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Modelling micro-habitat temperature for *Dendroctonus ponderosae* (coleoptera: scolytidae)

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Abstract

We evaluate two landscape-scale microhabitat temperature prediction models suitable for the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (coleoptera: scolytidae). Both models are based on maximum and minimum air temperatures measured at meteorological stations. The first, 'lapse' model employs temperature observations for a single nearby weather station, adjusting maximum and minimum temperatures based on elevation differences and appropriate historical vertical lapse rates. The second, 'geographic trend surface' model is based on the locations, elevations, and daily temperature measurements of surrounding weather stations. Predicted air temperatures are adjusted with a radiance-based exposure index to estimate sub-cortical phloem temperatures. Model parameters were estimated using original field measurements at three sites, and using 25 years of regional temperature measurements for sites in the western United States. Stand air temperature and phloem predictions were validated in comparisons with four withheld weather stations, and against one year of independently measured temperatures from four forest stands. Mean errors (observed minus predicted) of daily maximum stand air temperature ranged from −3.9 to 1.5°C, while mean prediction errors for daily minimum air temperatures ranged from −6.3 to 1.7°C. The geographic trend surface model performed slightly better across a range of sites, both for maximum and minimum air temperatures. Phloem temperature predictions were generally more variable, particularly for maximum temperatures on south sides of trees. Standard deviations in prediction errors were generally lower for minimum temperatures and did not differ by model form or tree exposures.

Keywords: Model; Temperature; Insect; Phenology; Landscape

1. Introduction

The mountain pine beetle (*Dendroctonus ponderosae* Hopk.) is a predominantly univoltine phloem feeder common in lodgepole (*Pinus contorta* Doug. ex Loud.) and ponderosa pine (*P. ponderosae* Doug. ex Laws.) forests of western North America. Due to periodic outbreaks the mountain pine beetle is an agent of large economic and ecological importance. Because the mountain pine beetle characteristically spends the majority of its life stages in the inner bark and phloem, knowledge of subcortical environmental conditions is key to understanding mountain pine beetle biology.

Temperature is among the most important factors governing mountain pine beetle population dynamics

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(Reid and Gates, 1970; Amman and Cole, 1983; Bentz et al., 1991, Safranyik, 1978). Cold temperatures are an important cause of mountain pine beetle mortality (Cole and Amman, 1980; Amman and Cole, 1983; Landgor, 1989; Bentz, in press) and hence key controllers of population densities. The effectiveness of stand density manipulations known to reduce mountain pine beetle-caused mortality (Amman et al., 1977; McGregor et al., 1987) may in part be due to modification of tree-phloem temperatures (Bartos and Amman, 1989; Schmid and Mata, 1992).

Air and phloem temperature regimes in stands inhabited by mountain pine beetle have been documented in a number of studies (Graham, 1924; Beal, 1934; Powell, 1967; Bartos and Amman, 1989; Schmid et al., 1991; Schmid et al., 1992). Night-time phloem temperatures have been reported as consistently warmer when compared to surface bark or air temperatures (Powell, 1967; Schmid et al., 1991). During the daytime, insolation-caused heating commonly results in elevated temperature maxima relative to air temperatures. However these effects are strongly influenced by crown density (Schmid et al., 1991; Schmid et al., 1992). Powell (1967) reported west and north-sides daytime temperatures which were the same and cooler (1°C), respectively, than air temperature. This previous work indicate temperatures on the south sides of trees show higher diurnal variation and have warmer maximas than north sides.

Studies by Logan and Amman (1986) and Bentz et al. (1991) have established the relationship between temperature and mountain pine beetle development. They noted optimum development temperatures for all life stages of between 23 and 25°C, in agreement with Safranyik and Whitney (1985). Bentz et al. (1991) also observed that each life stage has a specific optimum temperature regime and threshold for development, that over 'typical' annual temperature cycles provides a mechanism for synchronizing life stages and adult emergence.

Landscape-scale phenology models are the next step in our progression of understanding mountain pine beetle biology. Since most successful reproduction involves aggregation and mass attack, synchrony and concentration at stand to landscape scales may play an important role in outbreak dynamics. Microhabitat temperatures vary due to elevation, exposure, stand density, and a number of other factors. Relative temperature differentials may be greater in some years than others, e.g., cloudy versus clear summers, even though mean temperatures for the period may be quite similar. In this manner, environmental heterogeneity may affect outbreak dynamics, particularly for dispersing/aggregating species such as mountain pine beetle. This paper outlines two approaches for modelling stand air and phloem temperatures, and presents validation results for both models.

2. Model description

Two alternative methods were used to predict stand air and then phloem temperatures. Both methods first predict daily maximum and minimum stand air temperatures, based on air temperature measurements from one or more weather stations. Daily maximum and minimum phloem temperatures were then predicted for tree north and south sides. Finally, hourly phloem temperatures were interpolated using a modified sine-wave/exponential technique (Parton and Logan, 1981). The two methods differed in how daily stand air maximum and minimum temperatures were predicted.

The first method, hereafter referred to as the 'lapse' model, involves predictions of daily stand maximum and minimum air temperature from a single 'base' weather station

$$T_{\max} = T_{\max_b} + \Delta Z \cdot \mathrm{Lx}_{\mathrm{m}} + I_{\max} \cdot \mathrm{Ex}_{\mathrm{s,m}} \cdot \frac{\Delta T}{\Delta T_{95}} \tag{1}$$

$$\mathrm{Ex}_{\mathrm{s,m}} = \frac{R_{\mathrm{site}} - R_{\mathrm{flat}}}{R_{\mathrm{flat}}} \tag{2}$$

$$T_{\min_s} = T_{\min_b} + \Delta Z\, \mathrm{Ln}_{\mathrm{m}}, \tag{3}$$

where subscripts s, b, and m indicate stand, base and month, $T_{\max}$, $T_{\min}$ = daily maximum, minimum temperature, ΔZ = stand minus base elevation in meters, Lx_{m}, Ln_{m} = mean lapse rates for maximum and minimum temperatures, $I_{\max}$ = a constant, maximum temperature increase due to exposure, $\mathrm{Ex}_{\mathrm{s,m}}$ = exposure index, $(R_{\mathrm{site}} - R_{\mathrm{flat}})/(R_{\mathrm{flat}})$, where R is calculated monthly average potential daily diffuse plus direct solar radiation integrated from sunrise to sunset, assuming 21 km clear sky (Hottel, 1976) and adjusted for incidence angle (Swift and Knoerr, 1973), $\Delta T =$ daily $T_{\max_b} - T_{\min_b}$ ΔT_{95} is historical 95 percentile $T_{\max_b} - T_{\min_b}$.

The 'lapse' model assumes a significant proportion of the temperature difference between the base and stand derives from the lapse rate, the change in temperature with a change in elevation (usually °C per 100 m or 1000 m). The last term in (1) is an attempt to represent warming due to exposure. Previous studies dictate elevated temperatures on south-southwestern exposures and allow estimates of $T_{\max}$ and the relationship between $I_{\max}$ and daily R_s (Bristow and Campbell, 1984). While others have included aspect/slope relationships in site-specific temperature predictions (e.g., Hungerford et al., 1989), these models have been inadequately tested.

Lapse relationships or models have been widely used, in part because they require minimal input and are simple to apply. Potential disadvantages include base station bias, daily variation about mean seasonal or annual lapse rates, accuracy, appropriateness, or variations in exposure not represented in the model, and sensitivity to base-stand distance. Average lapse rates may vary by the time interval integrated, e.g., annually, seasonally, or daily. Predictions based on an annual average may be in error for a given day. Lapse characteristics and form are also known to vary by topographic position, e.g., observed temperature inversions in mountain valleys.

Our second stand air temperature prediction method involved estimating temperature based on maximum and minimum air temperature measurements for a number of weather stations in a region. This method involves fitting regression models to predict landscape temperature, and has been applied in previous studies of mean annual and seasonal temperature (Pielke and Mehring, 1977; Leffler, 1981; Boyer, 1984) and daily temperature (Russo et al., 1993). Regression models generally incorporate daily vertical and horizontal temperature gradients. In this study, the following forms for this 'geographic' model were used

$$T_{\max} = \beta_0 + \beta_1 z + \beta_2 \phi + \beta_3 \lambda + I_{\max} \cdot \mathrm{Ex}_s \cdot \frac{\Delta T}{\Delta T_{95}} \tag{4}$$

and

$$T_{\min} = \alpha_0 + \alpha_1 z + \alpha_2 \phi + \alpha_3 \lambda, \tag{5}$$

where α's and β's are estimated from daily regression models, latitude (ϕ) and longitude (λ) are in decimal degrees, and elevation (z) in meters.

For both methods, south facing phloem maxima were predicted from air temperature according to

$$\mathrm{TP}_{\max} = T_{\max_s} + \Delta P_{\max_{s,m}} \cdot \frac{\Delta T}{\Delta T_{95}}, \tag{6}$$

where $\mathrm{TP}_{\max}$ = south-side phloem maximum temperature, $\Delta P_{\max}$ = insolation increase in phloem maximum temperature, and the remaining terms are as previously defined in Eqs. (1) through (3). North and south side phloem temperature minima were assumed to be a constant 0.57°C warmer then stand minimum air temperature, and north phloem maximum temperature was assumed to be equal to stand air temperature

3. Study areas and data

Models were developed and validated in two regions, one bounded approximately by latitudes 40° and 43°N and 109° and 113°W, including portions of southern Idaho, western Wyoming, and northern and eastern Utah, USA (Utah study area), and one bounded by 42° and 46°N, and 112° and 116°W, including western Montana and central Idaho, USA (Idaho study area). Elevations in these areas generally range between 1200 and 3500 m with lower elevations dominated by grasslands and shrub steppe, mid-elevations dominated by coniferous forests, and upper elevations by alpine vegetation (Martson and Anderson, 1994). Model development, parameterization, and testing were based on data reported in the literature and on original field measurements.

3.1. Meteorological data

Average seasonal, monthly and daily maximum and minimum temperature lapse rates were obtained from the United States National Weather Service reporting network (NCDC) for the 25-year period 1964 through 1988. Seventy-six stations were available for the Utah study region, and 63 for the Idaho study region (Fig. 1). Stations were considered eligible if maximum and minimum temperature data were at least 90% complete for the period of record. Stations ranged in elevation from 1200 to 2700 m. Station density and distribution were non-uniform with respect to both geographic and terrain position, with a higher density in Utah and in river canyons, and skewed toward lower elevations. The effect of vertical station distribution was examined by analyzing NCDC data with data from 49 stations in a high elevation network maintained by the U.S. Soil Conservation Service (SNOTEL network). SNOTEL data were available for 1989 through 1993. Lapse rates were calculated based on the NCDC and combined NCDC/SNOTEL data, and compared. For the 25-year data set, lapse rates (°C/1000 m) were determined for Eqs. (1) through (3) from daily linear regression of temperatures on elevation, latitude, and longitude, restricted to days for which geographic coordinates by elevation interactions were not significant (8,749 days, $\alpha < 0.1$). Lapse rates were then summarized by month. Exposure indices ($R_{s,m}$) were ratios based on potential clear-sky radiation, integrating hourly approximations developed by Liu and Jordan (1960); Hottel (1976); and Nann and Riordin (1991), adjusted for latitude and daylength (Swift and Knoerr, 1973; Brock, 1981). Daily exposure-caused temperature differentials reported in the literature ranged from −2.0 to 10.2 (Parker, 1952; Fin-

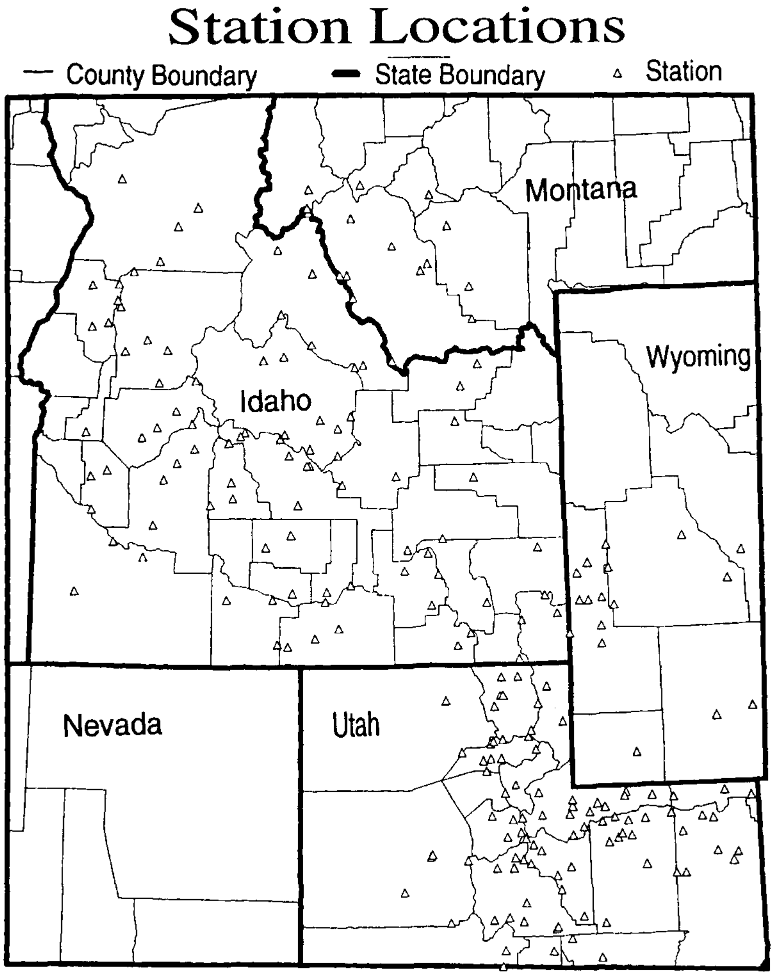

Fig. 1. Meteorological station locations.

klin, 1983; Bristow and Campbell, 1984; Kaufmann, 1984; Werling and Tajchman, 1984; Segal et al., 1985). We evaluated reported exposure-caused temperature differentials for use in parameterizing the models in our study areas. In addition, we measured exposure effects on air and phloem temperatures on three adjacent sites: northeast facing, southwest-facing, and ridgetop. These three 'Stanley Ridge' sites were in close proximity, at an elevation of 2713 m, on a ridge near Stanley, Idaho. Measurements began Julian day (JD) 287, 1993 and ended Julian day 258, 1994. Hourly phloem temperatures were measured using 24G copper–constantan thermocouples at each location on the north and south sides of each of two lodgepole pine bolts [1]. Bolts were approximately 30 cm in diameter, 1.4 m long, and had the ends waxed to reduce moisture loss. Cut bolts were used to approximate an attacked tree, and for comparisons to the other sites, where measurements were in infested trees. These data were the primary basis for estimates of I_{max}, the expected increase or decrease in temperature due to the slope and aspect (exposure) of the site.

Monthly south phloem to north phloem daily maximum temperature differentials (ΔP_{max}) were based on data from two sites in central Idaho. Copper–constantan thermocouples were inserted at 1.2 m in the north and south phloem of 4 trees in mature lodgepole pine stands. Temperatures were measured every 10 min and averaged hourly, from JD 230 1993 to JD 235 1994. Stand canopy closures were over 80% at the time of infestation, elevation at both sites was approximately 2240 m, slopes were 8% and 20%, and aspects SW and E respectively. These data are independent from all other model development and validation data used in this study.

Model validation was based on the comparisons of predicted and observed temperatures from two data sets. The first set consisted of four withheld NCDC temperature measurement stations. These stations were not used in estimating lapse rates or calculating other model parameters. Predicted versus observed air temperatures were compared for each station for each of three years: 1978 (typical year based on mean annual temperature), 1981 (warm year) and 1984 (cool year). A second validation set was based on independent air and phloem temperature measurements in four logdepole pine stands with active mountain pine beetle populations: (1) latitude N44° 07′, elevation 2260 m, (2) latitude N43° 54′, elevation 2347 m., (3) latitude N42° 45′, elevation 2120 m and (4) latitude N41° 56′, elevation 2042 m. The sites were all of low to moderate slope, with a range of aspects. Hourly phloem temperatures were determined for each of two to four trees in each stand for approximately one year, beginning JD 210, 1992 through JD 230, 1993. Temperatures were measured using 24-gauge copper–constantan thermocouples inserted into the phloem on the north and south sides of trees. All future references to north or south phloem refer to measurements on the north or south sides of trees, regardless of the aspect of the site. South slope and north slope will be used to indicate site aspect. In addition, shielded thermocouples were used to measure maximum and minimum air temperatures at 1.5 m and maxima and minima times were recorded. Because temperatures among trees did not differ significantly, measurements were averaged for each site.

4. Results and discussion

4.1. Model parameter ΔT_{95}, P_{max}, E_x and I_{max}

Daily maximum minus minimum air temperature differentials (ΔT) averaged 15.6°C for the 25-year NCDC data set, ranged from 0 to 37.9°C, with a standard deviation of 5.8°C. The observed 95th percentile used in the lapse and geographic models (ΔT_{95}) equalled 24.4°C.

Daily maximum south phloem temperature minus north phloem temperature (ΔP_{max}) measured at the Ranch II and Smiley Creek sites averaged 6.5°C, and varied considerably over the year (Table 1). Average monthly values ranged from 3.8 to 10.2°C, highest in early spring and again in fall, and lowest during the summer. Standard errors followed a similar pattern, as did the extreme maximum temperature differen-

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[1] All temperatures were recorded and stored using a Campbell Scientific 21x micrologger. The use of trade and company names does not constitute an official endorsement or approval of any service or product by the USDA to the exclusion of others that may be suitable.

Table 1
South versus north phloem temperature differentials observed at the Ranch II and Smiley Creek sites. Daily maximum values were recorded for each tree, and then averaged. Listed mean values were used for the monthly $\Delta P_{\max}$ parameters in the geographic and lapse models. All values are in °C

Month	Mean	Standard deviation	Maximum	Minimum
January	6.8	7.0	28.6	−0.9
February	5.5	6.9	31.3	−2.5
March	8.4	7.5	33.1	−2.0
April	5.2	4.8	23.8	−2.0
May	3.8	3.9	17.7	−1.4
June	5.0	3.7	15.7	−0.7
July	5.8	4.6	20.0	−0.7
August	7.2	5.5	24.0	0.3
September	10.2	7.0	30.0	0.7
October	8.0	7.6	31.4	−2.2
November	6.8	6.9	22.1	−1.9
December	6.1	5.8	19.4	−1.6

tials. Observed south phloem temperatures were as much as 33°C warmer than north phloem temperatures. Table 1 values were used for monthly $\Delta P_{\max}$ coefficients in both the geographic and lapse models. North and south phloem daily minima averaged 2.1 and 1.6°C warmer, respectively, than the daily minimum air temperature, and there was no difference between maximum daily north phloem and maximum air temperature. No patterns were discerned in monthly mean phloem-to-air temperature differences.

Site exposure indices ($E_{s,m}$) calculated for 43°N varied in a regular manner by time of year, slope, and aspect (Fig. 2a and b). The indices represent the proportional difference between the daily cumulative radiation for a slope/aspect combination and a horizontal site at the same latitude. Exposure indices are generally lower in summer than in winter. Winter exposures for study area latitudes are largest on steep, south-facing slopes, and lowest for steep north-facing slope. Winter exposure gradients vary considerably, with values approaching -1 (the lower limit for this exposure index) on north facing slopes $> 30°$.

Daily maximum south-phloem temperatures at the Stanley Ridge sites were typically warmer than maximum air temperatures, with differences ranging from -1 to over 21°C (Fig. 3, Table 2). Largest differential in late summer and early fall (Table 2). Phloem minimum temperatures more closely followed air temperatures across all seasons (Table 2 and Fig. 4).

4.2. Air temperature estimates

Summaries of the errors (observed minus predicted) in air temperature estimates for the withheld NCDC validation set are presented in Tables 3 and 4. In general they indicate the lapse model provides slightly less accurate and more variable estimates of daily maximum and minimum air temperature, when compared to the geographic model, at least when

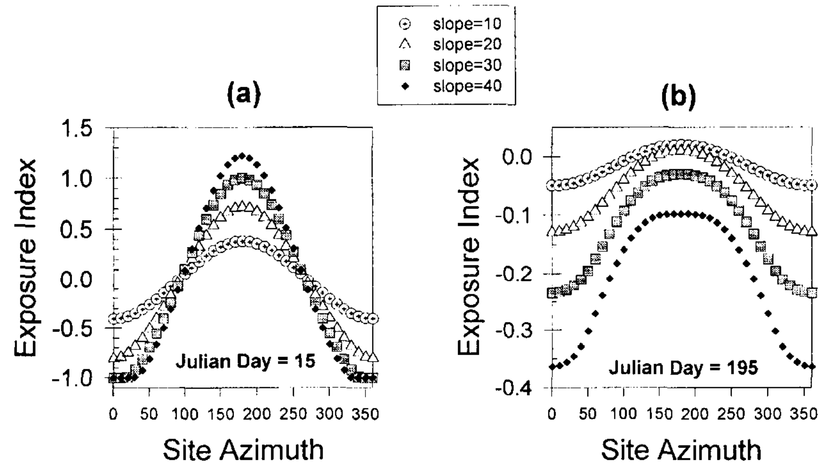

Fig. 2. Calculated exposure indices $(R_s - R_{\text{flat}})/(R_{\text{flat}})$ versus slope (degrees) for days in (a) winter, and (b) summer.

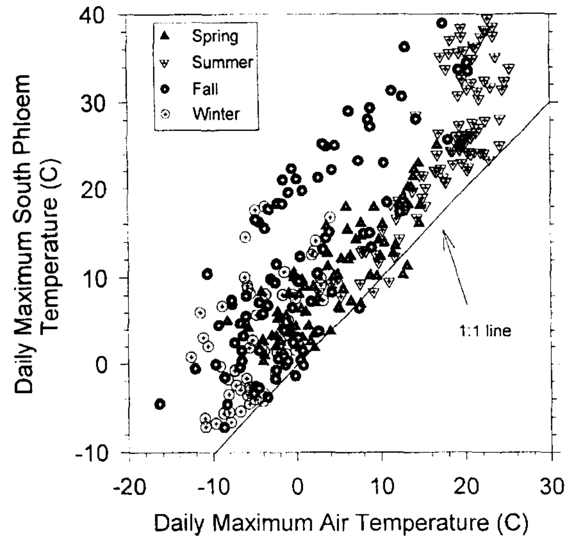

Fig. 3. Observed daily maximum south phloem temperature versus daily maximum air temperature, Stanley Ridge site. Daily maximum temperatures are based on hourly measurements of four trees, averaged after maximum identified.

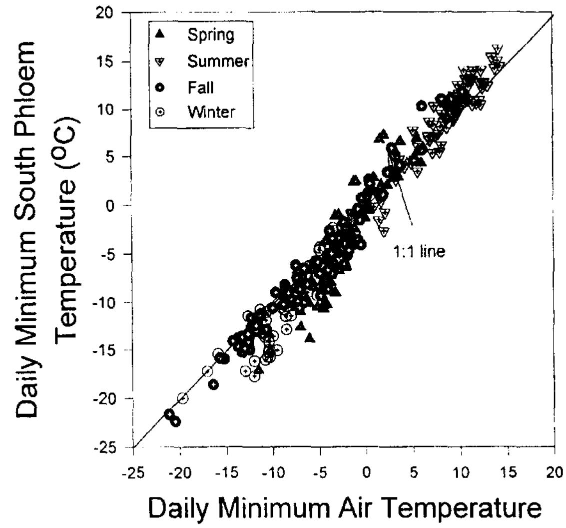

Fig. 4. Observed daily minimum south phloem temperature versus daily minimum air temperature, Stanley Ridge site.

predicting the temperatures at withheld weather stations. These differences were small, although they were generally statistically significant ($\alpha = 0.05$). Predicted maxima were both warmer and cooler than observed, and minimum air temperatures were generally warmer than the observed temperatures. Predictions for withheld NCDC sites were generally poorer for the Utah study area when compared to the Idaho study area.

Air temperature measurements for the four valida-

Table 2

Observed seasonal air and phloem temperature mean and standard deviations (..) for the Stanley Ridge sites, all bolts combined (2 each at NE, SW, and neutral exposures). Measurements at this site were used to aid selection of model parameters $I_{\max}$ and $P_{\max}$. Winter includes December through February, spring March through May, summer June through August, and fall September through November

Air temperature	Winter	Spring	Summer	Fall
Daily maximum	−4.6 (3.7)	4.6 (6.1)	17.6 (4.8)	3.8 (8.1)
Daily minimum	−10.3 (3.9)	−3.5 (5.6)	8.1 (5.4)	−3.8 (7.7)
Phloem temperature				
Southside, daily maximum temp.	1.6 (5.4)	10.9 (6.7)	25.3 (7.3)	13.9 (11.1)
Northside, daily maximum temp.	−4.5 (2.6)	4.5 (6.1)	21.4 (6.1)	4.4 (8.9)
South Phloem–North Phloem, Daily maximum temperature	6.1	6.4	3.9	9.5
Southside, daily minimum temp.	−9.7 (3.5)	−2.2 (4.4)	8.0 (4.8)	−3.3 (7.3)
Northside, daily minimum temp.	−9.6 (3.4)	−2.0 (4.5)	8.5 (4.8)	−3.3 (7.4)
South Phloem–North Phloem, Daily minimum temperature	−0.1	−0.2	−0.5	0.0
Phloem temperature minus air temperature				
South max. minus air max.	6.2	6.3	7.7	10.1
North max. minus air max.	0.1	−0.1	3.8	0.6
South min. minus air min.	0.6	1.3	−0.1	0.5
North min. minus air min.	0.7	1.5	0.4	0.5

Table 3
Air temperature prediction errors (observed minus predicted), Utah study area, based on four withheld NCDC meteorological stations for 1978 (typical year), 1981 (above average temperatures) and 1984 (below average temperatures). Test years were chosen based on average annual temperature, compared to the 25 year mean

Error (°C)	1978		1981		1984	
	Lapse	Geographic	Lapse	Geographic	Lapse	Geographic
T_{max}						
Mean	−0.5	−0.1	0.6	0.27	−0.7	−0.2
Maximum	19.6	7.6	15.5	9.5	12.4	11.3
Minimum	−11.7	−8.3	−14.1	−9.1	−11.5	−7.62
Std. dev.	3.5	2.1	3.6	2.1	3.3	2.1
n	1384	1452	1428	906	1464	1464
T_{min}						
Mean	−2.6	−1.8	−1.5	0.3	−2.3	−1.5
Maximum	12.1	8.3	12.3	9.5	13.9	8.6
Minimum	−14.9	−11.1	−14.4	−9.1	−17.0	−10.0
Std. dev.	3.6	2.4	3.4	2.1	2.1	2.3
n	1384	1451	1425	1458	1464	1464

tion stands indicate the geographic model generally performs slightly better than the lapse model (Table 5). Prediction errors for stand air temperature are greater than errors for withheld NCDC weather stations.

Table 4
Air temperature prediction errors (observed minus predicted), Idaho study area based on four withheld meteorological stations for 1978 (typical year), 1981 (warm year), and 1984 (cool year). Test years were chosen based on average annual temperature, compared to the 25 year mean

Error (°C)	1978		1981		1984	
	Lapse	Geographic	Lapse	Geographic	Lapse	Geographic
T_{max}						
Mean	0.5	0.0	0.0	0.0	0.3	0.2
Maximum	15.6	9.0	14.2	11.6	14.7	9.4
Minimum	−12.4	−10.2	−11.9	−8.7	−12.4	−7.0
Std. dev.	2.9	2.1	3.0	2.2	3.2	2.1
n	1444	1450	1427	1449	1465	1464
T_{min}						
Mean	−0.8	−0.9	−1.1	−1.1	0.2	−0.6
Maximum	14.9	7.1	10.5	7.9	15.2	7.6
Minimum	−15.0	−11.0	−18.5	−18.9	−12.7	−12.5
Std. dev.	3.7	2.3	3.6	2.3	3.8	2.5
n	1424	1451	1387	1412	1464	1464

4.3. Phloem temperature estimates

Predicted daily maximum phloem temperatures were generally warmer than observed temperatures for both the north and south sides of trees in our four validation stands (Tables 6 and 7), while predicted

Table 5
Stand air temperature prediction errors (observed minus predicted), four validation stands. Air temperatures measured with a shielded copper–constantan thermocouple, at 1.2 m height

Station								
Error (°C)	Galena		Moose		Logan Canyon		Ranch	
	Lapse	Geographic	Lapse	Geographic	Lapse	Geographic	Lapse	Geographic
T_{max}								
Mean	−3.9	−2.7	0.5	−3.03	−3.2	−3.1	1.5	0.0
Maximum	9.6	9.5	21.6	11.9	16.2	10.9	19.7	11.9
Minimum	−21.0	−15.8	−20.1	−19.3	−19.9	−18.7	−8.5	−11.3
Std. dev.	5.7	4.7	7.7	5.6	6.3	5.4	4.1	4.0
n	363	363	351	352	305	397	364	364
T_{min}								
Mean	3.8	−0.6	6.3	3.8	−1.7	−1.2	0.7	1.5
Maximum	17.9	10.4	34.7	29.9	19.6	17.3	11.2	18.2
Minimum	−11.8	−14.8	−5.1	−10.1	−14.0	−17.2	−12.5	−14.8
Std. dev.	5.6	4.4	7.5	7.4	5.5	5.3	3.2	4.8
n	363	363	351	352	305	396	364	364

Table 6

Errors (observed minus predicted) in daily southside phloem temperature estimates, four validation stands. Observed means based on daily maximum and minimum temperatures measured on each of four trees, then averaged for a stand estimate of south phloem maximum and minimum temperatures

Station								
Error (°C)	Galena		Moose		Logan Canyon		Ranch	
	Lapse	Geographic	Lapse	Geographic	Lapse	Geographic	Lapse	Geographic
T_{max}								
Mean	−1.1	0.1	−2.9	−2.3	−1.1	−2.4	1.3	−1.2
Maximum	10.5	10.9	12.9	10.5	14.3	8.4	11.8	9.2
Minimum	−16.3	−15.9	−19.3	−18.8	−18.9	−18.9	−17.9	−30.5
Std. dev.	5.5	4.6	5.7	4.8	6.4	5.4	8.1	8.4
n	363	363	351	351	305	397	364	364
T_{min}								
Mean	5.9	1.8	8.2	2.8	−0.7	0.1	1.5	1.4
Maximum	18.3	10.8	20.3	16.1	17.2	14.9	10.0	16.1
Minimum	−11.2	−14.5	−8.1	−15.2	−15.7	−14.6	−12.1	−14.1
Std. dev.	5.5	4.3	5.0	3.9	5.0	4.6	3.1	4.8
n	363	363	351	351	305	397	361	361

minimum temperatures were cooler than observed. These trends were not consistent for all sites and sides of tree. However, in general, the geographic model performed better than the lapse model when predicting daily maximum and minimum temperatures. Differences in mean prediction error between the two models were largest for minimum temperature. Mean errors for daily minimum phloem temperatures were larger in magnitude than those observed for maximum temperature. Extreme error magnitudes were quite large (Tables 6 and 7, Fig. 5). These extreme errors may be due in part to micro-scale

Table 7

Errors (observed minus predicted) in daily northside phloem temperature estimates, four validation stands. Observed means based on daily maximum and minimum temperatures measured on each of four trees, then averaged for a stand estimate of south phloem maximum and minimum temperatures

Station								
Error (°C)	Galena		Moose		Logan Canyon		Ranch	
	Lapse	Geographic	Lapse	Geographic	Lapse	Geographic	Lapse	Geographic
T_{max}								
Mean	−2.0	−0.8	−3.1	−2.5	−3.6	−4.7	−1.0	−1.9
Maximum	−10.7	13.3	11.5	8.0	11.4	6.7	15.0	8.2
Minimum	−16.9	−14.2	−18.4	−17.4	−18.9	−18.0	−13.8	−13.9
Std. dev.	5.2	4.3	5.2	4.3	5.6	4.8	5.3	5.5
n	363	363	351	351	305	397	364	364
T_{min}								
Mean	6.2	1.8	8.1	2.6	−1.7	−0.9	0.9	1.0
Maximum	−18.2	11.0	19.2	16.0	17.2	14.9	10.0	15.9
Minimum	−11.4	−15.0	−8.4	−15.4	−15.5	−14.5	−11.9	−12.8
Std. dev.	5.4	4.2	5.1	3.9	4.9	4.6	2.9	4.7
n	363	363	351	351	305	397	361	361

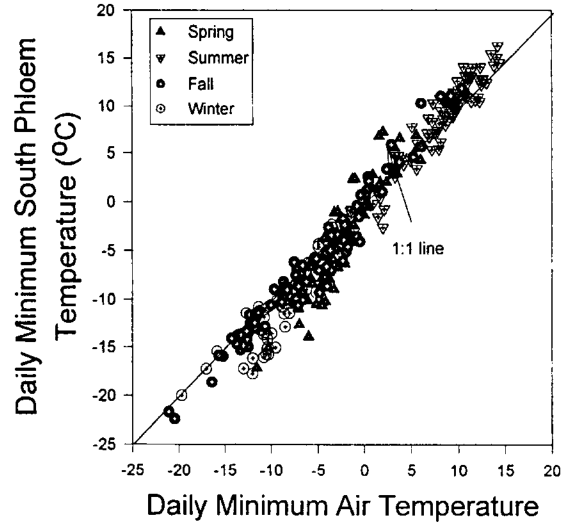

Fig. 5. Predicted daily south phloem temperatures, lapse model and geographic model, Galena site, in central Idaho.

spatial and temporal variation in phloem temperatures, largely caused by insolative heating. Current and future field experiments will better determine the nature of this within-bole variation.

The biological significance of these errors in predicted phloem temperatures will depend on how they affect predictions of mountain pine beetle phenology. Phloem temperature predictions are filtered through non-linear development rate curves (Bentz et al., 1991), in which the magnitude of the input error may not correspond to the magnitude of the output error. To adequately understand the significance of the errors in predicted phloem temperatures, we are currently evaluating phenology model output using observed and predicted phloem temperatures from both the lapse and geographic models. Results will provide insight into the sensitivity of temperature changes throughout a year, and the affect of these temperatures on the timing of mountain pine beetle larval development and adult emergence. This will help establish acceptable limits of error on phloem temperature estimates. With the microhabitat temperature predictors described here, we have the capability to project weather information over a complex landscape, at the scale of the bark beetle micro-habitat. This is a valuable tool in efforts to analyze the landscape-scale effects of weather and climate on mountain pine beetle population dynamics (Baker, 1944).

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