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Phloem Temperatures in Mountain Pine Beetle-infested Ponderosa Pine

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Phloem temperatures were recorded on the north and south sides of five mountain pine beetle-infested ponderosa pine in the Black Hills of South Dakota during the period of beetle habitation in 1989-1990 and 1990-1991. Phloem temperatures were frequently warmer than air temperatures during the nighttime hours and rarely cooled to the same extremes as air temperatures. During daylight hours, phloem temperatures on the south side were generally cooler or insignificantly different from air temperatures; rarely were they significantly warmer. Generally, phloem temperatures on the north side during daylight hours were significantly cooler than air temperatures. Although air temperatures dipped below -20°F for 6 hours in December 1989 and for 2 to 3 days in December 1990, brood mortality was insufficient to cause a decreasing population trend in the sample trees. The number of cumulative degree-hours to the appearance of adults was estimated to be between 20,000 and 22,000 using a base of 50°F . Mountain pine beetle rates of development and the synchronization of the life stages are discussed.

Keywords: Ponderosa pine, mountain pine beetle, temperatures

Introduction

Temperature is an important factor in the development and survival of the mountain pine beetle (MPB) (*Dendroctonus ponderosae* Hopkins). Temperature delimits growth and development, sets the rates of growth and development, regulates cold hardiness, and determines survival (Safranyik 1978). During the course of a typical 1-year life cycle—July-August of 1 calendar year to July-August of the following year—temperatures can increase or retard the rate of development, increase brood mortality, and restrain adult emergence. In this paper, we are concerned with temperature as it influ-

ences MPB survival and development within infested ponderosa pine (*Pinus ponderosa* Lawson) in an area where epidemics frequently develop.

MPB mortality can result from extremely cold and hot temperatures. Low temperatures of 12.5 to 0°F can be lethal to brood adults from ponderosa pine (Wygant 1937). Temperatures of -10°F can kill all MPB larvae in late October but temperatures of -25°F kill about 70% of the MPB larvae in February (Wygant 1937). Wygant's data was for naked larvae in petri dishes and therefore do not reflect the insulating properties of ponderosa pine bark. When air temperatures in the forest drop below zero, larval mortality beneath the bark of naturally infested trees may not correspond to Wygant's mortality levels because inside bark temperatures are warmer than air temperatures (Beal 1934). At the oppo-

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site extreme, temperatures $\geq 90^{\circ}\text{F}$ cause 100% mortality of first instar MPB larvae (Safranyik and Whitney 1985).

Between the temperature extremes that cause mortality, MPB development improves as temperatures depart from these extremes. Temperatures $\leq 35.6^{\circ}\text{F}$ will arrest larval development (McCambridge 1974). Larval development will proceed at 36°F but larvae reared at constant temperatures between 36 and 50°F fail to develop to the adult stage (Amman and Cole 1983; Safranyik and Whitney 1985). At a constant 59°F , larvae developed to adults in one study (Amman and Cole 1983) but not in another study (Safranyik and Whitney 1985). Optimum constant temperature for complete development is 68°F (Amman and Cole 1983), between 75 and 80°F (Safranyik and Whitney 1985), and between 73 and 75°F (Bentz et al. 1991).

How MPB larvae develop under variable temperatures in naturally infested trees may be quite different compared to their development under constant temperatures in the laboratory. Temperatures within the phloem of infested trees are seldom constant and the larvae can be exposed to a range of temperatures varying from critical to optimum. In apparent response to variable temperatures, each MPB life stage has acquired different temperature thresholds for development. First and second instars have lower temperature thresholds than do third and fourth instars (Amman and Cole 1983; Bentz et al. 1991). These temperature thresholds enable MPB larvae in lodgepole pine (*P. contorta* Douglas ex Loud.) to synchronize their life stages for mass attack (Amman and Cole 1983; Bentz et al. 1991).

Even though subcortical temperatures vary considerably in bark beetle-infested ponderosa pines, temperatures in the north and south sides follow definitive patterns in relation to air temperatures during winter months. Subcortical south-side temperatures are similar to air temperatures when air temperatures remain relatively constant (Beal 1934). On sunny days, south-side subcortical temperatures warm up between 1000 and 1500 hours when direct sunlight strikes the bark and they can exceed air temperatures by 16°F (Beal 1934). North-side subcortical temperatures are more constant than south-side temperatures but can rise rapidly on sunny days from heat reflected off the snow. When air temperatures drop sharply, subcortical temperatures frequently lag behind air temperatures (Beal 1934); thus, temporary subzero air temperatures may not cause significant beetle mortality because subcortical temperatures do not reach the same low level.

During summer, the relationship between subcortical bark temperatures of infested lodgepole pine trees and air temperatures is apparently opposite that of winter patterns. Subcortical bark temperatures are 3.5 to 5.4°F higher at night than air temperatures (Powell 1967). During midday, subcortical temperatures are about equal to air temperatures in the thin-barked trees

and cooler in the thick-barked trees (Powell 1967). The relatively equal or cooler temperatures during midday may have resulted because Powell averaged the temperatures for all four sides of his sample trees.

Except for the previously mentioned studies, little information is available on subcortical bark temperature patterns in MPB-infested trees, especially for the duration of MPB habitation in ponderosa pine. This note reports on the phloem temperatures of MPB-infested ponderosa pine in the Black Hills of South Dakota. More specifically, phloem temperatures on the north and south sides of five infested trees are compared to air temperatures. The phloem temperatures are then related to MPB survival and brood production during 1989-1990 and 1990-1991.

Methods

In 1987, a MPB epidemic was killing substantial numbers of ponderosa pines in Bear Basin which lies just north of the Bear Mountain Lookout and about 10 miles northwest of Custer, SD. The epidemic expanded in subsequent years and groups of 5 to 20 infested trees appeared in the upper Spring Creek and White House Gulch drainages in 1988 and 1989. By 1990, larger groups of 25 to 50 trees were evident in the landscape. Tree mortality in the Basin averaged 5.9 trees per acre for 1989, 17.8 for 1990, and 37.6 for 1991 (Pasek and Schaupp 1992).

Five MPB-infested trees in stands in the White House Gulch area were selected for temperature monitoring on September 21, 1989 and August 20, 1990. The trees were infested in August 1989 and August 1990, respectively. They ranged in diameter at breast height from 10.2 to 14.6 inches in 1989 (average = 12.2) and from 11.6 to 14.6 in 1990 (average = 12.8). They were surrounded by other uninfested trees of similar diameter, crown development, and spacing. Basal area was $\geq 150\text{ ft}^2$ per acre around both sets of trees. Elevation of the infested trees was around 6,200 ft and both sites were essentially flat.

On September 21, 1989, and on August 20, 1990, a Campbell Scientific 21X micrologger² was set up amongst the infested trees to record phloem temperatures. Temperatures were recorded via YSI thermilinear thermistor networks² attached to cables that were connected to the micrologger. A thermistor bead from each thermilinear network was placed in the phloem about 4.5 ft aboveground on the north and south sides of each of the five infested trees. Ambient air temperature was monitored by a thermistor bead hang-

²The use of trade and company names is for the benefit of the reader; such use does not constitute an official endorsement or approval of any service or product by the U.S. Department of Agriculture to the exclusion of others that may be suitable.

ing just below the micrologger and about 4 ft aboveground.

Instantaneous phloem and air temperatures were recorded every 4 hours from September 21, 1989 to August 20, 1990. A power loss soon after installation caused the loss of data from September 21 to October 18, 1989. Animal damage in June and July 1990 caused the loss of some data from June 6 to June 20, and from June 26 to July 12, 1990.

Instantaneous phloem and air temperatures were also recorded every 4 hours from August 20, 1990 to August 21, 1991. Data was lost from February 18, 1991 to March 19, 1991 because of battery failure.

Instantaneous temperatures from the north sides for each recording time of each day (i.e., 0400, 0800 hours, etc. of October 20, 21, etc.) were compared against their respective temperatures from the south sides in a series of *t*-tests, $\alpha = 0.05$. The temperatures for each recording time were tested for each day rather than a single test of all days pooled together because we wanted to determine if the frequency of significant differences varied from month to month. After the *t*-tests were performed, the frequency of significant differences between the north and south sides were determined for each time of day by summarizing the results of the *t*-tests.

Mean temperatures for the north and south sides were compared for each recording time. Linear regressions of the mean north and south temperatures against the respective air temperature were used to derive the equations predicting phloem temperatures from air temperature. Mean north-side and south-side temperatures for 1989-1990 and 1990-1991 were also plotted for their respective recording time to derive the general trend in temperatures over the period of beetle habitation. Air temperatures for 1989-1990 and 1990-1991 were not plotted with the respective north-side and south-side temperatures because their presence obliterated the details in the day to day trend of the north-side or south-side temperatures.

To determine either density of attacks or brood density and development, bark samples were taken from the 1989- and 1990-infested trees. Samples 6 inches by 12 inches were taken on September 17, 1989 to determine density of attacks in 1989 and on August 23, 1990 to determine density of attacks in 1990. Samples 6 inches by 6 inches were taken on December 5, 1989; May 24, 1990; June 6 and 21, 1990; and July 17, 1990 from five 1989-infested trees to determine brood development for 1989-1990 and on August 22, 1990; October 25, 1990; March 19, 1991; May 21, 1991; and June 11 and 21, 1991 from five 1990-infested trees to determine brood development for 1990-1991.

To determine the number of MPB emerging per square foot of bark surface, 1-ft by 2-ft emergence cages were attached between 4 and 6 ft aboveground to the 5

trees monitored for temperature in 1989-1990 and 1990-1991. Two cages were attached to each tree on July 17, 1990 and May 21, 1991, well before MPB emergence usually starts. The cages were attached to the north and south sides of four trees and the east and west sides of one tree in 1990. Cages were attached to north and south sides in 1991. MPB emergence into the cages was monitored daily from July 19 to August 12, 1990 and again on August 20 and 23, 1990. Emergence in 1991 was monitored on July 17 and 18, daily from July 28 to August 10, and again on August 13, 14, 15, 29, and 30, 1991. Beetle counts were totaled for each year and converted to numbers emerging per square foot of bark surface.

The trend in MPB numbers was determined by calculating a population trend ratio (PTR). The PTR is determined by dividing the number of MPB emerging per square foot of bark by the number of attacking beetles. The number of attacking beetles is derived by doubling the density of attacks. The attack density is doubled because we assumed that even though the female beetle makes the attack and creates the gallery, a male beetle is needed in every gallery before the female can produce viable brood. Using the doubled attack density may understate the PTR because the sex ratio usually favors females and is rarely 1:1 (see Cole et. al 1976). If males are not present in some galleries because one male mates with females in different galleries, then the number of attacking beetles would be less than twice the density of attacks and the PTR, therefore, underestimated. However, all of the attacking beetles may not be within the sample when it is taken so we have no way of knowing if their number is less than twice the number of attacks; therefore we use a doubled attack density. If the PTR exceeds 1, the population is increasing because the number of emerging beetles (the brood of the attacking beetles) exceeds the number of attacking beetles. If the PTR is less than 1, the population is decreasing.

To determine the number of degree-hours (Allee et. al 1955) at various times in the life cycle of the MPB, degree-hours per day were calculated from August 15, 1989 to August 15, 1990 and August 20, 1990 to August 21, 1991 using threshold temperatures of 50 °F (Reid 1962) and 40° F (McCambridge 1974).

Degree-hours for 1989-1990 were calculated by using our mean temperatures from each recording time for the periods October 18, 1989 to June 6, 1990; June 21 to June 25, 1990; and July 13 to August 15, 1990. For the periods that our phloem temperatures were missing, we first estimated air temperatures for our site by using equations developed from the correlations between our air temperature data and air temperature data from Hill City, SD, a town about 8 miles northeast of the study area. Then we estimated phloem temperatures by using equations developed from the relationships between our air and phloem temperatures.

Degree-hours for 1990-1991 were calculated by using our mean temperatures for each recording time for the periods August 20, 1990 to February 17, 1991 and March 19 to August 21, 1991. We derived phloem temperatures for the 1991 period of missing data in the same manner as we did for the 1989-1990 calculations.

The number of degree-hours for specific time periods or for a specific life stage was derived by cumulatively summing the values for each from August 15, 1989 or August 20, 1990 to the specific date of interest. We considered the 1990-1991 data to be more accurate because we had less missing data than in 1989-1990. The cumulative degree-hours for a specific life stage represent when the first individuals in that stage appeared and are not average values for the entire population.

Results and Discussion

Temperature Patterns

Air and phloem temperatures generally declined from October to December, remained relatively uniform from December to late February, increased from late February to late June, and then remained relatively uniform from late June to the end of the recording period in August. Surges of cold and warm air masses periodically interrupted this general pattern so that air and phloem temperatures temporarily exceeded or fell under the general trend.

North-side phloem temperatures were generally below 50°F from November to April in 1989-1990 (fig. 1) and from late November to April in 1990-1991 (fig. 2). South-side phloem temperatures were generally below 50°F from November to early April in 1989-1990 (fig. 3) and from November to the first days in April in 1990-1991 (fig. 4).

Figure 1.—Mean north-side phloem temperatures at the Black Hills study location from August 1989 to August 1990.

Figure 2.—Mean north-side phloem temperatures at the Black Hills study location from August 1990 to August 1991.

Figure 3.—Mean south-side phloem temperatures at the Black Hills study location from August 1989 to August 1990.

Figure 4.—Mean south-side phloem temperatures at the Black Hills study location from August 1990 to August 1991.

Phloem temperatures were strongly influenced by air temperatures as indicated by the following equations:

1989-1990

$$\text{NPT}_{\text{win}} = .75\text{AT} + 7.78 \quad R^2 = 87\% \quad \text{S.E. of Est.} = 3.81$$

$$\text{NPT}_{\text{sum}} = .85\text{AT} + 8.70 \quad R^2 = 92\% \quad \text{S.E. of Est.} = 3.56$$

$$\text{SPT}_{\text{win}} = .86\text{AT} + 5.83 \quad R^2 = 93\% \quad \text{S.E. of Est.} = 3.11$$

$$\text{SPT}_{\text{sum}} = .91\text{AT} + 6.80 \quad R^2 = 95\% \quad \text{S.E. of Est.} = 3.00$$

1990-1991

$$\text{NPT}_{\text{win}} = .92\text{AT} + 2.85 \quad R^2 = 97\% \quad \text{S.E. of Est.} = 2.50$$

$$\text{NPT}_{\text{sum}} = .90\text{AT} + 6.61 \quad R^2 = 95\% \quad \text{S.E. of Est.} = 2.89$$

$$\text{SPT}_{\text{win}} = .96\text{AT} + 3.18 \quad R^2 = 95\% \quad \text{S.E. of Est.} = 3.48$$

$$\text{SPT}_{\text{sum}} = .98\text{AT} + 3.73 \quad R^2 = 95\% \quad \text{S.E. of Est.} = 3.28$$

where

NPT_{win} = north phloem temperatures during October through March

AT = air temperature

SPT_{win} = south phloem temperatures during October through March

NPT_{sum} = north phloem temperature during April through September

SPT_{sum} = south phloem temperature during April through September

Because solar radiation also influences bark temperatures by heating the bole (Schmid et al. 1991), these equations will become more precise when a term reflecting the interaction of cloud cover and solar radiation is added to them.

Although phloem temperatures were strongly influenced by air temperatures, phloem temperatures were generally warmer when the lows occurred, especially when cold air masses lowered the temperatures below freezing. Phloem temperatures became equal to below-freezing air temperatures only when below-freezing temperatures persisted for at least 24 hours. During December 10-11, 14-15 and 20-22, 1989, air temperatures were 5° to 10°F lower than north- and south-side phloem temperatures (fig. 5) and phloem temperatures did not drop as low as air temperatures. Similarly, below-freezing air temperatures between December 18, 1990 and January 4, 1991 were colder than phloem temperatures until the air temperatures persisted continuously for more than 24 hours (fig. 6).

Peak air temperatures during the daytime were warmer than phloem temperatures, but this relationship varied by month and side of the tree. North-side phloem temperatures were frequently 5 to 10°F cooler than air temperatures when maximum temperatures occurred and were 5 to 10°F warmer when minimum air temperatures occurred, but were equal to air temperatures during the transition from one extreme to the other. South-side phloem temperatures were generally warmer than air temperatures when minimum tempera-

Figure 5.—Air, mean north-side, and mean south-side phloem temperatures during December 1989 at the Black Hills study location.

Figure 6.—Air, mean north-side, and mean south-side phloem temperatures during December 18, 1990 to January 4, 1991 at the Black Hills study location.

tures occurred but varied considerably in relation to air temperature when maximums occurred. We suspect the variability in the relationship of maximum air and south-side phloem temperatures reflected the amount of cloud cover. When days were overcast to partly cloudy, south-side phloem temperatures were less than or nearly equal to air temperatures. When days were mostly clear, south-side phloem temperatures generally exceeded air temperatures.

The magnitude of differences between the mean phloem temperatures for the north and south sides varied by the time of day, month, and year (table 1). The greatest differences in north- and south-side temperatures occurred at midday when south-side temperatures exceeded north-side temperatures by more than 7°F in some months (table 1). Similarly, south-side temperatures exceeded north-side temperatures by 1°F to 3°F at 1600 hours. The pattern of temperature differences for the 1200 and 1600 hour time periods was surprising because maximum differences were expected during

Table 1.—Magnitude of differences between the mean north-side and south-side temperatures (°F) of five mountain pine beetle-infested trees by time of day by month. Minus indicates the mean south temperatures are warmer. The first rows of temperature differences for each time represent 1989-1990 and the second rows represents 1990-1991.

Hour	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.
0000			0.15	0.42	0.26	0.33	0.76	0.80	0.61	0.13	-0.23	-0.15	-0.14
	-0.91	-1.23	-0.77	-0.57	-0.20	-0.39	-0.40	-0.23	-0.27	0.05	-1.53	-0.82	-0.55
0400			0.55	0.54	0.30	0.60	0.85	0.90	0.64	0.21	-0.57	-0.15	-0.08
	-0.63	-0.81	-0.51	-0.47	-0.22	-0.27	-0.39	-0.06	-0.17	0.15	-1.28	-0.61	-0.30
0800			0.65	0.65	0.37	0.54	0.88	0.81	0.22	-0.53	-1.44	-0.50	-0.61
	-0.51	-0.49	-0.50	-0.44	-0.20	-0.19	-0.24	-1.14	-0.48	-0.13	-1.50	-0.74	-0.72
1200			-2.23	-3.20	-3.17	-3.09	-5.34	-8.67	-5.77	-3.27	-1.93	-1.84	-2.09
	-6.24	-6.56	-4.34	-3.73	-2.92	-5.81	-8.21	-6.73	-3.89	-4.51	-7.50	-7.06	-10.46
1600			-2.38	-2.09	-1.76	-2.34	-3.13	-3.27	-2.26	-1.47	-1.52	-1.87	-2.61
	-0.95	-2.11	-2.22	-1.49	-0.82	-1.50	-3.61	-1.55	-0.75	-0.16	-1.13	-0.76	-1.80
2000			0.06	-0.04	-0.02	-0.05	0.25	-0.12	-0.11	-0.06	0.03	-0.12	-0.51
	-1.13	-1.42	-0.96	-0.82	-0.43	-0.71	-0.97	-0.69	-0.28	-0.11	-1.43	-0.62	-0.53

the 1200 and 1600 hour time periods in the months of June, July, and August but not in October and January to March. With only a few exceptions, mean north-side temperatures differed from mean south-side temperatures by $\leq 1^\circ\text{F}$ from 2000 to 0800 hours throughout each year (table 1).

The frequency of significant difference between north- and south-side temperatures reflected the magnitude of differences between the two sides. North-side temperatures were most frequently different from south-side temperatures at 1200 hours when differences were significant on more than 70% of the days of the year and at 1600 hours when differences were significant on more than 60% of the days of the year. In contrast, significant differences between the two sides from 2000 to 0800 hours existed less than 30% of the time during the months of April to August. Significant differences between the two sides from 2000 to 0800 hours were surprisingly more prevalent in September to February than in April to August.

We believe the magnitudes of temperature differences between the two sides, and therefore the frequencies, reflect the seasonal and daily patterns of solar radiation as influenced by weather patterns and stand density. During clear days in the winter months, the south sides of trees heat up primarily during the midday hours because of the low angle of the sun. Significant differences occur frequently at 1600 hours despite the setting of the sun because the tree boles retain the heat gained during the midday hours. These differences may also occur at night because the equal rates of heat loss from the north and south sides would tend to maintain the differences. The low percentage of time when midday temperatures on the north and south sides were not different probably reflects the presence of cloud cover.

As the season progresses from winter to spring to summer, the sun's angle is rising, so south-side temperatures can rise quite dramatically on clear days. At the same time, the months of February and March, and to a lesser extent April, are usually months of low

precipitation, which contributes to the high magnitude and frequency of temperature differences at midday. In contrast, the months of May and June are wet months with periods of rain or general overcast during the day. Cloud formation during the midday hours also becomes more frequent because of convection heating in July and August; the clouds screen out solar radiation, and temperature differences thus become less frequent. The infrequency of significant differences during the summer months also results from the greater variability in temperatures within each side as influenced by stand density (Schmid et al. 1991), and thus the lesser chance for significant differences. In winter, the decreased variability allows smaller mean differences to be significant.

The mean differences in phloem temperatures of $\leq 1^\circ\text{F}$ from 2000 to 0800 hours were probably much less significant in terms of more rapid MPB development on either side than midday differences because the means for the nighttime hours represent a mixture of warmer north-side temperatures on some days and warmer south-side temperatures on other days. In contrast, mean differences at 1200 and 1600 hours represent predominantly warmer temperatures on the south-side. Thus, if MPB development proceeds more rapidly on the south side than on the north side, it occurs during midday to late afternoon when south-side temperatures may substantially exceed north-side temperatures.

Brood Survival

The PTR in 1990 was 1 or more for 4 of the 5 infested trees and less than 1 for the fifth tree but averaged 2.0 for the 5 trees. In 1991, the PTR was 1 or more for 3 of the 5 infested trees and less than 1 for the other 2 trees but averaged 2.0 for the 5 trees. The population trend was thus increasing, which indicates that the cold temperatures in December of both years did not kill enough brood to cause the populations to decline. According to Wygant (1937), temperatures of -20°F are critical in

October but will kill less than 50% of the brood in February. Apparently the brood had developed enough cold hardiness by December to withstand nearly continuous -20° F temperatures for 1 to 2 days in 1989 (fig. 5) and for 2 to 3 days in 1990 (fig. 6).

The relationship between air and phloem temperatures indicates that pest managers should not quickly assume significant brood mortality when air temperatures drop well below 0° F. When air temperatures went to -23° F on December 22, 1989, phloem temperatures barely reached -20° F (fig. 5). Similar differences were apparent in December 1990 although the differences narrowed as -20° F temperatures were maintained (fig. 6). On other days in 1989-1990, air temperatures were 5 to 10° F colder than phloem temperatures so the effect of cold air temperatures in December may not be as great as suspected, especially when the duration of below-zero temperatures is short. We suspect air temperatures ≤-20° F in December must continually exist for at least 7 days before they influence brood survival and cause a decreasing population trend.

Short-term below-zero temperatures are more influential if they occur in October before the larvae are cold hardy or in April when larvae are resuming development and losing their cold hardiness. On October 30 and 31, 1991, unseasonably cold temperatures dropped to -9° F and -5° F in Hill City, SD (NOAA 1991a). Minimum temperatures on November 2 and 3, 1991 dropped to -8° F and -13° F (NOAA 1991b). The PTR for 29 1991-infested trees in and nearby the 1989 and 1990 study areas averaged 0.4 with only 2 trees having a ≥1

PTR; thus indicating a decreasing population (J.M. Schmid, unpublished data). Because temperatures in December 1991 and January 1992 were similar in extent and duration to temperatures during 1989-1990 and 1990-1991, we believe the major differences in PTRs for the three generations of MPB results from low temperatures in October and November 1991. As indicated by Wygant (1937), short-term below-zero temperatures in October were more influential than short-term below-zero temperatures in December.

Degree-hours and MPB Development

Several MPB stages were present in each of the 1989-1990 and 1990-1991 samples (tables 2,3). Pupae were present in the June 21 samples but not in the June 6 samples, thus indicating that the larvae transformed into pupae between June 6 and June 21, 1990 (table 2). Similarly, pupae were absent in the May 21 samples but were present in the June 11 samples, thus indicating the larvae transformed into pupae between May 21 and June 11, 1991 (table 3). We estimate formation of first pupae in ponderosa pine requires between 16,000 and 18,000 degree-hours using a 50° F base and between 37,000 and 41,000 degree-hours using a 40° F base. The values for the 50° F base are at least 5,000 degree-hours more than the 11,000 degree-hours of Reid (1962) for lodgepole pine.

Callow adults were absent from the June 21 samples but were present in the July 17 samples in 1990 (table 2). Similarly, adults were absent in the June 11 samples but

Table 2.—Percentage of brood in each stage at each sampling date for the 1989-1990 MPB life cycle.

Date	Instar				Pupae	Callow	Adult
	1st	2nd	3rd	4th			
Dec. 5	3	52	45				
May 24	12	8	47	33			
June 6			20	80			
June 21			2	61	37		
July 17					<1	8	91
Aug. 1						First emergence	

Table 3.—Percentage¹ of brood in each stage at each sampling date for the 1990-1991 MPB life cycle.

Date	Egg	Instar				Pupae	Callow	Adult
		1st	2nd	3rd	4th			
Aug. 22	100							
Oct. 25			2	29	70			
Mar. 19		4	18	53	24			
May 21				29	71			
June 11				3	75	22		
June 21					17	69	13	
July 17							First emergence	

¹Percentages may not add to 100 due to rounding.

were present in the June 21 samples in 1991 (table 3). The cumulative degree-hours for the formation of the first callow adults appears to be 20,000 to 22,000 which indicates the formation of adults also occurred well beyond the approximate values of 12,000 degree-hours of Reid (1962) and 15,000 degree-hours of Powell (1967). Thus, the degree-hours needed for completion of the various stages appears greater for the MPB in ponderosa pine in the Black Hills as compared to the MPB in lodgepole pine in Canada.

The range of 2,000 degree-hours for the formation of pupae and callow adults suggests our estimates of degree-hours necessary for the formation of these stages are imprecise. However, cumulative degree-hours within the phloem varies with bark thickness, so that broods in thin-bark trees may receive in excess of 2,000 degree-hours more than broods in thick-bark trees (Powell 1967). In our situation, the thermistor beads were probably not at the same depth, and therefore functioned as if they were in bark of different thicknesses. In addition, phloem temperatures may have also indirectly influenced MPB development by affecting phloem quality. Higher temperatures on the south side may have caused the phloem to dessicate more than on the north side. Drying of the phloem deprives developing brood of necessary moisture (Amman and Cole 1983) and may, in this case, have delayed transformation of fourth instar larvae to pupae. Or perhaps, the higher phloem temperatures on the south side are causing changes in the nutritional quality of the phloem such that larval development is retarded. In any case, the cumulative degree-hours are variable but definitely higher than Reid's 1962 values.

Since Reid's 1962 publication, additional information on temperature thresholds and rates of development for the MPB have been determined. The threshold for development of first instar MPB larvae apparently occurs between 36 and 40° F (McCambridge 1974) and the rate of development for all larval stages increases with increasing temperature (McCambridge 1974; Bentz et al. 1991). Using a threshold temperature of 40° F (McCambridge 1974) for eggs laid in early August 1989, we estimate that 43,000 to 46,000 degree-hours would be needed for the formation of teneral adults.

In a similar context, Amman and Cole (1983) and Bentz et al. (1991) have indicated that MPB first and

second instars in lodgepole pine have lower thresholds for development than do third and fourth instars and pupae. These lower thresholds presumably allow first and second instar larvae originating from eggs deposited late in the attack period to "catch up" to larvae originating from eggs deposited early in the attack period that have progressed to the third and fourth instars. Based on the distribution of the life stages in our samples (tables 2, 3), the different MPB larval instars in the Black Hills do *not* generally "catch up" and individuals only become synchronized during the adult stage. We say generally because some "catch up" may occur on south sides. In some 1991 samples, one or two instars were present on the south side while three were present on the north side (table 4). This data may be an example of synchronization. On the other hand, the presence of three instars in the north sides of three trees and in the south side of one tree (table 4) suggests that population synchronization is not generally occurring.

Although the thresholds for development of the four instars may be quite different (Amman and Cole 1983; Bentz et al. 1991), the rate of development below 50° F is low for all instars: first instar larvae would require 100 days to advance to second instars and second instar larvae would require 60 days at 50° F to advance to the third instar (see Bentz et al. 1991). Further, development is probably longer at lower temperatures. If the population synchronized between October 15 and April 15, 1991—the period when phloem temperatures were generally below 50° F (fig. 1, 2, 3, 4) and very few degree-hours above 50° F or 40° F are available (fig. 7, 8)—the four instars would not have been present in the May 24, 1990 (table 2) and March 19, 1991 (table 3) samples. Therefore, even though the first and second instars may continue development between October 15 and April 15 when third and fourth instars are generally temperature limited, their rate of progress is not great enough to overcome the progress of the third and fourth instars.

The presence of first and second instars in the May 1990 and March 1991 samples suggests that they may have originated from eggs laid in the spring and therefore, cannot be cited as evidence against the hypothesis of synchronization (G.D. Amman, personal communication). This argument cannot be discounted with our 1989-1990 data because we did not determine if the parent adults were alive in the December 1989 samples.

Table 4.—Number of individuals in each instar in north- and south-side samples from three trees on March 19, 1991.

Tree	North-side				South-side			
	Instar				Instar			
	1st	2nd	3rd	4th	1st	2nd	3rd	4th
1	1	12	6				2	6
2		2	23	5	3	5	19	3
3		1	1	12				3

Figure 7.—Cumulative degree-hours above threshold temperatures of 40°F and 50°F from August 15, 1989 to August 15, 1990.

Figure 8.—Cumulative degree-hours above threshold temperatures of 40°F and 50°F from August 20, 1990 to August 29, 1991.

However, we found no eggs in our December samples and we believe the first instar larvae in our May 1990 sample originated from eggs deposited late in the 1989 gallery construction phase (i.e., October). Further, the 1990-1991 bark samples had only live parent adults in the October samples and no eggs or live adults in the March samples. Thus, we believe the first instar larvae overwintered in this stage, and that their presence is evidence against population synchronization in ponderosa pine.

The number of life stages present at any specific time during MPB development is mostly a function of the density of attacks, the duration of the attack, and egg deposition periods. Thus, any particular bark sample may have several stages because of the nature of MPB attacks and gallery construction. For example, sampling within 2 to 3 weeks after attacks, galleries are intermingled but contain essentially 1 or 2 stages. Sampling in successive weeks will generally yield several stages because each sample will usually contain the beginning portion of some galleries wherein are found the oldest larvae (instar III and IV) plus the terminal portions of other galleries wherein are found only first and second

instars. Because trees are attacked at different times, samples drawn from such trees will exhibit distributions as shown in table 4. Yet when the samples are combined, the overall distribution may contain more stages than the individual samples (i.e., tables 2, 3).

The MPB population in the Black Hills becomes morphologically synchronized (i.e., all one stage) only during the adult stage because the first individuals becoming adults do not emerge immediately but wait for some mechanism to trigger emergence. This delay allows most of the larvae and pupae emerging from late-deposited eggs to complete development and become adults before the population emerges. Even then, synchronization seems questionable because adults emerge over at least a 30-day period (Schmid 1972). If all adults were fully synchronized, they would emerge in a much shorter period.

Beetles first emerged on July 27, 1990 and July 17, 1991. The emergence of the first MPB corresponds to approximately 29,000 for 1990, and 31,000 degree-hours for 1991 (fig. 7, 8) as calculated using the 50°F base and 61,000 for 1990, and 65,000 for 1991 using the 40°F base. These cumulative degree-hours are at least 9,000 degree-hours more than we estimated as necessary to reach the callow adult stage. We assume that adults must require additional degree-hours to complete physiological development after they attain morphological maturity or other mechanisms are necessary to trigger emergence. We expect to ascertain in future research whether approximately 30,000 degree-hours from time of attack is a good tool for predicting emergence.

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