CHAPTER 15.

Monitoring Mountain Pine Beetle Life Cycle Timing and Phloem Temperatures at Multiple Elevations and Latitudes in California

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Barbara Bentz
James Vandygriff
Camille Jensen
Tom Coleman
Patricia Maloney
Sheri Smith
Amanda Grady
Greta Schen-Langenheim

INTRODUCTION

The mountain pine beetle (MPB) (*Dendroctonus ponderosae* Hopkins, Coleoptera: Curculionidae, Scolytinae), a native of western North America, mainly infests and reproduces in live trees within the genus *Pinus,* and successful offspring production often results in the death of the host tree. The range of MPB is expansive, spanning from Baja California Norte, Mexico, to northern British Columbia (BC) and western Alberta, Canada, yet suitable pine hosts extend beyond the current northern and southern geographical extent (Bentz and others 2010, Safranyik and others 2010). Mountain pine beetle has been at outbreak levels across parts of western North America over the past 2 decades. Ongoing changes in climatic conditions are hypothesized to be driving a northward expansion of MPB in northern BC and Alberta, Canada (Safranyik and others 2010) and contributing to sustained population outbreaks in high elevation forests where persistent activity was previously constrained by cold temperatures (Amman 1973). Increasing minimum temperatures increase brood survival (Régnière and Bentz 2007, Weed and others 2015), and at high elevations increasing summer temperatures allow some individuals to shift from one generation every two years to one generation every year (Bentz and others 2014). It is clear that in addition to susceptible stand conditions and drought (Chapman and others 2012), warmer temperatures are influencing MPB.

Mountain pine beetle life cycle timing has historically been reported as univoltine (i.e., one generation per year) at low elevations with a mix of univoltine and semivoltine (i.e., one generation every 2 years) at high elevations (Amman 1973, Reid 1962). The capacity for MPB to complete two generations in a single year (i.e., bivoltinism) is unclear. Bivoltinism was reported to have occurred in California and Oregon (Evenden and others 1943, Furniss and Carolin 1977) and speculated to occur with warming temperatures at 3000 m in Colorado (Mitton and Ferrenberg 2012). Bentz and Powell (2014), however, suggest that bivoltinism across the current range of MPB is constrained by a lack of sufficient thermal energy and evolved developmental thresholds that ensure overwintering success.

Little information is available on MPB life cycle timing in California. To predict future MPB response to changing climatic conditions, baseline information is needed. Our objectives were (1) to develop a baseline database of MPB life cycle timing and associated phloem temperatures in several host trees at multiple elevations and latitudes across California (CA) and (2) using the field-collected data, to evaluate a current MPB phenology model in areas other than where model parameters were derived. This information will provide a reference for evaluating potential future population response to changing climate and help identify areas with high probability of climate-induced shifts in population success and where management interventions may be most effective. Here, we provide a brief description of our methods and highlight results from the project. A more complete description of data collected and results can be found in Bentz and others (2014).

METHODS

Mountain pine beetle adults emerge from trees and fly to attack new live trees where mating and oviposition occur, and new brood will develop within the phloem throughout the next 1 to 2 years. The timing of emergence and flight is dependent on temperature and typically occurs in the summer months. For our study, we define a brood to be a group of individuals that develop from eggs laid by parents that attacked trees in the same season. The length of time for brood to develop and emerge from a tree is considered a generation. We classified brood that emerged from a tree the summer following parent attacks as univoltine and the brood that required 2 years to complete a generation as semivoltine. To be considered a bivoltine brood, two complete generations must occur within 1 year.

Data from six sites were included in this study (fig. 15.1). At each site, data were collected for a period of 1 to 3 years, including two MPB generations and associated phloem and air temperatures (table 15.1). Prior to MPB flight, three to five live trees were selected at each site

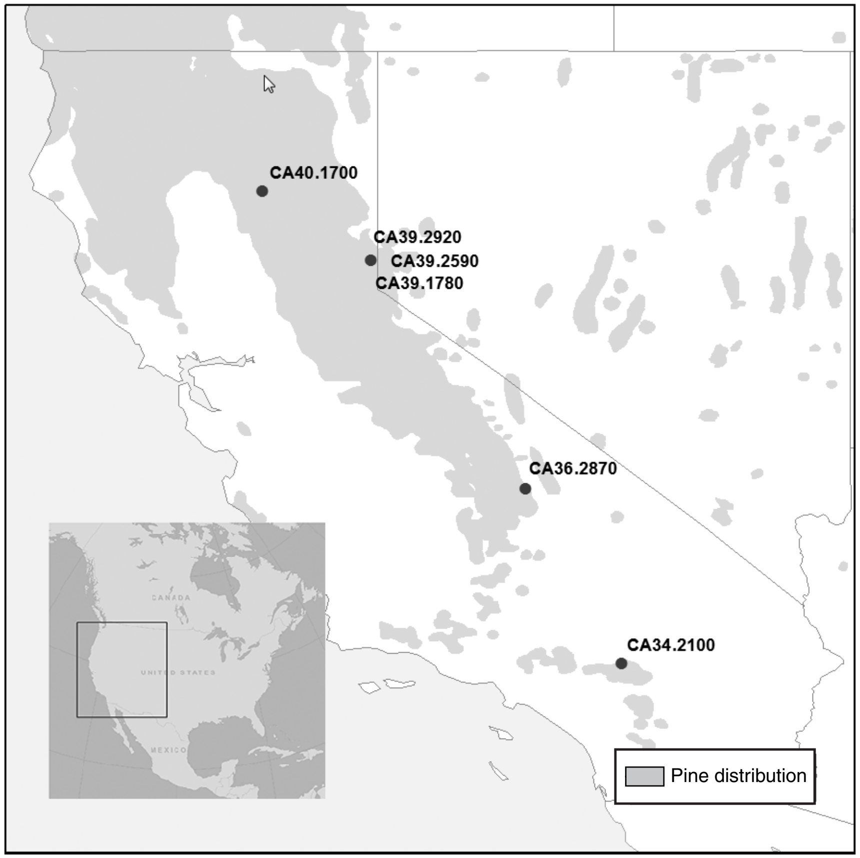

Figure 15.1—Map of study sites in the Western United States. Also shown is the distribution (Little 1971) of major pine host species for mountain pine beetle (i.e., Pinus albicaulis, P. contorta, P. flexilis, P. lambertiana, P. monticola, *and* P. ponderosa). *Three sites were installed along an elevational gradient at CA39, shown here as a single point. See table 15.1 for site information.*

Table 15.1—Study site location in California, years the site was sampled, mountain pine beetle population phase, and *Pinus* host tree species

Forest	Site name	Years	Population phase	DBH (mean ± SD)	Latitude	Longitude	Elevation	Host tree species
							m	
Lassen	CA40.1700-09	2009–10	Endemic	50.55 ± 6.4	40.2238	-121.4331	1700	*P. lambertiana*
Lassen	CA40.1700-10	2010–11	Endemic	39.37 ± 8.6	40.2103	-121.4341	1700	*P. lambertiana*
Tahoe	CA39.1780-09	2009–10	Endemic	33.27 ± 5.3	39.3926	-120.1841	1780	*P. contorta*
Tahoe	CA39.1780-10	2010–11	Endemic	33.78 ± 6.1	39.3922	-120.1863	1780	*P. contorta*
Lake Tahoe Basin Management Unit	CA39.2590-09	2009–11	Endemic	46.74 ± 8.1	39.2984	-119.9330	2590	*P. monticola* *P. contorta*
Lake Tahoe Basin Management Unit	CA39.2590-10	2010–12	Endemic	44.96 ± 4.6	39.2998	-119.9310	2590	*P. monticola* *P. contorta*
Lake Tahoe Basin Management Unit	CA39.2920-09	2009–12	Endemic	33.53 ± 2.8	39.3218	-119.9390	2920	*P. albicaulis*
Lake Tahoe Basin Management Unit	CA39.2920-10	2010–12	Endemic	39.12 ± 3.1	39.3217	-119.9386	2920	*P. albicaulis* *P. contorta*
Inyo	CA36.2870-09	2009–10	Endemic	43.43 ± 18.5	36.4693	-118.1252	2870	*P. flexilis*
Inyo	CA36.2870-10	2010–11	Endemic	47.24 ± 19.6	36.4695	-118.1253	2870	*P. flexilis*
San Bernardino	CA34.2100-09	2009–10	Endemic	50.89, 46.2	34.2653	-116.9089	2100	*P. monophylla*
San Bernardino	CA34.2100-10	2010–11	Endemic	33.27	34.2635	-116.9087	2100	*P. monophylla*

Note: site names are a combination of the State abbreviation, approximate latitude, elevation (m), and parent attack year and are arranged by latitude with the most northerly sites at the top. Also shown is the mean (± SD) d.b.h. (diameter at breast height) of trees sampled at each site.

based on tree size (> 20.2 cm diameter at breast height, or d.b.h.). To ensure MPB attacks, an aggregation lure [(S) *trans*-verbenol and racemic *exo*-brevicomin, Synergy Semiochemicals Corp., Burnaby, BC, Canada] was placed on each live tree when MPB flight activity was observed in the area (based on pheromone traps and emergence cages in the vicinity). Aggregation lures were removed once attacks were initiated on each tree to allow the natural attack process to continue. Beetle attacks were monitored twice weekly on the entire circumference of each tree bole from 0.305 m to 1.524 m above ground until attacks ceased. Attacks were not monitored at the CA36.2870 site. After the entire circumference of each tree bole was successfully mass attacked, based on the total number of attacks, emergence cages were installed at 1.4 m above the ground on the north and south bole aspects. A centrifuge tube attached to the bottom of the enclosure collected all beetles emerging from under the bark within each cage. Adult MPB emergence into cages was monitored twice weekly at each site. The date of median attack and median emergence among all trees at a site was calculated.

We used the field collected data to evaluate a mechanistic MPB phenology model. The model was originally parameterized using lab-derived data on lifestage-specific development times at a range of constant temperatures (Bentz and others 1991, Powell and Bentz 2014, Régnière and others 2012). Populations from central Idaho and northern Utah were used in model parameterization. The model predicts lifestage-specific development timing, including adult emergence, given hourly temperatures and an input distribution of attacks. To evaluate how well the model predicts adult emergence in CA, we initiated model runs with the observed number of attacks on a single tree. Observed hourly phloem temperatures from that same tree, on the north and south bole aspects, were used to drive the model. Predicted emergence of adults was then graphically compared to field-observed emergence.

RESULTS

Life cycle timing and air temperature varied among sites and among years at the same site (figs. 15.2 and 15.3). A strictly univoltine life cycle was observed both years at two sites (CA40.1700, CA39.1780). At CA36.2870, we were unable to monitor attacks, although the emergence timing suggested univoltinism. At the highest elevation sites (CA39.2920, CA39.2590), we observed a mixture of univoltine and semivoltine brood (often within the same tree). At the warmest site, CA34.2100-09, some brood adults emerged from a single tree (T2) the fall following attacks earlier that summer (faster than univoltine). Median attacks on a second tree (T5) at that site coincided with emergence from T2, and peak brood adult emergence from this tree was on July 24, 2010. To be classified as bivoltine, brood from attacks made in the fall 2009 would need to have completed development and emerged

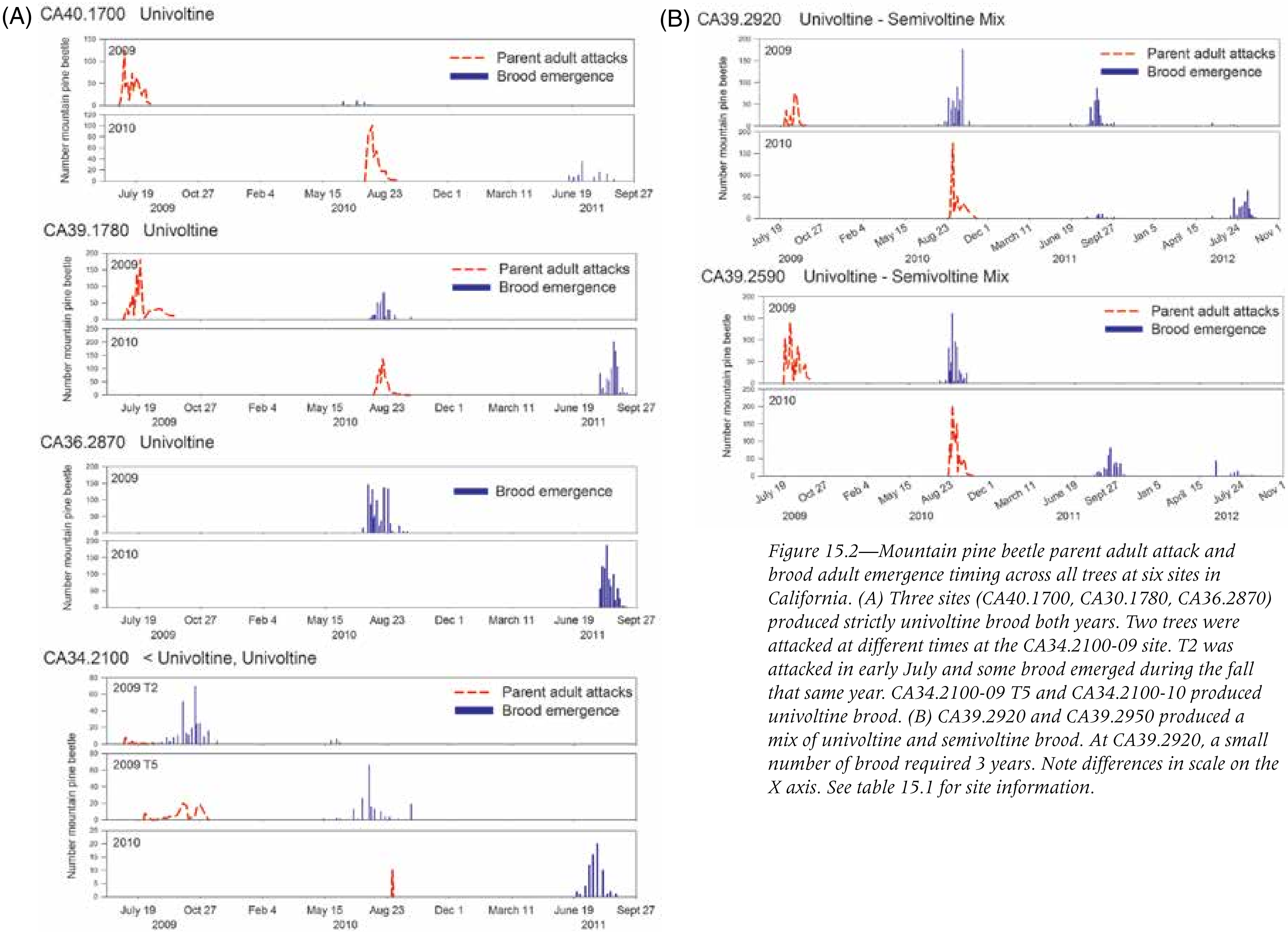

Figure 15.2—Mountain pine beetle parent adult attack and brood adult emergence timing across all trees at six sites in California. (A) Three sites (CA40.1700, CA30.1780, CA36.2870) produced strictly univoltine brood both years. Two trees were attacked at different times at the CA34.2100-09 site. T2 was attacked in early July and some brood emerged during the fall that same year. CA34.2100-09 T5 and CA34.2100-10 produced univoltine brood. (B) CA39.2920 and CA39.2950 produced a mix of univoltine and semivoltine brood. At CA39.2920, a small number of brood required 3 years. Note differences in scale on the X axis. See table 15.1 for site information.

by June 2010 (i.e., two complete generations in a single year). This did not happen. The next generation at CA34.2100 was initiated from attacks that occurred in July and August 2010, and brood from these attacks emerged in July 2011, a strictly univoltine life cycle. Therefore, the CA34.2100 site produced three generations in 2 years, a fractional voltinism faster than strict univoltinism, but not bivoltinism (fig. 15.2). The opposite extreme was the highest elevation site, CA39.2920, where 1.1 percent of offspring from attacks in 2009 emerged in 2012, a life cycle that required 3 years to complete (fig. 15.2).

With the exception of the summer generation at the most southern site and the mostly semivoltine generation at the highest elevation site, generation time (number of days between median attack and median emergence) across sites and years was between 300 and 400 days (fig. 15.4, table 15.2). The thermal energy required to complete a generation, however, varied between 86 and 447 degree days (DD) >15 °C (table 15.2). The site with the shortest generation time (110 days) accumulated the greatest thermal heat during the generation (484 DD), and the site with the longest generation time (695 days) accumulated the smallest thermal heat over the generation (74.6 DD) (fig. 15.4).

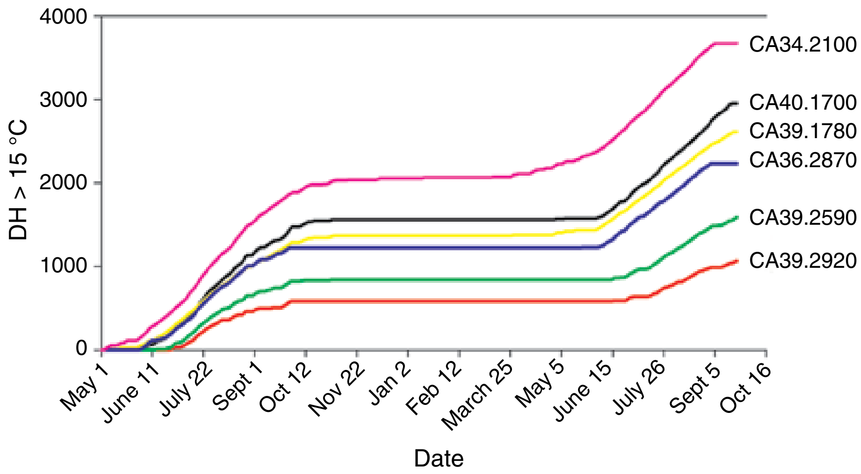

Figure 15.3—Cumulative degree hours (DH) > 15 °C (based on air temperature) accumulated between May 1 and September 30 the year following 2009 attacks at each site. See table 15.1 for site information.

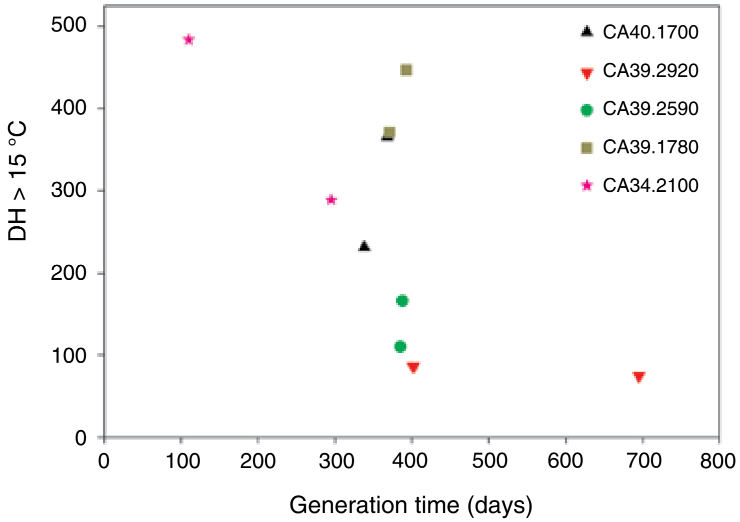

Figure 15.4—Generation time (number of days between median attack and median emergence) of mountain pine beetle at five California sites and the degree days (DD) > 15 °C required to complete a generation at each site. Generation time and air temperature were monitored for two beetle generations at each site. See table 15.1 for site information.

Table 15.2—Proportion brood that emerged in 1 year (univoltine) and the associated total number of brood adults sampled from cages at each site (N)

Site	Proportion univoltine (N)	Generation time	DD > 15 °C	Average air temp.	Average July–Aug. max. air temp.	Average Dec.–Jan. min. air temp.
		days		---------------------*°C*-------------------------		
CA40.1700-09	100 (32)	368	365.95	5.9	25.2	-3.9
CA40.1700-10	100 (101)	338	231.37	6.2	24.0	-2.8
CA39.2920-09[a]	64.2[b] (944)	402	86.27	1.3	16.8	-8.4
CA39.2920-10[a]	13.8 (319)	695	74.59	1.2	16.3	-7.1
CA39.2590-09	100 (616)	388	166.20	3.3	21.3	-6.6
CA39.2590-10[a]	71.5 (884)	385	110.16	2.4	19.1	-6.2
CA39.1780-09	100 (454)	393	447.00	5.0	25.8	-8.7
CA39.1780-09	100 (863)	371	371.32	4.5	26.2	-8.1
CA36.2870-09	100 (968)	–	–	4.4	20.6	-7.5
CA36.2870-10	100 (839)	–	–	4.6	20.5	-5.7
CA34.2100-09 T2	4.0[c] (170)	110	484.16	8.8	27.0	-3.8
CA34.2100-09 T5	100 (176)	295	288.75	8.8	27.0	-3.8
CA34.2100-10	100 (69)	–	–	8.1	25.7	-3.7

– = timing of the attacks on the trees was not recorded, so generation time and DD were therefore not quantifiable.

[a] Remainder of brood emerged > 1 year following attacks.

[b] 1.1 percent emerged in 3 years.

[c] Remainder of brood emerged < 1 year following attacks.

Note: Sites are arranged with the most northerly at the top (see table 15.1 for site information). Generation time (days) is the number of days between median attack and median emergence at each site, information available for a portion of the sites. DD >15 °C is the accumulated degree days warmer than 15 °C between median attack and median emergence. Average annual temperature, average daily maximum air temperature in July and August, and average daily minimum air temperature in December and January were calculated using sensors located at each site.

Median predicted univoltine MPB emergence at the CA39.1780-09 site was within a few days of observed emergence (fig. 15.5A). Similar results were observed for emergence of univoltine beetles at the CA39.2920-09, although predicted median emergence timing of semivoltine beetles the following year at the same site was 20–30 days slower than observed (fig. 15.5B and 15.5C). Model-predicted MPB emergence timing was substantially faster than observed in a tree at the warmest and most southern site (CA34.2100-09 T2) that produced a generation of beetles between June and November of the same year (fig. 15.5D).

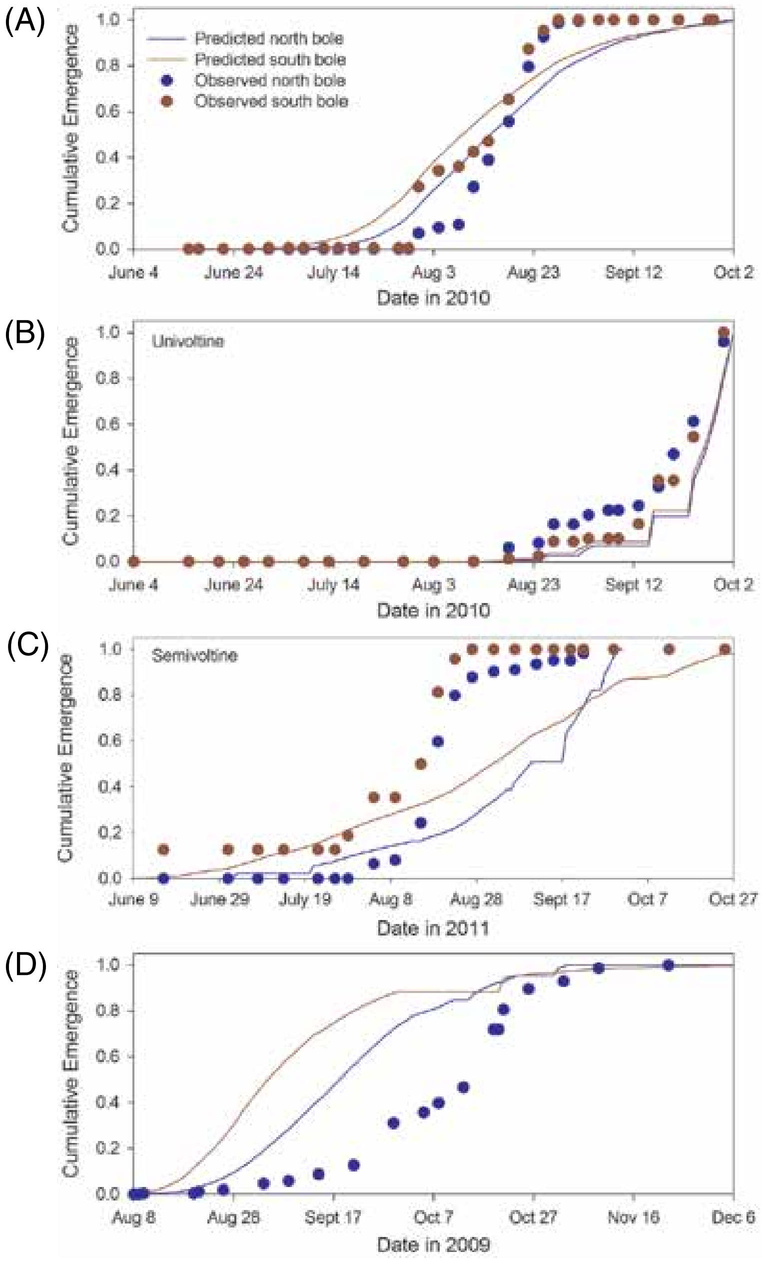

Figure 15.5—Model-predicted and observed mountain pine beetle emergence from the north and south bole aspect of a single tree at three sites: (A) CA39.1780-09, (B) CA39.2920-09 univoltine, (C) CA39.2920-09 semivoltine, and (D) CA34.2100-09 T2. Emergence predictions were generated from a MPB phenology model using hourly phloem temperatures measured in the field for each beetle generation.

DISCUSSION

Our results show that MPB lifecycle timing in California is univoltine at warmer sites and a mix of univoltine and semivoltine at cooler sites, similar to findings in other parts of the range of MPB (Amman 1973, Bentz and others 2014, Reid 1962). The DD >15 °C required to complete a generation varied considerably. The cooler the site, the fewer thermal units were needed for completion of a generation regardless of the number of days (figs. 15.3 and 15.4). In fact, the site with the shortest generation time accumulated more than six times the thermal heat of the site with the longest generation time. Despite this, we did not observe bivoltinism at the warmest site, which was also at the most southern location. Although a generation was completed in a single summer (i.e., between June and October) at the most southern site, the thermal energy and timing of that energy were not sufficient to complete a second generation across winter (i.e., between October and June). Adult emergence the second summer did not occur until July, potentially shifting the population to a univoltine lifecycle the next year (i.e., July to July).

One explanation for this pattern is the different thermal thresholds and rates of development among lifestages that serve to maintain seasonality. A high threshold for pupation (15–17 °C) has evolved in MPB to enable adult emergence synchrony and to reduce the likelihood that cold-sensitive lifestages (i.e., eggs and pupae) will be present during winter (Logan and Bentz 1999, Régnière and others 2012). These thresholds also play an important role in univoltinism, a trait important to population success. Results from this project suggest that the evolved adaptations that promote univoltinism and emergence synchrony allow populations in cool environments to efficiently use available thermal energy and provide flexibility to shift from semivoltine to univoltine cycles in warm years. In contrast, at the warmest sites excess thermal units beyond what is needed by specific lifestages are acquired and the use of thermal energy is therefore less efficient. The adaptations have served to maintain univoltinism at both warm and cold sites but may also constrain a shift to bivoltinism (Bentz and Powell 2014). The amount and seasonality of thermal energy required to surpass this constraint is currently unclear.

The MPB phenology model can provide predictions of thermal regimes under various future climate conditions that will be advantageous for MPB population success based on predicted emergence timing (Bentz and others 2010). When combined with a demographic model (Powell and Bentz 2009, 2014), population growth under multiple future climate conditions can also be predicted. Because of genetic differences in MPB temperature response across the Western United States (Bentz and others 2011), however, it is unclear where the model, which was parameterized using populations from central Idaho and northern Utah, can be used. Field collected data from this project were ideal for evaluating the model at sites in California. We initiated the MPB phenology with observed tree attack information in one year, used observed hourly phloem temperature measurements to drive the model, and then compared model predictions of adult emergence 1 and 2 years later with observed emergence from field plots. Model predictions of median MPB adult emergence 1 year later were within a few days of observed emergence at univoltine sites in central and northern CA. Although the model accurately predicted that semivoltine brood emergence would occur, predicted timing was slightly less accurate than for univoltine brood. A majority of brood emerging the second year of attack could have overwintered as a brood adult (Bentz and others 2014), and the model did not adequately capture emergence timing of these overwintered adults. Model predictions of the timing of brood emergence from a tree in southern California, where a generation was completed in a single summer, were earlier than what was observed in the field. This result, however, was anticipated. In common garden laboratory experiments, MPB from southern populations required significantly more days to complete a generation at a constant temperature compared to a population from a northern population reared at the same constant temperature, implying genetic differences among populations along a latitudinal cline (Bentz and others 2011). Our results suggest the MPB phenology model best predicts temperature-dependent traits of MPB in central and northern California, compared to southern California.

CONCLUSIONS

MPB lifecycle timing in CA is univoltine at warmer sites and a mix of univoltine and semivoltine at cooler sites. Due to nonlinearities in thermal thresholds among lifestages, degree days did not adequately explain MPB lifecycle timing. Instead, a mechanistic model that inherently includes these nonlinearities provides an enhanced tool for predicting MPB phenology and ultimately population success. Based on preliminary runs using field-collected temperature and lifecycle timing data, the current MPB phenology model can be used to predict thermal regimes advantageous for MPB from central to northern California. New laboratory data and model parameters that describe MPB response to temperature in southern populations are needed. Warming temperatures are influencing range expansion in Canada into habitats previously too cool for MPB. A model parameterized for southern populations would provide a tool for evaluating thermal regimes with a high probability of climate-induced shifts in population success and potential MPB range expansion into habitats in the Southwest United States and Mexico that are currently too warm.

CONTACT INFORMATION

Barbara Bentz: bbentz@fs.fed.us.

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