Evaluation of Multiple Funnel Traps and Stand Characteristics for Estimating Western Pine Beetle-Caused Tree Mortality

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J. Econ. Entomol. 102(6): 2170–2182 (2009)

ABSTRACT The western pine beetle, *Dendroctonus brevicomis* LeConte (Coleoptera: Curculionidae: Scolytinae), is a major cause of ponderosa pine, *Pinus ponderosa* Dougl. ex Laws., mortality in much of western North America. This study was designed to quantify relationships between western pine beetle trap catches [including those of its primary invertebrate predator *Temnochila chlorodia* (Mannerheim) (Coleoptera: Trogositidae)], and levels of tree mortality attributed to western pine beetle at 44 trapping sites (stands) and within five general locations (forests) in California. Furthermore, we evaluated relationships between forest stand characteristics and levels of western pine beetle-caused tree mortality. Preliminary analyses were conducted by Pearson's correlation coefficient (r) using tree mortality per hectare and percentage of tree mortality and 10 potential predictor variables. All predictor variables that had significant correlations (western pine beetle per day, western pine beetle: *T. chlorodia*, percentage of western pine beetle [percentage of total trap catch represented by western pine beetle], trees per hectare, basal area of all tree species, basal area of *P. ponderosa*, mean diameter at breast height [dbh] and stand density index) were considered for linear and multiple linear regression models for predicting levels of western pine beetle-caused tree mortality. Our results suggest monitoring western pine beetle populations through the use of pheromone-baited multiple funnel traps is not an effective means of predicting levels of western pine beetle-caused tree mortality. However, levels of western pine beetle-caused tree mortality can be efficiently predicted (adjusted $R^2 > 0.90$) at large spatial scales (forests; ≈3,000–14,000 ha of contiguous host) by simply measuring stand density, specifically the basal area of all tree species or stand density index. The implications of these results to forest management are discussed.

KEY WORDS *Dendroctonus brevicomis*, *Pinus ponderosa*, risk, stand density, trapping

Bark beetles (Coleoptera: Curculionidae: Scolytinae), a large and diverse group of insects consisting of ≈550 species in North America (Wood 1982), are commonly recognized as important tree mortality agents in coniferous forests of western North America (Furniss and Carolin 1977). To reproduce, bark beetles must successfully locate suitable and susceptible hosts using a variety of sensory modalities. Successful colonization of living hosts requires recruitment of a critical minimum number of beetles to initiate mass attack and overcome tree defenses (Franceschi et al. 2005). This threshold (i.e., the number of beetles required) varies with host tree vigor (Raffa and Berryman 1983). Depending on the bark beetle species and numerous other factors (Fettig et al. 2007), the extent of tree mortality may be limited to small spatial scales (e.g., single trees or small groups of trees) or impact large areas (e.g., >9 million ha) such as recently observed in British Columbia, Canada (Westfall and Ebata 2008). The resultant tree mortality can influence forest ecosystem structure and function by regulating certain aspects of primary production, nutrient cycling, ecological succession and the size, distribution and abundance of forest trees (Mattson et al. 1996). Bark beetle infestations also impact timber and fiber production, water quality and quantity, fish and wildlife populations, recreation, grazing capacity, real estate values, biodiversity, carbon storage, endangered species, and cultural resources (Coulson and Stephen 2006).

The western pine beetle, *Dendroctonus brevicomis* LeConte (Coleoptera: Curculionidae: Scolytinae), causes extensive amounts of ponderosa pine, *Pinus ponderosa* Dougl. ex Laws., mortality in much of western North America (Miller and Keen 1960) and particularly California (DeMars and Roettgering 1982). During initial phases of host tree colonization, female western pine beetle produce (+)-*exo*-brevicomin and males produce frontalin. Both elicit an aggregation response (Wood et al. 1976), and myrcene, a host monoterpene of *P. ponderosa*, enhances the response (Bedard et al. 1969). These semiochemicals have been synthesized

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and are commercially available as lures and baits (Skillen et al. 1997). The use of semiochemicals, in particular pheromones, has led to advances in management through the forecasting of infestation trends (Billings 1988), development of containment methods (Borden et al. 1983), stand protection and spot suppression (Shea et al. 1992, Ross and Daterman 1994, Clarke et al. 1999), and successful mass trapping efforts (Shea and Neustein 1995). Semiochemicals also have been used to describe the spatial and temporal distributions or flight activity patterns of several bark beetles, including western pine beetle (Sánchez-Martínez and Wagner 2002; Fettig et al. 2004, 2005; Gaylord et al. 2006, Williams et al. 2008).

In the western United States, bark beetle populations are often monitored using pheromone-baited traps, typically multiple funnel traps (Lindgren 1983, hereafter referred to as funnel traps), but often without knowledge of the relevance and usefulness of these data in pest management decision-making (e.g., for predicting trends in levels of bark beetle-caused tree mortality). Models have been developed for predicting tree losses based on trap catches of spruce beetle, *Dendroctonus rufipennis* Kirby, in Utah (Hansen et al. 2006); European spruce bark beetle, *Ips typographus* (L.), in Europe (Faccoli and Stergulc 2004, 2006); and southern pine beetle, *Dendroctonus frontalis* Zimmermann, in the southeastern United States (Billings 1988). Hansen et al. (2006) conducted a 4-yr study in Utah to examine the relationship between trap captures of *D. rufipennis* and mortality of Engelmann spruce, *Picea engelmannii* Parry ex Engelm. In general, these models produced relatively poor fits (i.e., explaining <40% of the variation in the data) when current-year tree mortality was modeled by seasonal trap catch at 1-, 4- and 10-ha scales. However, classification-tree analyses indicated that captures of ≈842 *D. rufipennis* during a season (late May to mid-August) from a single funnel trap represented a threshold between endemic conditions (less than two mass-attacked trees per ha) and epidemic conditions (two or more mass-attacked trees per ha) for either the current or subsequent year relative to deployment of the funnel trap. In Italy, the amount of *I. typographus*-caused tree mortality was very strongly correlated (R^2 >0.90) with trap catches, which led to the development of strong predictive models based on linear regression (Faccoli and Stergulc 2004). In Scandinavia, the number of *I. typographus*-infested trees was also strongly correlated with trap catch (Weslien et al. 1989, Hubertz et al. 1991). In the southeastern United States, Billings (1988) developed a practical method of forecasting population trends and infestation levels of *D. frontalis* based on captures of *D. frontalis* per day and the ratio of *D. frontalis* to one of its major predators *Thanasimus dubius* (F.) (Coleoptera: Cleridae). This method deploys funnel traps on a county-basis that are monitored for four consecutive weeks during spring. Since its initiation, this system has received widespread use and is generally regarded as an accurate means of forecasting *D. frontalis* population trends (i.e., increasing, declining or static) and infestation levels (i.e., low, moderate, high or outbreak).

The primary objective of this study was to determine the relationship between western pine beetle trap catches and levels of tree mortality attributed to western pine beetle (hereafter referred to as western pine beetle-caused tree mortality). Specific objectives were to 1) quantify the relationship between annual trap catch and levels of western pine beetle-caused tree mortality at two spatial scales (stand, forest); 2) quantify the relationship between early season trap catch and levels of western pine beetle-caused tree mortality at two spatial scales; 3) quantify relationships between stand characteristics and levels of western pine beetle-caused tree mortality at two spatial scales; and 4) determine whether trap catches and/or stand characteristics are useful in predicting levels of western pine beetle-caused tree mortality. If such relationships exist, they could serve as an effective tool for land managers, allowing the targeted implementation of integrated strategies to reduce the susceptibility and vulnerability of forests to western pine beetle attack.

Materials and Methods

Study Locations. This study was conducted over a 2-yr period on five national forests: 1) Goosenest Adaptive Management Area (GAMA), Klamath National Forest (41.6° N, 121.9° W; 1,502-m mean elevation); 2) McCloud Ranger District (McCloud), Shasta-Trinity National Forest (41.3° N, 122.0° W; 1,184 m); 3) Blacks Mountain Experimental Forest (BMEF), Lassen National Forest (40.7° N, 121.1° W; 1,759 m); 4) Placerville Ranger District (Placerville), Eldorado National Forest (38.6° N, 120.5° W; 1,497 m); and 5) Mountaintop Ranger District (Mountaintop), San Bernardino National Forest (34.2° N, 116.9° W; 1,650 m) (Fig. 1). These forests were selected on the basis of variation in the amount of anticipated western pine beetle-caused tree mortality (i.e., Mountaintop > McCloud > BMEF > Placerville > GAMA) based on our experience working in these areas and preliminary surveys of active western pine beetle infestations. Live tree composition was predominately *P. ponderosa* (Table 1), but it also included incense cedar, *Calocedrus decurrens* (Torr.) Florin; white fir, *Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.; Jeffrey pine, *Pinus jeffreyi* Grev. & Balf.; black oak, *Quercus kelloggii* Newb.; sugar pine, *Pinus lambertiana* Dougl.; Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco; and miscellaneous species. *P. ponderosa* was the only host of western pine beetle present in these stands with the exception of a few (<5% of basal area; total amount of cross-sectional area of trees at 1.37 m in height) Coulter pine, *Pinus coulteri* D. Don, at Mountaintop. Existing forest structure and topography were variable, with slopes ranging from <2 to 48% with all aspects represented, and reflected both past natural and human-caused disturbances.

Beetle Trapping. At each forest, six (Mountaintop, due to limited availability of suitable hosts) or 10 (all

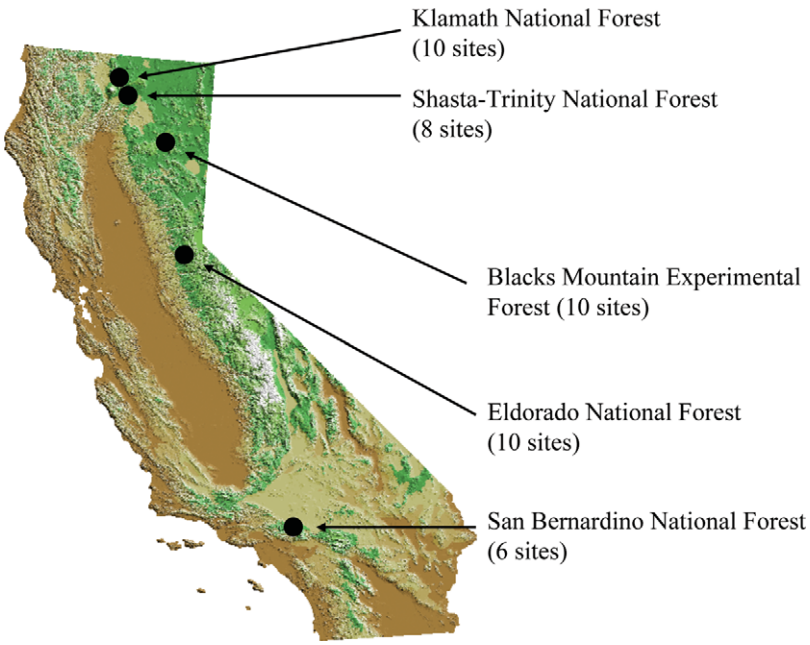

Fig. 1. Data were collected in 44 trapping sites (stands) distributed among five national forests in California. (Online figure in color.)

others), 16-unit funnel traps were deployed in stands along existing roads (i.e., placed in the forest ≈100 m perpendicular from the road edge) at >800-m intervals when each first became accessible in spring after sufficient snowmelt. This time varied among forests and included 1 April (BMEF), 9 April (McCloud), 20 April (Placerville), and 5 May (GAMA) 2003. Two trapping sites were discontinued at McCloud in June 2003 as a result of repeated disturbance of these traps by black bears, *Ursus americanus* Pallas. On 15 April 2004, Mountaintop was added to the study based on the extensive amounts of western pine beetle activity reported on that forest (USDA Forest Service 2003). In all cases, traps were hung on 3-m metal poles with collection cups ≈1 m from the ground and >8 m from any living pine, and baited with western pine beetle tree baits (Pherotech [Contech] International Inc., Delta, BC, Canada) consisting of the aggregation pheromone components *exo*-brevicomin (racemic, 97% chemical purity, 3 mg/d at 24°C) and frontalin (racemic, 98% chemical purity, 3 mg/d at 24°C), and the host volatile myrcene (90% chemical purity, 18 mg/d at 24°C). All semiochemicals were released from individual polyethylene tubes (250 μl, 250 μl, and 1.8 ml [2×], respectively). Baits were placed on the eighth funnel of each trap and were removed and replaced every 6 wk during the field season. A 3-cm time-released insecticidal Prozap Pest Strip (2,2-dichlorovinyl dimethyl phosphate, Loveland Industries Inc., Greeley, CO) was placed in the trap cup to kill arriving insects, and prevent damage or loss by invertebrate predation. These strips were replaced twice annually. This trapping system is commonly used for sampling western pine beetle in California and allows for efficient collection of large numbers of individuals (e.g., >500 per trap per d under some circumstances; C.J.F., unpublished data).

Insects captured in funnel traps were collected every 7–14 d from the end of May through mid-October of each year, which covers the majority of western pine beetle flight that occurs in these areas (Fettig et al. 2004, 2005). Samples were returned to the lab-

Table 1. Stand characteristics at western pine beetle trapping sites throughout California

Forest	*n*	dbh (cm)	Trees/ha	Ponderosa pine/ha	SDI	BAA (m^2/ha)	BAP (m^2/ha)
GAMA	10	39.3 ± 2.1	197.7 ± 18.3	173.0 ± 25.8	171.9 ± 12.5	26.2 ± 2.1	23.3 ± 3.1
BMEF	10	26.8 ± 1.5	376.8 ± 53.3	295.3 ± 52.4	177.3 ± 18.2	23.4 ± 2.5	16.1 ± 2.0
Placerville	10	41.8 ± 3.2	201.4 ± 23.1	91.4 ± 12.8	206.2 ± 22.3	32.9 ± 4.0	20.6 ± 3.3
Mountaintop[a]	6	35.4 ± 3.8	271.8 ± 37.1	57.7 ± 18.8	241.5 ± 54.8	37.6 ± 10.2	8.9 ± 3.2
McCloud[b]	8	55.8 ± 4.8	166.8 ± 37.3	137.4 ± 40.6	261.9 ± 36.1	46.8 ± 6.1	43.5 ± 5.8

Values are means ± SEM. dbh, diameter at breast height (1.37 m in height); SDI, stand density index; BAA, basal area of all trees; BAP, basal area of ponderosa pine.

[a] Only six sites were available that met selection criteria due to limited availability of suitable hosts.

[b] Ten sites were established but two were removed shortly thereafter due to repeated disturbance by black bears.

oratory for identification and tally using available keys (Wood 1982) and reference collections. Specifically, the number of western pine beetle and predators *Temnochila chlorodia* (Mannerheim) (Coleoptera: Trogositidae), *Enoclerus lecontei* (Wolcott), *Enoclerus sphegeus* F., and *Thanasimus undatulus* (Say) (Coleoptera: Cleridae) were of interest. However, few *E. lecontei* and *E. sphegeus* were collected (Fettig and Dabney 2006) and therefore were not considered in our analyses. Although *T. undatulus* occurs in northern California (Papp 1960) and is attracted to frontalin (Pitman and Vité 1970), it was not collected (Fettig and Dabney 2006). Voucher specimens are housed at the USDA Forest Service Bark Beetle and Common Associates Collection in Placerville, CA.

Stand Characteristics and Levels of Tree Mortality. In each stand ($n = 44$), one 0.081-ha circular plot was established surrounding each trap from which we obtained stand structure and composition data by conventional means. Only trees >5 cm diameter at breast height (dbh, 1.37 m in height) were tallied. A 2-ha circular plot was established surrounding each trap from which all recently attacked and/or killed pines were identified, tallied and causal agent of mortality recorded. A 100% cruise (census) was conducted in May of the first year (yr-1) of the study for trees that had been attacked and/or killed by western pine beetle before the study. These trees were excluded from our analyses. Subsequent cruises were conducted in fall of yr-1 and yr-2. In all cases, the bole of each tree was carefully examined for bark beetle attacks (i.e., oxidized phloem material present in pitch tubes or points of attack containing phloem boring dust and/or dry frass). Tree species, dbh, crown color (i.e., lime, yellow or red and used as an indicator of time since tree death), and colonizing bark beetle species were recorded. In some cases, a section of bark ≈625 cm^2 was removed with a hatchet at ≈2 m in height to determine whether any bark beetle galleries were present in the phloem or cambium, but only after the tree had died. The shape, distribution and orientation of galleries are commonly used to distinguish among bark beetle species (Furniss and Carolin 1977). In all cases, all trees identified as attacked by western pine beetle during yr-1 or yr-2 were checked the following fall to confirm mortality based on crown fade.

Statistical Analyses. To standardize the collection period, we began calculations of trap catch data at the second collection date disregarding the first collection period, which differed greatly in length among sites. Thus, the beginning of the trapping period used in these analyses ranged from 28 May to 2 June 2003 for GAMA, McCloud, BMEF and Placerville, and began 28 May 2004 for Mountaintop. Levels of western pine beetle-caused tree mortality were expressed as both the number of stems per hectare (mortality per hectare) and proportion of *P. ponderosa* stems killed (percentage of mortality). Using mortality assessments conducted for yr-1 and yr-2, sites were also classified by population phase [endemic <1 tree per ha per yr killed by western pine beetle, building = 1–5 trees per ha per yr killed by western pine beetle, or epidemic >5 trees per ha per yr killed by western pine beetle (Miller and Keen 1960, Hansen et al. 2006)].

Because we were interested in the effect of scale, analyses were conducted using independent and response variables calculated at the stand ($n = 44$; 2-ha) and forest ($n = 5$; ranging from ≈3,000–14,000 ha of contiguous host) scales. Preliminary analyses were conducted by Pearson's correlation coefficient (r) (SigmaStat 2.03, SPSS Inc., Chicago, IL) by using mortality per hectare and percentage of mortality, and several potential predictor variables: 1) western pine beetle trapped per day (western pine beetle per day); 2) western pine beetle trapped per day in June (June western pine beetle per day); 3) western pine beetle to *T. chlorodia* ratio (western pine beetle: *T. chlorodia*); 4) percentage of western pine beetle of overall trap catch [(western pine beetle/western pine beetle + *T. chlorodia*) × 100; percentage of western pine beetle]; 5) trees per hectare of all species (TPH); 6) basal area of all tree species (BAA); 7) basal area of *P. ponderosa* (BAP); 8) mean dbh; 9) percentage of basal area represented by *P. ponderosa* (% PP); and 10) stand density index (SDI).

All independent variables that had significant correlations ($\alpha = 0.10$; western pine beetle per day, western pine beetle: *T. chlorodia*, percentage of western pine beetle, TPH, BAA, BAP, mean dbh, and SDI) were considered for linear and multiple linear regression models for estimating levels of western pine beetle-caused tree mortality. Simple linear regressions were run for all significant independent variables, along with all combinations of two predictor variable multiple regressions at both spatial scales. Identification of more complex models (i.e., from small scale analyses due to sufficient sample size) was done using forward stepwise analysis (SigmaStat 2.03). Criteria used for selection of models reported here included model P value ($P < 0.05$), even distribution of plotted standardized residuals, low partial P values for individual independent variables, and R^2 values (minimum adjusted [adj.] $R^2 = 0.20$).

Results

Pinus ponderosa was the dominant tree species at all forests except Mountaintop (Table 1). Mean BAA ranged from 26.2 (GAMA) to 46.8 m^2/ha (McCloud), and the mean number of *P. ponderosa* stems ranged from 57.7 (Mountaintop) to 295.3 trees per ha (BMEF). Placerville and McCloud had relatively high trap catches (>50 western pine beetle per trap per d) throughout both years, with occasional discernible peaks (Fig. 2). BMEF also had relatively high trap catches, but experienced more defined peaks in July of yr-1 and June and September of yr-2. At the GAMA, western pine beetle trap catches were low throughout much of yr-1, peaking in September, and were elevated throughout yr-2 (Fig. 2). Mountaintop experienced the highest trap catches of any forest in yr-1, peaking at 592 western pine beetles per trap per d and then decreasing in September, followed by greatly reduced catches in yr-2 relative to yr-1 (Fig. 3).

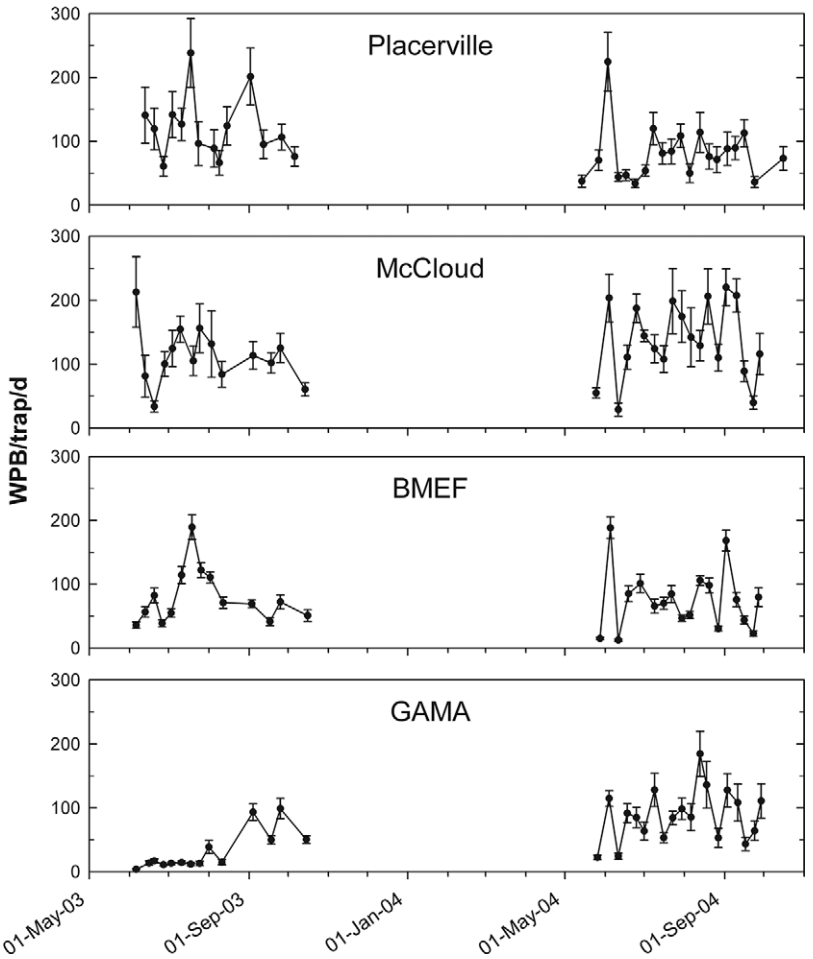

Fig. 2. Seasonal flight periodicity of western pine beetle (WPB) at four forests in California, 2003–2004. Points and error bars represent mean ± SEM for trap catches taken weekly to bimonthly (n = 8–10).

All three population phase classifications were represented in this study (Table 2). As defined by these classifications, western pine beetle-caused tree mortality increased from yr-1 to yr-2 at GAMA, remained constant at Placerville, and decreased at BMEF, Mountaintop, and McCloud (Table 2). Throughout the study, mean levels of western pine beetle-caused tree mortality ranged from 0.7 (Mountaintop) to 6.2 trees per ha per yr (McCloud), which represented 0.6–6.2% of *P. ponderosa* at these locations (Table 2). At the individual stand level, mean levels of western pine beetle-caused tree mortality ranged from 0 to 14.3 trees per ha per yr, which represented 0–15.2% of *P. ponderosa.*

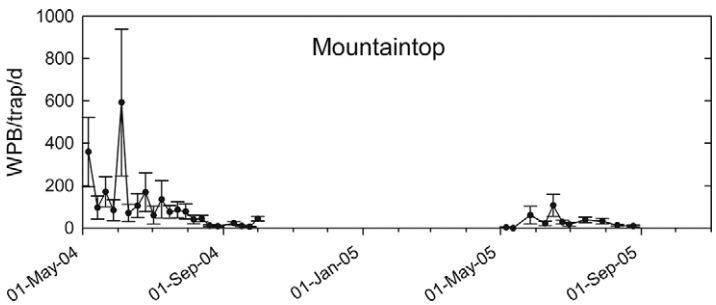

Fig. 3. Seasonal flight periodicity of western pine beetle (WPB) at Mountaintop, San Bernardino National Forest, 2004–2005. Points and error bars represent mean ± SEM for trap catches taken weekly to bimonthly (n = 6).

Table 2. Mean daily trap catches and levels of western pine beetle (WPB)-caused tree mortality at five forests in California

Forest	Yr-1				Yr-2			
	Beetle stage[a]	WPB/trap (/d)	Mortality (/ha)	% mortality	Beetle stage[a]	WPB/trap (/d)	Mortality (/ha)	% mortality
GAMA	Endemic	41.8 ± 4.0	0.7 ± 0.3	0.3 ± 0.1	Building	81.6 ± 10.4	1.2 ± 0.3	0.7 ± 0.2
BMEF	Building	74.6 ± 5.1	1.8 ± 0.5	0.6 ± 0.1	Endemic	67.8 ± 4.9	0.7 ± 0.2	0.3 ± 0.1
Placerville	Building	109.6 ± 22.7	1.8 ± 0.5	1.8 ± 0.4	Building	78.8 ± 13.0	1.4 ± 0.5	1.5 ± 0.5
Mountaintop	Building	88.3 ± 41.2	3.0 ± 1.4	4.8 ± 2.8	Endemic	33.4 ± 13.8	0.7 ± 0.2	0.6 ± 0.3
McCloud	Epidemic	107.6 ± 15.1	6.2 ± 0.9	6.2 ± 1.4	Building	126.7 ± 10.9	4.0 ± 1.7	2.4 ± 0.6

Values are means ± SEM.
[a] Beetle stage defined as endemic <1, building 1–5, or epidemic >5 trees killed per ha per yr by WPB.

None of the yr-1 western pine beetle trap catch variables (western pine beetle per day, June western pine beetle per day, western pine beetle: *T. chlorodia* or percentage of western pine beetle) was significantly correlated with either yr-1 or yr-2 mortality levels expressed as the number of trees per hectare (mortality per hectare) or proportion of *P. ponderosa* stems killed (percentage of mortality). In yr-2, western pine beetle: *T. chlorodia* and percentage of western pine beetle had significant positive correlations with yr-2 mortality at the stand scale (Table 3). At the forest scale in yr-2, there were positive correlations between western pine beetle per day and mortality per hectare, and percentage of western pine beetle and mortality per hectare, albeit at the 0.10 α level.

Several stand characteristics were significantly positively correlated with levels of western pine beetle-caused tree mortality at both spatial scales (Table 3). At the stand scale, BAA, BAP, mean dbh and SDI had numerous significant positive correlations with tree mortality, but with low r values ($r = 0.28–0.61$) (Table 3). Furthermore, % PP was significantly positively correlated with yr-2 mortality per hectare at the stand scale. At the forest scale, BAA and SDI had strong positive correlations with both yr-1 mortality per hectare and percentage of mortality ($r = 0.90–0.99$). In yr-2, again at the forest scale, BAP and mean dbh had significant positive correlations with mortality with high r values (BAP × yr-2 mortality per hectare, $r = 0.96$; mean dbh × yr-2% mortality, $r = 0.96$), but BAA and SDI did not (Table 3).

At the stand scale, many significant regression models ($P < 0.005$, all cases) were identified, but all had high levels of unexplained variation (adj. $R^2 < 0.35$, all cases) (Table 4). All models contained one of the stand characteristics (i.e., mean dbh, TPH, or BAA), and one model contained a trap catch variable, western pine beetle per day (Table 4, model B). In the model containing western pine beetle per day, western pine beetle per day and mean dbh both had pos-

Table 3. Pearson's correlation coefficients (r) between levels of western pine beetle (WPB)-caused tree mortality (dependent variable) and all independent variables at stand (2-ha) and forest scales, California 2003–2005

Independent variable[a]	Stand scale				Forest scale			
	Yr-1 mort/ha[b]	Yr-1% mort[c]	Yr-2 mort/ha[b]	Yr-2% mort[c]	Yr-1 mort/ha[d]	Yr-1% mort[d]	Yr-2 mort/ha[d]	Yr-2% mort[d]
Yr 1								
WPB/d	0.06	0.09	−0.12	−0.05	0.65	0.65	0.48	0.66
June WPB/d	0.01	0.06	−0.07	−0.03	0.43	0.72	−0.01	0.16
WPB: *T. chlorodia*	−0.02	0.06	−0.07	−0.04	0.10	0.46	−0.37	−0.30
% WPB	0.22	0.19	0.05	0.08	0.40	0.70	−0.09	−0.02
Yr 2								
WPB/d	0.28	0.18	0.03	0.07	0.55	0.25	0.84*	0.76
June WPB/d	0.10	0.85	−0.06	−0.11	0.42	0.03	0.69	0.59
WPB: *T. chlorodia*	0.01	−0.04	0.30*	0.43***	0.67	0.75	0.56	0.77
% WPB	0.19	−0.005	0.30**	0.28*	0.87*	0.61	0.87*	0.72
Stand data								
TPH	0.02	−0.30*	0.07	−0.24	−0.34	−0.39	−0.66	−0.77
BAA	0.55***	0.44***	0.44***	0.42***	0.90**	0.96***	0.44	0.82*
BAP	0.56***	0.28*	0.61***	0.50***	0.68	0.43	0.96***	0.87*
Mean dbh	0.43***	0.57***	0.17	0.43***	0.73	0.66	0.92**	0.96**
% PP	0.22	0.01	0.25*	0.17	0.18	−0.17	0.62	0.45
SDI	0.48***	0.29*	0.46***	0.33**	0.90**	0.99***	0.64	0.20

Significance of r: *, $P \leq 0.10$; ** $P \leq 0.05$; *** $P \leq 0.01$. mort/ha, *P. ponderosa* mortality per hectare; % mort, percentage of *P. ponderosa* killed by WPB; June WPB, WPB captures in June; % WPB, (WPB/WPB + *T. chlorodia*) × 100; TPH, trees/ha; BAA, basal area of all trees; BAP, basal area of *P. ponderosa;* dbh, diameter at breast height (1.37 m in height); % PP, percentage of basal area represented by *P. ponderosa;* SDI, stand density index.
[a] Yr-1 and yr-2 trap catch variables. Stand data assumed constant during the course of this study.
[b] $n = 44$.
[c] $n = 43$, one trap site removed due to missing data.
[d] $n = 5$.

Table 4. Six small-scale (stand) regression models (A–F) relating percentage of ponderosa pine killed by western pine beetle (WPB) in yr-1, and yr-1 and yr-2 (combined) to trap catches and various forest stand characteristics in California, 2003–2005

Model	Independent variables (x_i)				Model statistics			
	Variable	Range of values	Coefficient (SEM)	Partial *P*	*F*	df	*P*	Adj. R^2
A. $y = \sqrt{}$ Yr-1% *P. ponderosa* mortality ($n = 43$) (range of values, 0.0–3.9%)								
	Constant		−0.42 (0.40)	0.30	18.0	1,41	<0.001	0.29
	x_1 Mean dbh	19.5–75.4 cm	0.10 (0.02)	<0.001				
B. $y = \sqrt{}$ Yr-1% *P. ponderosa* mortality ($n = 43$) (range of values, 0.0–3.9%)								
	Constant		−0.71 (0.42)	0.10	11.2	2,40	<0.001	0.33
	x_1 WPB/d	18.1–285	0.004 (0.002)	0.08				
	x_2 Mean dbh	19.5–75.4 cm	0.02 (0.02)	<0.001				
C. $y = \sqrt{}$ Yr-1% *P. ponderosa* mortality ($n = 43$) (range of values, 0.0–3.9%)								
	Constant		0.91 (0.38)	0.02	6.5	2,40	0.004	0.21
	x_1 TPH	61.8–766.0	−0.002 (0.001)	0.04				
	x_2 BAA	14.3–77.3 m^2/ha	0.006 (0.002)	0.004				
D. $y = \sqrt{}$ Combined % *P. ponderosa* mortality ($n = 43$) (range of values, 0.0–4.1%)								
	Constant		0.64 (0.32)	0.05	10.7	1,41	0.002	0.19
	x_1 BAA	14.3–77.3 m^2/ha	0.03 (0.01)	0.002				
E. $y = \sqrt{}$ Combined % *P. ponderosa* mortality ($n = 43$) (range of values, 0.0–4.1%)								
	Constant		−0.23 (0.40)	0.57	22.6	1,41	<0.001	0.34
	x_1 Mean dbh	19.5–75.4 cm	0.05 (0.01)	<0.001				
F. $y = \sqrt{}$ Combined % *P. ponderosa* mortality ($n = 43$) (range of values, 0.0–4.1%)								
	Constant		1.26 (0.37)	0.002	10.1	2,42	<0.001	0.30
	x_1 TPH	61.8–766.0	−0.003 (0.001)	0.01				
	x_2 BAA	14.3–77.3 m^2/ha	0.03 (0.008)	<0.001				

dbh, diameter at breast height (1.37 m in height); TPH, trees/ha; BAA, basal area of all trees.

itive regression coefficients indicating that stands with a combination of high trap catches and large-diameter trees had the highest yr-1% mortality. However, this model offered only a small improvement (adj. R^2 = 0.33) over the model containing mean dbh alone (adj. R^2 = 0.29; Table 4, model A). A third model included TPH and BAA as predictor variables in which TPH had a negative regression coefficient and BAA had a positive regression coefficient, indicating that stands with fewer trees and higher basal area had higher levels of tree mortality (Table 4, model C).

When considering both yr-1 and yr-2 data combined, two linear regression models and one multiple regression model were selected at the stand scale (Table 4). In the two linear regressions, both mean dbh and BAA (Table 4, models D and E) had positive regression coefficients, but neither model explained much of the variation (adj. R^2 <0.35, both cases). Finally, another model with TPH with a negative regression coefficient and BAA with a positive regression coefficient was identified (Table 4, model F). This model used the same predictor variables as a previous model (Table 4, model C), but explained more of the variation in the data (adj. R^2 = 0.30).

At the forest scale, three predictor variables were used in our models, BAA, SDI, and mean dbh (Table 5). A measure of stand density, BAA or SDI, was used in all chosen models, having positive regression coefficients in each case. The models selected were all significant, simple, and had very high adj. R^2 values. Simple models were identified for explaining yr-1% mortality using the predictor variables BAA and SDI alone, with each having positive regression coefficients and adj. R^2 values of 0.90 and 0.98, respectively (Table 5, models A and B). Another model of Yr-1% mortality added mean dbh to BAA (Table 5, model C). In this model, BAA had a positive correlation coefficient and mean dbh had a negative correlation coefficient. The response surface graph shows that locations with more BAA and smaller mean dbh (i.e., closer to 25 cm dbh) had higher levels of western pine beetle-caused tree mortality (Fig. 4). Finally, when we combined Yr-1 and Yr-2 mortality we found two models that included a measure of stand density, either BAA or SDI. Both models had positive correlation coefficients and explained high levels of the variation in the data, with adj. R^2 >0.95 (Table 5, models E and F; Fig. 5).

Discussion

Throughout this study, western pine beetle activity and associated levels of tree mortality were elevated in many areas of California (USDA Forest Service 2003, 2004, 2005). For example, the amount of tree mortality attributed to western pine beetle reached unprecedented levels in the mountains of San Bernardino and Riverside Counties, CA, where ≈61,000 ha were impacted (USDA Forest Service 2002). That said, we chose forests that included a range of levels of western pine beetle-caused tree mortality (i.e., from endemic to outbreak). Trap catches varied widely (Table 2), with the greatest mean daily trap catch >2.6× the lowest in yr-1 (Placerville and GAMA) and >3.7× the lowest in yr-2 (McCloud and Mountaintop).

Table 5. Five large-scale (forest) regression models relating percentage of ponderosa pine killed by western pine beetle (WPB) in yr-1 (A–C), and yr-1 and yr-2 (combined, D and E) to various forest stand characteristics in California, 2003–2005

Model	Independent variables (x_i)				Model statistics			
	Variable	Range of values	Coefficient (SEM)	Partial *P*	*F*	df	*P*	Adj. R^2
A. y = Yr-1% *P. ponderosa* mortality (n = 5) (range of values, 0.3–6.2%)								
	Constant		−6.28 (1.51)	0.02	37.8	1,3	0.01	0.90
	x_1 BAA	23.4–46.8 m^2/ha	0.27 (0.04)	0.01				
B. y = Yr-1% *P. ponderosa* mortality (n = 5) (range of values, 0.3–6.2%)								
	Constant		−11.27 (1.01)	0.002	197.6	1,3	<0.001	0.98
	x_1 SDI	171.9–261.9	0.07 (0.004)	<0.001				
C. y = Yr-1% *P. ponderosa* mortality (n = 5) (range of values, 0.3–6.2%)								
	Constant		−5.37 (0.88)	0.03	68.3	2,2	0.01	0.97
	x_1 BAA	23.4–46.8 m^2/ha	0.37 (0.04)	0.01				
	x_2 Mean dbh	19.5–75.4 cm	−0.11 (0.04)	0.10				
D. y = Combined % *P. ponderosa* mortality (n = 5) (range of values, 0.9–8.6%)								
	Constant		−7.60 (0.78)	0.002	229.8	1,3	<0.001	0.98
	x_1 BAA	23.4–46.8 m^2/ha	0.34 (0.02)	<0.001				
E. y = Combined % *P. ponderosa* mortality (n = 5) (range of values, 0.9–8.6%)								
	Constant		−13.20 (1.89)	0.006	83.9	1,3	0.003	0.95
	x_1 SDI	171.9–261.9	0.08 (0.009)	0.003				

BAA, basal area of all trees; SDI, stand density index.

Daily catches of western pine beetle were much greater in our study than those reported for similar studies in Arizona (Gaylord et al. 2006, Williams et al. 2008), but comparable to others in California (Fettig et al. 2004, 2005). Gaylord et al. (2006) caught <15 western pine beetle per d and Williams et al. (2008) caught less than three western pine beetle per d during similar length trapping periods in studies that used the same lure (bait) type. In our study, the lowest mean daily trap catch for any forest was 33 western pine beetle per d (Mountaintop, yr-2). Differences in trap catches could reflect higher western pine beetle population levels in California compared with Arizona but also may reflect geographical variation in the attractiveness of lures to western pine beetle. For example, Hofstetter et al. (2008) found geographical

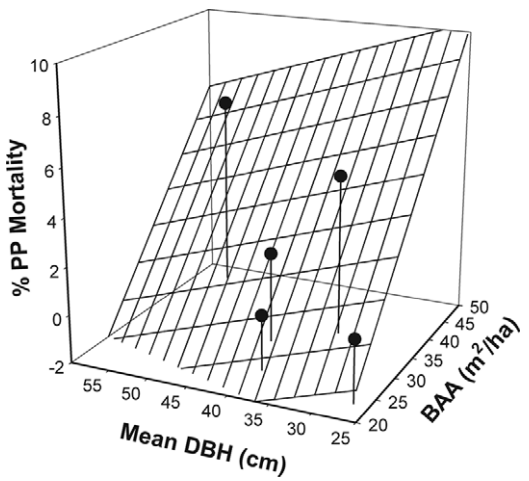

Fig. 4. Three-dimensional multiple regression response surfaces overlaid on observed data points for mean percentage of ponderosa pine killed by western pine beetle in yr-1. Response surface represents percentage of ponderosa pine mortality (% PP) to basal area (BAA) and mean dbh of all tree species (see Table 5, model C for statistics).

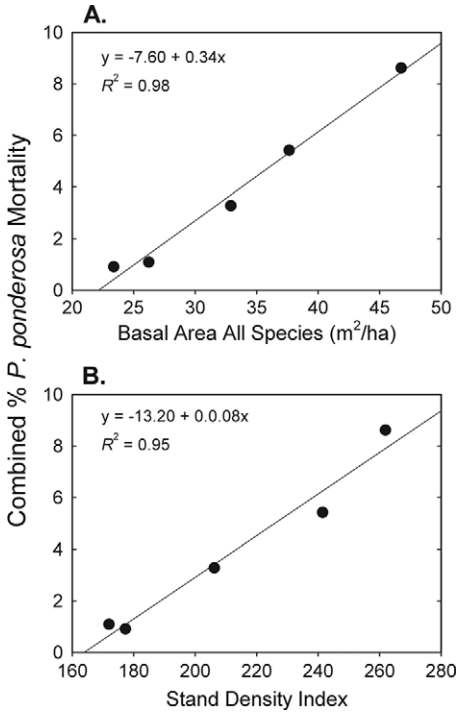

Fig. 5. Linear regressions overlaid on observed data points for (A) basal area of all tree species and mean percentage of ponderosa pine killed by western pine beetle in yr-1 and yr-2 combined (see Table 5, model D for additional statistics), and (B) stand density index and mean percentage of ponderosa pine killed by western pine beetle in yr-1 and yr-2 combined (see Table 5, model E for additional statistics).

variation in the attractiveness of western pine beetle to the standard western pine beetle lure in Arizona, and reported substituting α-pinene for myrcene significantly increased captures. This is problematic in regard to developing a monitoring tool for widespread use throughout the beetle's range. In our study, mean daily western pine beetle catches for forests defined as having endemic western pine beetle populations by our classification system ranged from ≈33–68 western pine beetles per trap per d.

Flight periodicity, as indicated by western pine beetle captures in funnel traps, varied among forests (Figs. 2 and 3). In yr-2 at both McCloud and GAMA, no distinct peaks were found. Other forests in both years experienced one or two distinct peaks with early season peaks ranging from June to July and late season peaks ranging from August to September. In these locations, western pine beetle is thought to have two to three generations annually (Miller and Keen 1960), with considerable overlap among them. Peaks in June are likely a result of captures of dispersing overwintering adults, while subsequent peaks are emerging brood adults resulting from June attacks (Fettig et al. 2004).

Overall, trap catch levels were found to be poor indicators of western pine beetle-caused tree mortality (Table 3). Our lowest trap catch in yr-1 was recorded at GAMA, which had the lowest tree mortality (Table 2). Beyond that, however, we found little evidence of a relationship between trap catch variables and levels of western pine beetle-caused tree mortality, with the exception of significant correlations between western pine beetle per day, western pine beetle: *T. chlorodia* and percentage of western pine beetle, and tree mortality during yr-2 only (Table 3). The trap catch variable western pine beetle per day was included in only one regression model, and added only a small amount of predictive power to that model (Table 4, model B). Although little work has been done in this area, trap catches have been found to be weak indicators of levels of bark beetle-caused tree mortality in *P. ponderosa.* For example, Hayes et al. (2008) reported weak and inconsistent relationships between bark beetle trap catches and levels of bark beetle-caused tree mortality in Arizona, an area with a high species richness of tree-killing bark beetles. However, trap catch data and data from gallery identifications in bark samples produced statistically similar relative abundances, suggesting, in this case, that captures in funnel traps may be good predicators of the relative abundance of bark beetles, but not associated levels of bark beetle-caused tree mortality. This is probably due to temporal variation in host vigor and thus large variation in the critical minimum number of beetles required to mass attack a tree and overcome host defenses (Fettig et al. 2007). The complexity of forest ecosystems in the western United States, including substantial climatic, topographic and ecological gradients, and its influence on trapping efficiency is also probably a contributing factor.

Many factors may impact the number of western pine beetle caught in a funnel trap, including heterogeneity in western pine beetle distribution. For example, brood trees close to traps may serve as a source of beetles and attractive semiochemicals (e.g., host volatiles and pheromones) that may pull beetles into the vicinity of the trap (Hayes et al. 2008). As a result trap catch may be biased in relation to the overall density of flying beetles for a given area. Pheromone-baited traps may not capture all beetles attracted to them, which may result in spillover attacks on neighboring trees depending on their proximity (Borden 1989, Laidlaw et al. 2003, Bentz 2006). It is possible for spillover to confound trap catches by serving as a beetle sink (i.e., competitor with traps through natural aggregation pheromone component release during initial phases of host tree colonization) or source (i.e., through natural release of anti-aggregation pheromone components or upon beetle emergence) (Hayes et al. 2008). During the course of this study, we did observe trees attacked by western pine beetle that seemed to result from spillover.

In addition to trap placement, stand conditions and the physical environment within stands are thought to influence the spacing and distribution of bark beetles within forests. Schmitz et al. (1989) sampled the flight behavior of mountain pine beetle, *Dendroctonus ponderosae* Hopkins, in thinned and unthinned stands in Montana. Most beetles were caught in the least intensely thinned plots and unthinned control, which were shown by McGregor et al. (1987) to have significantly higher levels of tree mortality. Safranyik et al. (2004) analyzed the number of bark beetles (several species) captured in British Columbia and unlike some studies in lodgepole pine, *Pinus contorta* Dougl. ex Loud. (Schmitz et al. 1989), and *P. ponderosa* (Zausen et al. 2005); but in agreement with others (Sánchez-Martínez and Wagner 2002), significantly more bark beetles (several species) were captured in thinned stands. Stand structure and composition may influence trap catches in a number of ways, including, but not limited to, effects on pheromone plume distributions (Thistle et al. 2004), the complexity of the olfactory environment (Shepherd et al. 2007), and host finding behavior (Turchin and Odendaal 1996).

Fettig et al. (2007) provide a review of tree and stand factors associated with bark beetle infestations, and discuss the effectiveness of reducing stand density for preventing bark beetle infestations. Factors such as stand density, tree diameter and host density are consistently identified as primary attributes associated with bark beetle infestations. Craighead (1925) and Miller (1926) were among the first to demonstrate that slower growing trees were more susceptible to western pine beetle attack. Since that time, a considerable amount of effort has been devoted to the identification of tree and stand conditions associated with bark beetle attack in *P. ponderosa.* Negrón and Popp (2004) established 35 clusters of *D. ponderosae*-infested and uninfested plots in *P. ponderosa* forests of north central Colorado. Based on data collected from the plots, the authors developed several classification models for estimating the probability of infestation. The simplest model indicated a 50% greater probability of infesta-

tion when *P. ponderosa* basal area was >17.1 m^2/ha than when *P. ponderosa* basal area was ≤17.1 m^2/ha (Negrón and Popp 2004). In the Pinaleño Mountains of Arizona, plots infested with roundheaded pine beetle, *Dendroctonus adjunctus* Blandford, had significantly higher stand densities compared with uninfested plots (Negrón et al. 2000). In the Southern Cascades of California, Fettig et al. (2009) reported significant correlations between the percentage of pines killed by bark beetles (several species) and basal area, trees per hectare, and SDI, but trees per hectare was the best predictor of levels of tree mortality (R^2 = 0.76).

Our results suggest that stand density, measured as BAA or SDI, is the most important predictor of western pine beetle-caused tree mortality at large spatial scales. That is not to say that we found that high stand densities cause outbreaks, but rather that, during times of increased levels of western pine beetle-caused tree mortality, areas with the highest stand densities will experience the highest levels of tree mortality on both an absolute (trees per hectare) and proportion (percentage of mortality) basis. This is probably due to the effect of stand density on individual tree vigor and water availability (Feeney et al. 1998; Kolb et al. 1998; Wallin et al. 2004, 2008; Sala et al. 2005; Skov et al. 2005; Zausen et al. 2005) and pheromone plume distributions (Thistle et al. 2004). Surprisingly, BAP and % PP were of less predictive power than other measures of stand density (Tables 3–5), suggesting tree competition is more important that host availability. In studies conducted in *P. ponderosa* in Arizona, soil water content was higher in thinned treatments than untreated controls (Feeney et al. 1998), and increased phloem thickness and resin flow was found with decreasing stand density, suggesting increased tree vigor and reduced likelihood of successful bark beetle attack (Kolb et al. 1998).

Scale seems to be an important factor in developing regression models for predicting levels of bark beetle-caused tree mortality. Faccoli and Stergulc (2004) identified powerful regression models with repeated measures (seven consecutive years) with intensive trapping (weekly collection of 40 traps) of a large area (≈10,100 ha). By plotting mean trap totals of *I. typographus* for the entire trapping season against volume of trees, *Picea abies* Karsten, lost in each trapping season they found a linear model with a R^2 of 0.93. It seems that averaging a large sample over a large area reduced the high variance reported in other bark beetle sampling studies (Hansen et al. 2006, Hayes et al. 2008). Similarly, our results suggest that predicting western pine beetle-caused tree mortality on a small scale basis is difficult (adj. R^2 <0.35), but that at large spatial scales stand density is a strong predictor of levels of western pine beetle-caused tree mortality (adj. R^2 >0.90).

Stand density index (Reineke 1933) is a common measure of the density of a stand of trees based on tree size (i.e., dbh of trees of average basal area known as quadratic mean diameter) and numbers of trees per unit area. Because SDI is an indicator of the amount of growing space available, and thus well correlated with tree growth, it is not surprising that SDI would be useful in predicting levels of western pine beetle-caused tree mortality. However, basal area is usually preferred over SDI because it is a satisfactory measure of stand density and is easier to calculate. Oliver (1995) reported maximum SDI for even-aged *P. ponderosa* stands in northern California was regulated by *D. ponderosae* and western pine beetle infestations. A SDI value of 230 defined a threshold for a zone of imminent bark beetle-caused tree mortality within which endemic populations kill a few trees but net growth is positive. Maximum SDI was defined at 365. Our data suggest that western pine beetle-caused tree mortality begins below the SDI 230 threshold and may begin as low as 170. Careful consideration of the models presented here (Table 5, models E and F; Fig. 5) may lead to lower threshold densities. DeMars and Roettgering (1982) stated that reducing stand stocking to 55–70% of the basal area needed for full site utilization will relieve competitive stress among residual trees, improve their vigor, and make them less prone to successful attack by western pine beetle.

In this study, we demonstrated that monitoring western pine beetle populations through the use of pheromone-baited funnel traps is not an effective means of predicting levels of western pine beetle-caused tree mortality. However, levels of western pine beetle-caused tree mortality, when considering the possibility of future outbreaks, can be efficiently predicted (adj. R^2 >0.90) at large spatial scales by simply measuring stand density, specifically BAA or SDI. Although adding mean dbh to BAA in our model increased the amount of variation explained (adj. R^2 = 0.97; Table 5, model C), the predictive power is likely not increased enough in practical terms to warrant input of this variable. Our large spatial scale model that predicts low tree mortality in locations with low basal area (<30 m^2/ha) and large diameter trees (>40 cm, mean dbh) (Table 5, model C; Fig. 4) is strong evidence that current fuels reduction and forest restoration treatments that aim for a stand structure with relatively few large diameter trees (Kolb et al. 2007) are also prudent approaches for reducing risk to western pine beetle infestations.

Acknowledgments

We thank T. Blubaugh, R. Borys, C. Dabney, W. Dobrowolski, J. Fenn, E. Hanson, S. McKelvey, and J. Nowak (USDA Forest Service); C. Mautner (University of California); M. Patterson (University of Reno), A. Piscitelli (Humboldt State University), C. Stoll (Chico State University); and J. Young (Oregon State University) for technical assistance. In addition, we are grateful to the staff of Blacks Mountain Experimental Forest, Eldorado National Forest, Klamath National Forest, Shasta-Trinity National Forest, and San Bernardino National Forest (USDA Forest Service) for providing study sites. We thank R. Billings (Texas Forest Service), J. Hayes (Pacific Northwest Research Station, USDA Forest Service), and M. Haverty (Pacific Southwest Research Station) for helpful insight. A special thanks to J. McMillin

(Forest Health Protection, USDA Forest Service) and S. McKelvey for critiques that greatly improved earlier versions of this article. This research was supported, in part, by a USDA Western Bark Beetle Initiative grant (2004-1) (to C.J.F., L.M., and J. Negrón), a U.S. President's Early Career Award for Scientists and Engineers (to C.J.F.), the Pacific Southwest Research Station, and Forest Health Protection.

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Received 8 May 2009; accepted 16 September 2009.