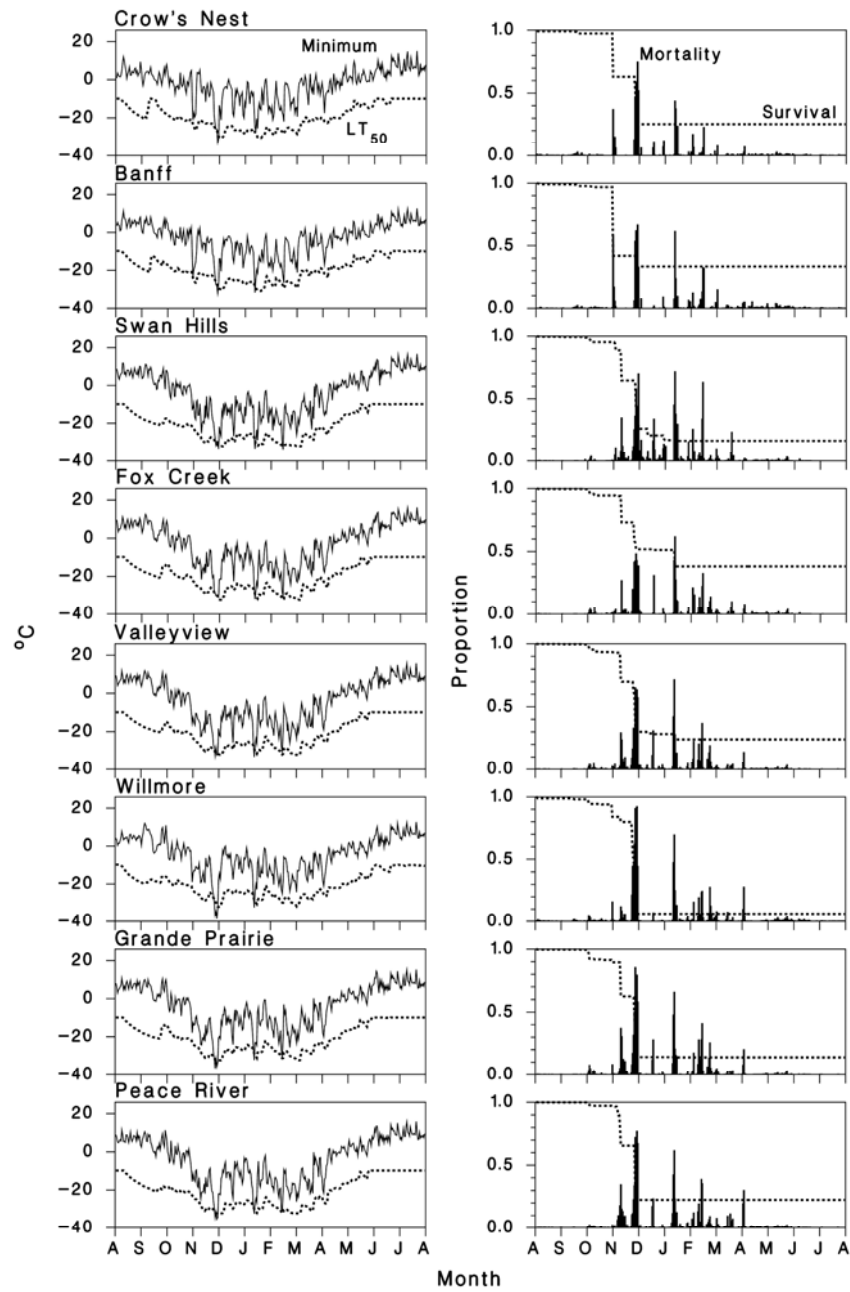
Figure 7. Daily model output. Examination of the model's daily output indicates the relative impact of the 2006-07 winter's several low-temperature events on end-of-season survival, and illustrates the high degree of sensitivity of the model to exact temperature values occurring near the LT_{50}.

Frequency of instar per region
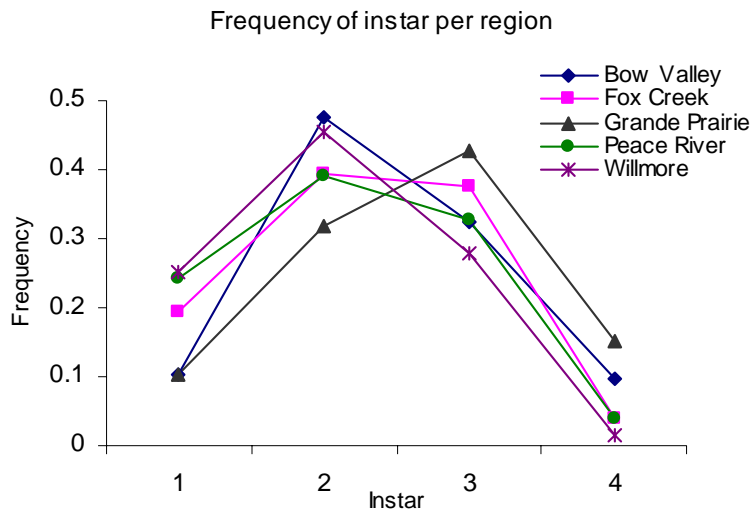
Figure 8. Phenological differences observed between regions during winter 2006-07. Phenology differed slightly, but significantly between regions (X-squared = 397.5834, df = 12, p = 2.2e-16), with the Grande Prairie region exhibiting the most advanced phenology and the Bow Valley region the least advanced phenology. Additional simulations of MPB phenology (not shown) indicate that this low proportion of 4th instars is inconsistent with the hypothesis of immigration prior to August 12.
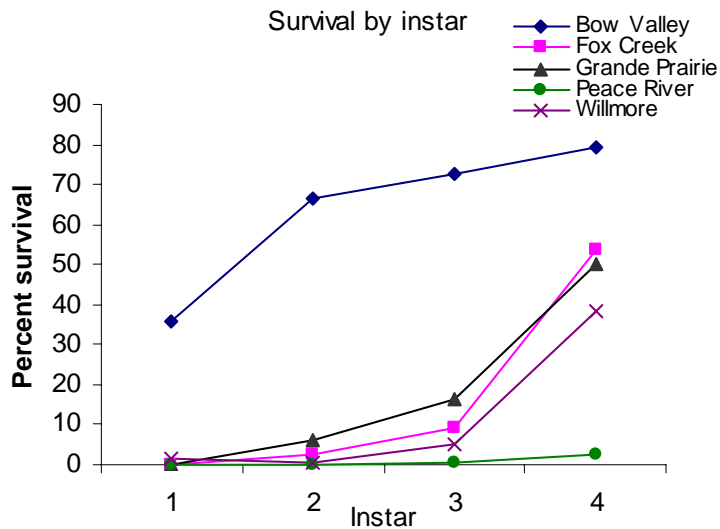
Figure 9. Effect of phenology on winter survival. Survival rate was positively related to larval age in all five regions.

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MPB survival above and below snow
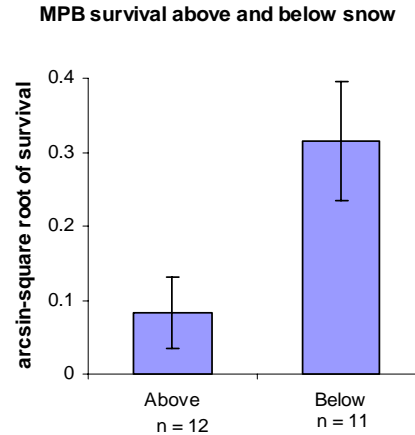
Figure 10. Effect of snow depth on survival. Survival was compared above and below the February snow-line, which was located at a height of 42 inches above ground. After arcsin-square-root transformation, the between-treatment difference in sample variance was stabilized and survival differed significantly (t = - 2.49, df = 21, p = 0.010): survival was significantly higher below snow.
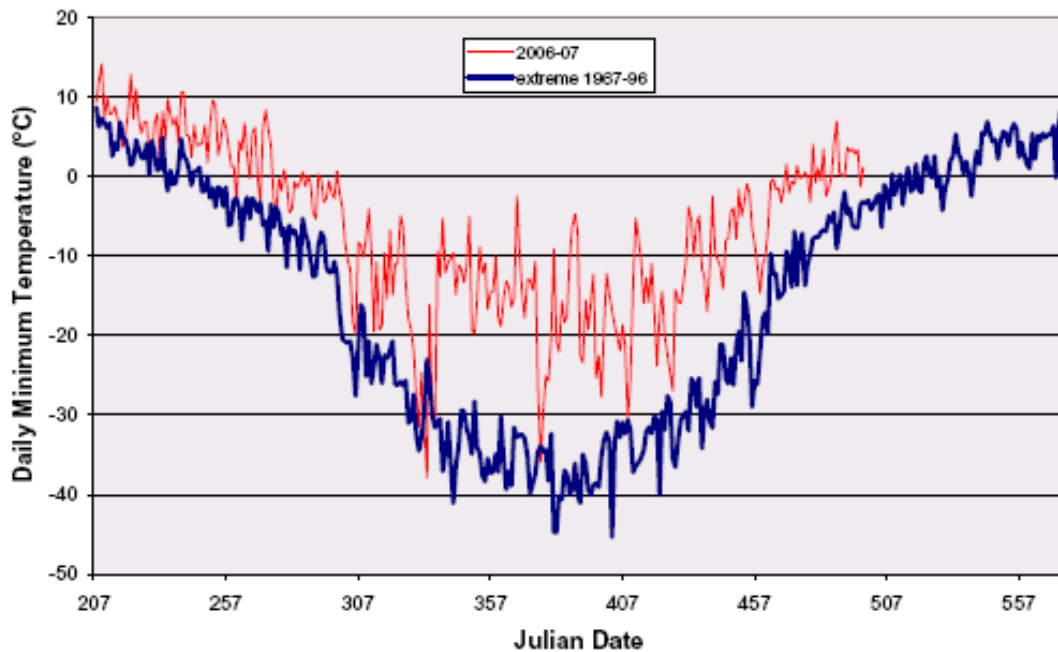
Figure 11: The 26-28 Nov 2006 cold snap in context. Comparing the 2006-07 daily minimum vs. the 30-year extreme daily minimum (1967-96) for Edmonton International Airport shows that the observed MPB-killing cold snap was highly anomalous for that particular date, although not necessarily for that general time of year.

3.1.2 *Field validation, winter 2007-08*

Predictions

The spatial pattern of predicted winter mortality for 2007-08 (Fig. 12) was similar to that for 2006-07 (Fig. 3), although (i) the overall rate of mortality was higher and (ii) the late January cold snap did not appear to penetrate as deeply from the Northeast across the Rocky Mountains westward into the MPB-infested areas of northeastern BC.
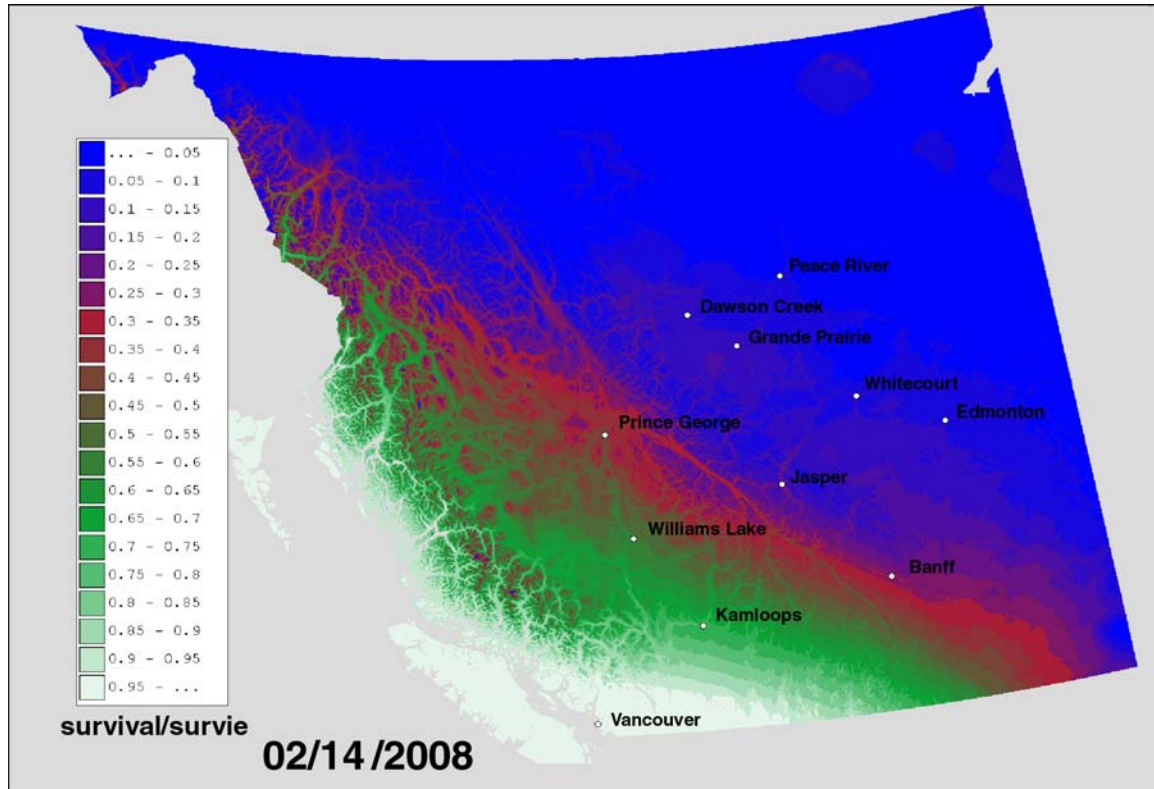
Figure 12. Predicted cumulative daily survival rate of mountain pine beetle populations in western Canada, as simulated by MPB/BioSIM 14 February 2008.

Observations

Mortality surveys in Edmonton indicated a significant increase in mortality in the period between the first and second survey (Table I). In the first survey (24 Jan), the percent mortality of mountain pine beetle was only 18.2%. However, when the air temperature dropped to -38.1ºC and -39.9ºC on January 28 and 29 respectively, it was sufficient to reach a cumulative mortality of 93.3% in the Edmonton samples. According to our experimental results, the temperature required to achieve 93.3% mortality is -39.1ºC, which represent a trivial difference of 0.8ºC from the observed temperature.

In the Crowsnest Pass area, the temperature only dropped to -37.3ºC, which resulted in only 47.1% mortality. Accordingly, experimental temperature required to achieve this level of mortality was -36.5ºC, which represents a temperature difference of 0.8ºC. The difference in mortality between the two locations appears to be attributable largely to differences in air temperature during the late January 2008 cold snap.

Table 1. Mortality survey for two regions in Alberta, along with minimum temperature realized up to that date. The "experimental temperature" refers to Figure 16 and shows the temperature needed to achieve the observed mortality.

Location	date	n	observed mortality (%)	air temperature observed (ºC)	experimental temperature needed to match observed mortality (ºC)
Edmonton	24 Jan	1004	18.2	-26.6	-33.9
	01 Feb	180	93.3	-39.9	-39.1
Crowsnest Pass	12 Feb	210	47.1	-37.3	-36.5

Historical context

Similar simulations for the five winters of 2001-02 through 2005-06 in Alberta indicate that the last two winters were fairly cold for MPB, though not as cold as 2003-04 or 2004-05 (Fig. 13).
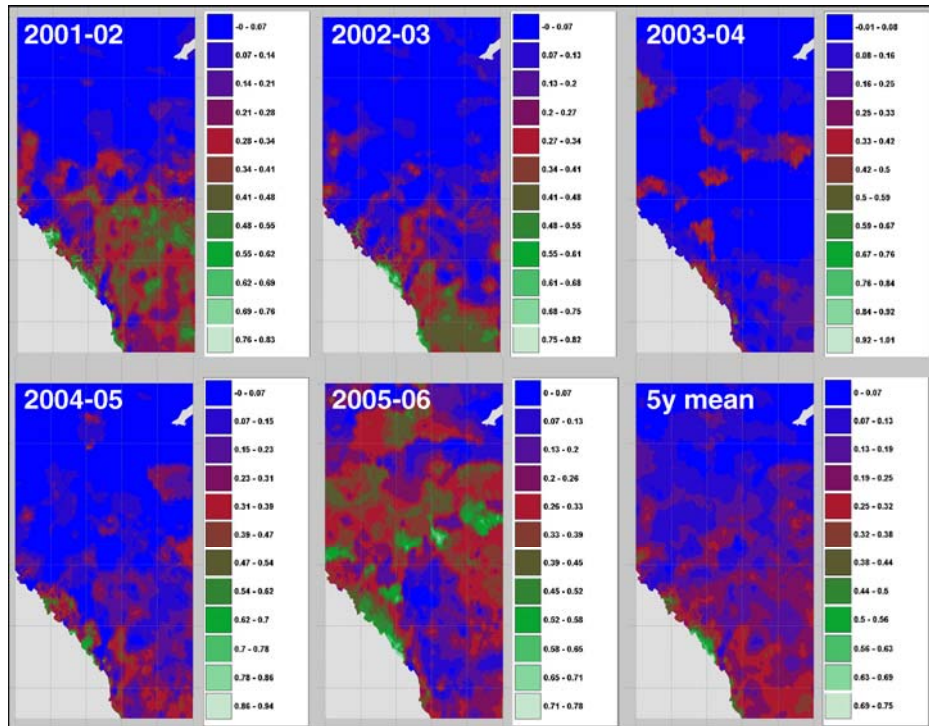
Figure 13. MPB/BioSIM backcasts for the previous five winters (data as in Fig. 12).

Increasing the scope of investigation over the last 58 winters, it is helpful to examine how the various winters rank, in terms of MPB winter mortality. According to the results in Table 2, the winter of 2007-08 was the 32nd coldest winter of the last 58, much harsher than 2006-07, which was only 52nd out of 58. By comparison, the winter of 2003-04 was the 8th coldest – far colder than either 2006-07 or 2007-08. Meanwhile, 2002-03 and 2004-05 were the 28th and 29th. In contrast, 2005-06 was the 4th warmest. To put some bounds on the process, the coldest beetle winter was 1952-53 and the warmest was 1991-92.

Table 2. Winter severity among years (1951-2008), ranked from coldest/lowest survival (=1) to warmest/highest survival (=58).

year	survival rank
1952-53	1
2003-04 [1]	8
2002-03 [1]	28
2004-05 [1]	29
2007-08 [2]	32
2001-02 [1]	51
2006-07 [3]	52
2005-06 [1]	55
1991-92	58

[1] Winter survival for this year mapped in Fig. 13.

[2] Winter survival for this year mapped in Fig. 12.

[3] Winter survival for this year mapped in Fig. 3.

Examining weather station time-series, it is clear that MPB winter survival is highly variable over time (Fig. 14). The average predicted survival rate in the northern boreal region (Peace River, Grande Prairie, Whitecourt) was 0.13, associated with an average minimum winter temperature of -38.0°C. The average predicted survival rate in the Rocky Mountains (Jasper, Banff) and southern boreal plains region (Edmonton) was 0.27, associated with an average minimum winter temperature of -33.6°C. Temporally, the correlation between annual minimum winter temperatures and annual winter survival varied slightly among regions, from $r = 0.79$ to 0.87.

These fluctuations in predicted MPB survival rates (and hence minimum winter temperatures) tended to track the Pacific Decadal Oscillation (PDO), but only when PDO was in its "negative phase" (i.e., until 1976, but not afterward) (Fig. 14). Prior to 1976, when PDO was averaging -4.18, winter temperatures (and therefore MPB winter survival rates) were moderately correlated with PDO (average $r = 0.42$ among regions). After 1976, when PDO was averaging 1.52, winter temperatures were uncorrelated with PDO (average $r = -0.00$ among regions).
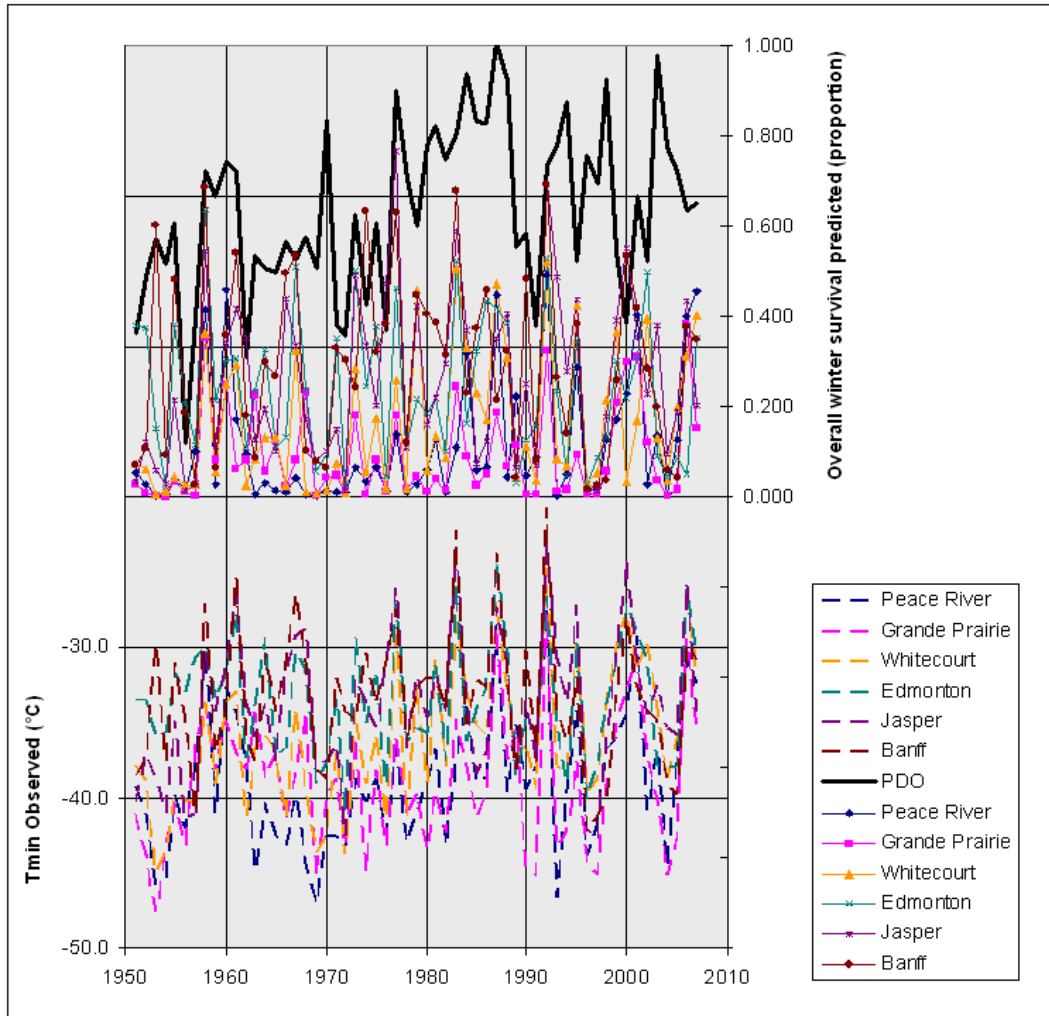
Figure 14. Fluctuations in minimum winter temperature (dashed lines) and predicted MPB survival (solid lines) for six locations in Alberta, as compared to the PDO index**.**

3.2 Laboratory Testing

3.2.1 MPB supercooling points and temperature over time

Due to high variation in phloem temperature on the south side of the bolts, only larvae from the north side of the bolts were used in the measurement of supercooling point. Fig. 15 shows the relationship between the phloem temperature and the variation in supercooling point of the mountain pine beetle. From this graph it is clear that on 29 January the phloem temperature got colder than the average supercooling point, which translated into very high mortality.
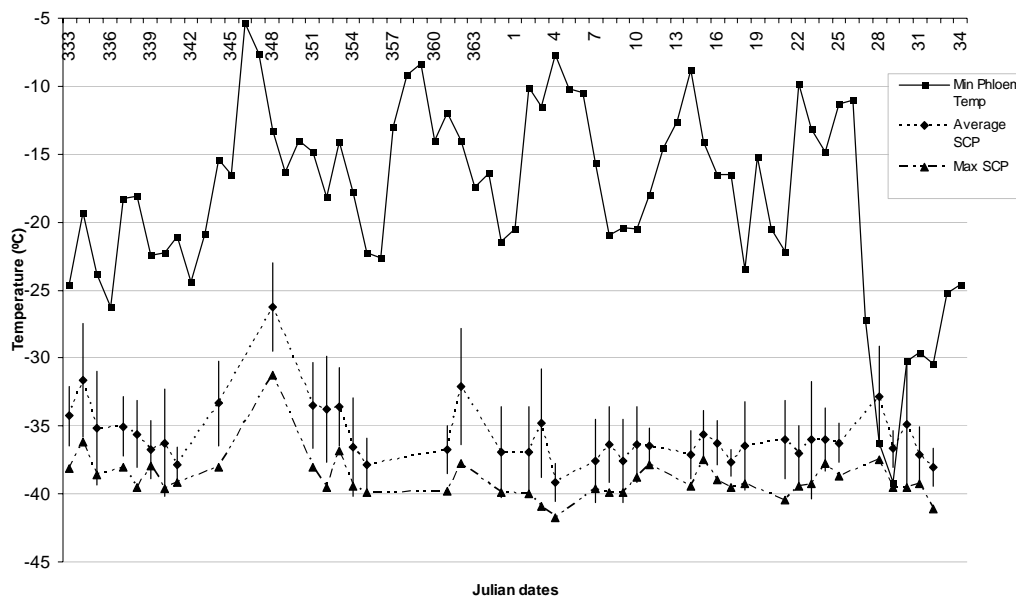
Figure 15. Daily minimum phloem temperature of infested bolts and average (+/- SD) and maximum supercooling point temperature of MPB larvae. Plot starts 29 Nov 2007 (JD 333) and runs through 3 Feb 2008 (JD34).

The experimentally derived cumulative mortality curve indicated that a temperature of

-36.7ºC killed 50% of larvae (LT$_{50}$), while a temperature of -39.3ºC killed 95% of larvae (LT$_{95}$) (Fig. 16). To kill one hundred per cent of the experimental sample population required a temperature of -41.7ºC.

Figure 16. Temperature dose-response curve for MPB mortality as a function of temperature at which larvae died (i.e., SCP). Curve is based on all larvae measured.

3.2.2 Phloem temperature above and below snow

As a general trend, the below snow phloem temperature was warmer than the above snow (Fig. 17). There were days where the difference was minimized (day 346, below = -5.2ºC, above= -5.6 for a difference of 0.4ºC), but others where th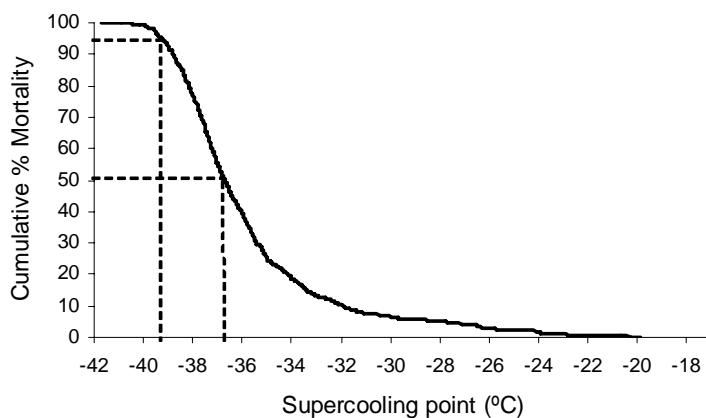e differences was much greater (day 29, below =-22.2, above = -37.5 for a difference of 15.3ºC). The average difference between the above and below was 4.6ºC over a period of 99 days.
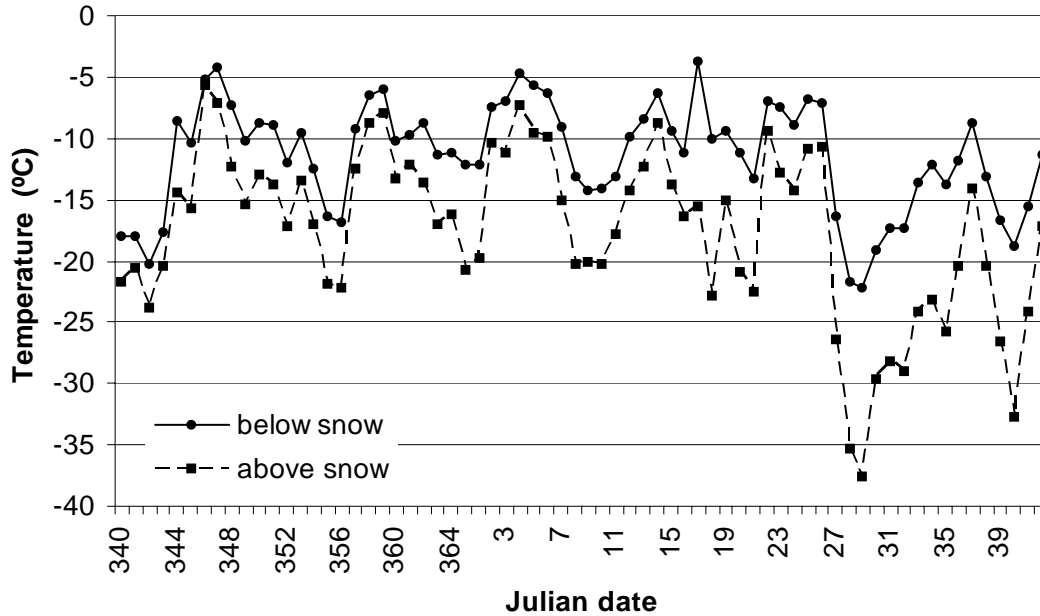
Figure 17. Minimum phloem temperature measured on a MPB infested bolt at a height of 10 cm (below snow) and 30 cm (above snow).

3.2.3 Phloem temperature on south and north facing exposures

Variation in temperature between the north- and south-facing phloem was larger during sunny days but minimized during cloudy days (Fig. 18). The direct radiation from the sun increased the phloem temperature of the south side of the bolt by as much as 25ºC at its warmest point. During cloudy days or during night time, the south and north facing phloem shows similar temperature.
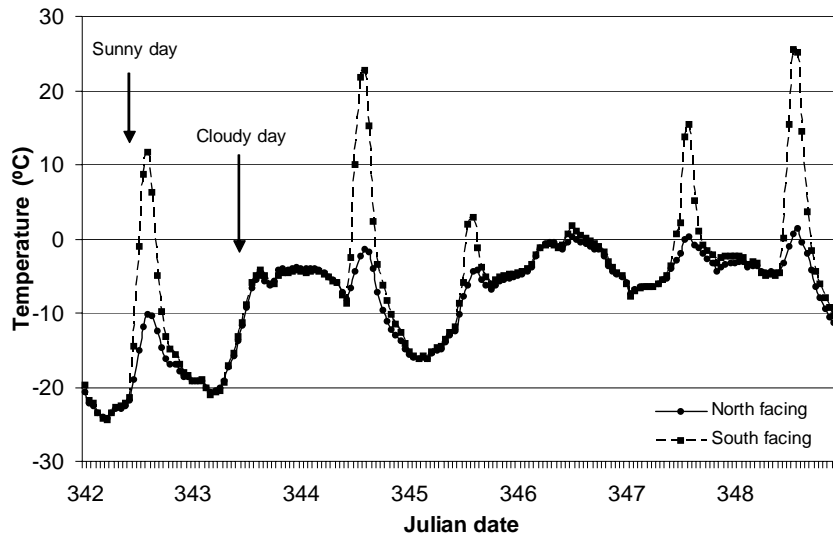
Figure 18. Seven days of hourly phloem temperature measurement on the north- and south-facing side of a lodgepole pine bolt infested with mountain pine beetles. Temperature measured with type E thermocouple and recorded with a Campbell 21X.

3.2.4   *Phloem temperature at different heights on a bolt*

Only minor and non-significant differences could be found in the phloem temperature measured at different heights along the bolt (Fig. 19). There is a lag of approximately four hours for the phloem temperature to equilibrate with the air temperature.

Figure 19. Three days of hourly measurement of phloem temperature at different heights along a bolt and air temperature. The air temperature curve is indicated with an arrow.

3.2.5   Supercooling point (SCP) estimation on living and dead larvae

An experiment was done in order to investigate if it was possible to differentiate between the cooling profiles of live and dead larvae. If dead larvae cool differently from living larvae, then it would be possible to screen them out of a sample without having to pre-warm them to conduct an activity assay. Fourteen live l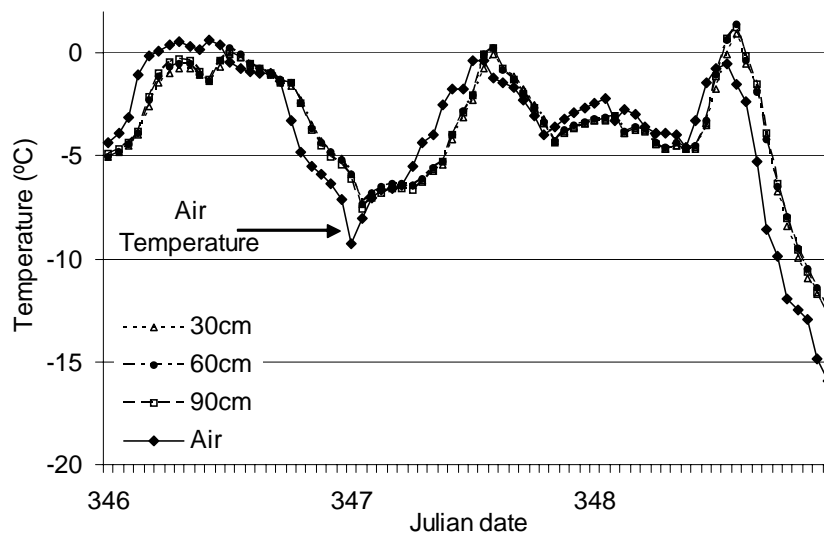arvae were used in a preliminary SCP estimation test. The same larvae, killed by the first cooling, were then cooled again to generate a second signal to be compared with the first one. Fig. 20 shows only the signals of three sample larvae and clearly indicates that there was no detectable difference in the signal given by the live or freshly dead larvae.
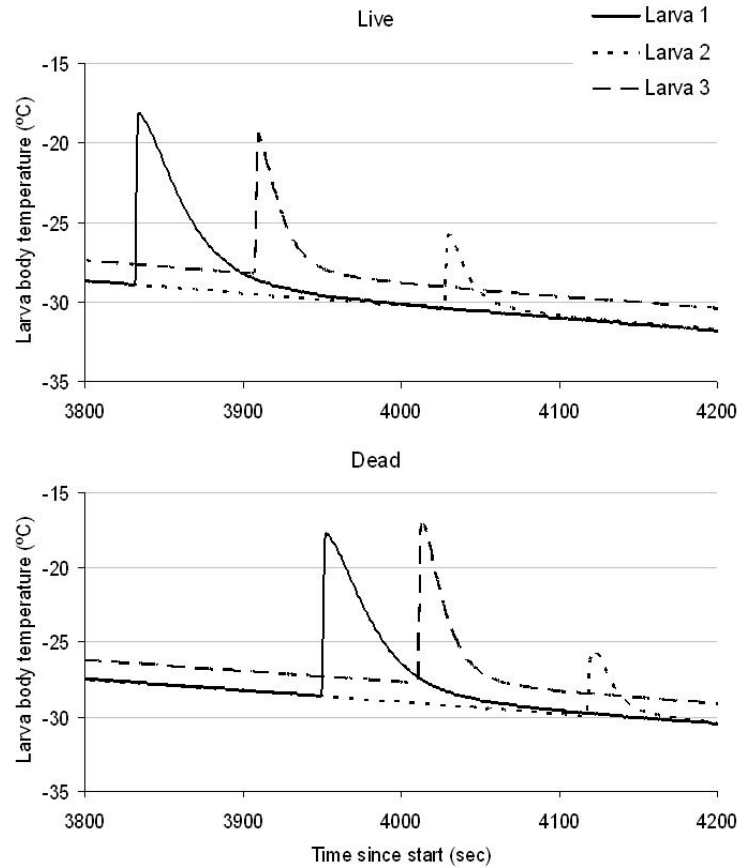
Figure 20. Supercooling point signals of living (top) and dead (bottom) MPB larvae.

3.2.6   Effect of pre-warming prior to SCP estimation

Given that it is not possible to distinguish living and dead larvae on the basis of cooling profiles, the simplest alternative is to conduct an activity/response assay, whereupon larvae are pre-warmed in order to amplify an activity response. We sought to quantify the impact of a 24h warming on SCPs by calculating the difference in larval SCPs between samples tested immediately after removal from a bolt (n=42) versus samples warmed at room temperature for 24 hours after extraction (n=24). Those tested immediately upon extraction showed an average supercooling point of SCP of 35.1 ± 3.9ºC while the larvae subjected to 24h room temperature showed an average SCP of 31.1 ± 2.3ºC (Fig. 21). The means significantly differed from each other (t-test, p <0.001). Warming the larvae before testing the supercooling point will therefore result in a positively biased SCP measurement.

Figure 21. Frequency distribution of larval supercooling points measured immediately after extraction from field versus 24h at room temperature. Warming by 24h resulted in a ~4°C rise in supercooling point.
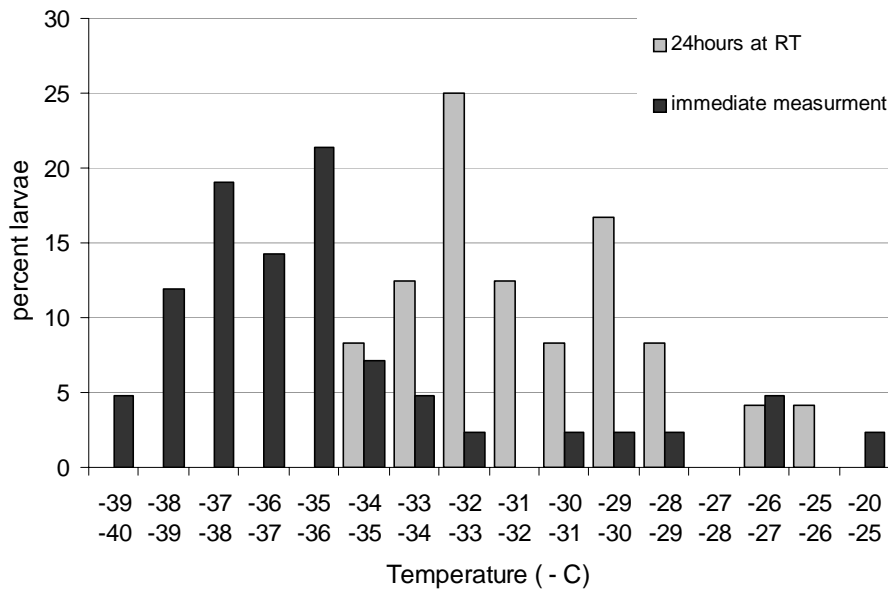
3.3   Technology Transfer and Follow-up

3.3.1   *Operationalization of the MPB/BioSIM forecasting tool*

The province of Alberta was sufficiently satisfied with the quality of the model predictions that these were used to optimize the re-deployment of their control resources. Working closely with the province, we discovered that a number of mapping-related computational details needed to be addressed in order to move from research forecasting to operational forecasting. Two issues in particular required significant follow-up:

(1) *Mapping interpolation method*. Mapping involves using high-resolution digital elevation models (DEM) to generate high-resolution spatial maps from a coarser-resolution grid of simulation points. Two methods of mapping were investigated for real-time forecasting. Spatial regression was found to be much faster than kriging, but introduced extrapolation errors that ASRD considered unacceptable for operational forecasting. These data extrapolation/spatial interpolation errors were exacerbated when the spatial extent of mapping was extended from just Alberta to include BC. The reason is because of the large extent in longitude and elevation in BC, and the increase in error this causes in the Alberta spatial/data domain, where the geographic data do not span the same range. In addition, we found it advantageous to transform the dependent variable (survival rate) using a logit transform prior to kriging and then back-transform prior to mapping. This served to minimize the cross-validation mapping error. Alberta Sustainable Resource Development preferred the accuracy of the kriged product. The difference between the regression and kriged maps highlighted just how sparse the weather network was, because the two methods produced very different fits in areas where weather stations were absent over large areas.

(2) *Extent of weather station network*. The Environment Canada weather station network in northern BC and Alberta appears to be sparse enough that additional sources of weather data should be investigated. The numerous stations that are used for fire weather prediction do not report in winter time, leading to a network that yields predictions of unacceptably

low accuracy in areas where MPB populations are growing fastest, in the northern foothills of the Alberta-BC borderlands. This network could be bolstered by including provincial weather stations not in the Environment Canada network. This would require coordination and support beyond the level committed to this project.

3.3.2   Communication of forecasts

Model results were transferred directly to the provinces of Alberta and BC, and to the media and the public through the creation of a new Natural Resources Canada website, hosted at the Northern Forestry Centre in Edmonton. Software has been written such that model backcasts can now be communicated in near real-time (with a delay of 3-5 business days). The costs and benefits of implementing a fully automated map-generation procedure should be investigated. As it stands, the software requires user intervention at multiple stages.

3.3.3   Overwintering mortality in 2006-08 put in context

Compared to BC standards, the winters of 2006-07 and 2007-08 were quite hard on MPB in northern Alberta, although southern populations survived at levels high enough to allow populations to continue rapid growth and expansion. A retrospective study of past beetle weather in Alberta from 1951-2008 indicated that the rates of MPB mortality predicted and observed in 2007-08 were similar to the rates of mortality we would have expected in the mid 1970s and mid 1980s. The winter of 2007-08 thus represented a sudden reversion back to nominally "normal" winter conditions: colder than the 1990s, but warmer than the 1950s.

It is unreasonable to assume, based on just two winters, that Alberta's winter climate is too cold to allow MPB to invade eastward into the boreal forest. There are years when Alberta's winter climate – even in the north – is favourable to population growth. A string of successive warm winters could allow for a rapid rebuilding-up of populations over the next decade, suggesting there could be some value in long-range climatological forecasting where low-frequency variations in oceanic circulations and atmospheric radiative forcings are taken into consideration.

3.3.4   Future research

Supercooling point (SCP) estimation bias

One problem that we encountered in the course of this work which needs to be resolved is the inevitable bias that results from the presence of dead larvae in a sample taken from a natural population. Whereas the SCPs of living larvae respond dynamically to changes in temperature, this is not the case with dead larvae. If dead larvae are included in a test sample, the SCP estimate will be biased, with the direction and magnitude of bias depending on SCPs of the dead larvae at the time of death relative to those of the living population at the time of testing. Excluding dead individuals prior to testing is a valid option, but requires the use of an assay to distinguish living from dead. A common practice (e.g., Bentz & Mullins 1999) is to pre-warm all larvae, so that the living are active and responsive to a probing test. However, this introduces a different bias, in that the sample SCPs of the living larvae will rise as a result of warming. There are three possible avenues of resolution: (1) estimate the mortality-caused SCP bias, (2) find a better assay that does not affect SCPs, or (3) estimate the warming-caused SCP bias.

Effect of cooling rate

We chose a cooling rate of 0.5°C/min in order to simulate the rapid drop in temperature associated with the passage of an arctic air mass. However, the rate of cooling is known to be an important factor in the temperature at which an insect freezes and dies. It has been shown in other beetle species that 0.5°C/min is far more lethal than lower cooling rates, with a cooling rate of ~0.35°C/min acting as a critical threshold between high and low survival (Miller 1978).

Sublethal effects of cold

In some cases we encountered larvae which showed limited activity after supercooling. However, these larvae seemed so impaired in function as to be effectively moribund. An experiment examining the ability of these beetles to re-establish and feed is recommended.

On the possible evolution of increased cold tolerance

Given the high rates of natural selection against cold-intolerant MPB, it is reasonable to ask whether there is enough genetic variability in cold tolerance to allow for the rapid evolution of a new cold-tolerant race of MPB. That some MPB can tolerate temperatures as low as -41.7°C suggests this is a possibility. This question merits increased attention. The genetic basis of cold tolerance in MPB is not currently known, but should be investigated. The process of natural selection could influence genetic susceptibility to cold even from one year to the next. This also requires investigation. Finally, it is not clear what the fitness consequences might be for individuals with extremely high cold tolerance. It may be that any fitness benefits are outweighed by fitness costs which are unknown. These tradeoffs could imply a hard upper limit to the degree of cold tolerance that may be achieved through natural selection.

Winter climatology

Why did winter temperatures and MPB winter mortality in Alberta track the PDO while PDO was in its cool phase, up until 1976? Are these correlations in fact causative, and therefore predictive? If the PDO no longer correlates with winter temperature, does some other index, such as the Arctic Oscillation, now play that role (Stahl et al. 2006)? If the PDO switches back to its negative phase – which some climatologists suggest could be happening (Hartmann & Wendler 2005) – will it regain the predictive power it had prior to 1976? Are such switches predictable? Answers to these questions could help in forecasting future winter climates and thus MPB winter survival rates. Given that this is the single biggest mortality factor affecting MPB rates of population growth and invasive spread, research in this area is viewed as a high priority.

4   Conclusions

A landscape-scale ecophysiological model of mountain pine beetle (MPB) overwintering mortality was developed and validated for the province of Alberta. The model describes daily overwintering survival in the above-snow component of the MPB population. With some additional research, the below-snow survival process could be included in the model.

Field validation showed that the model is yielding some promising results, although it remains to be seen if model performance is as high during milder winters. Despite the overall predictive power of the model, there appears to be substantial unexplained variation in observed mortality. The nature of this discrepancy should be investigated, as small errors in mortality estimates can be a major concern for operational decisions when the degree of predicted mortality is in the neighbourhood of 95%.

Experimental data appear to match the observational data very closely, suggesting that the model's assumptions are valid. This needs to be investigated further during a winter in which low mortality is observed due to the absence of any major cold snap.

Retrospective studies of winter climate suitability over the past six decades suggest that northern Alberta is only marginally suitable for MPB invasion. Some years, populations will thrive. Other years, they will not. This implies that population monitoring and adaptive, strategic pest management is going to continue to be a high priority as the MPB invasion front ebbs and flows according to the vagaries of the harsh and variable boreal climate. Accordingly, winter climate warming will pose an increasing threat of outbreaks and eastward range expansion, suggesting regional scale winter climate modeling is an area of high priority.

5   Acknowledgements

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