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RESEARCH ARTICLE

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Interactions of White Pine Blister Rust and Mountain Pine Beetle in Whitebark Pine Ecosystems in the Southern Greater Yellowstone Area

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ABSTRACT: Whitebark pine (*Pinus albicaulis*) is a fundamental component of alpine and subalpine habitats in the Greater Yellowstone Ecosystem. The magnitude of current white pine blister rust (WPBR) infection caused by the pathogen *Cronartium ribicola* and mountain pine beetle (MPB; *Dendroctonus ponderosae*) impacts, combined with the effect of climate change on beetle population dynamics, are placing this foundation species in a precarious state. We collected stand- and tree-level data in three whitebark pine systems in the southern Greater Yellowstone Ecosystem to evaluate current conditions and to determine how characteristics of individual whitebark pine trees, including the presence and severity of white pine blister rust, influence host selection by the MPB. Data revealed that 45% of all whitebark pine trees sampled were dead. In addition, 67% of all trees sampled were attacked by MPB, 83% were infected with WPBR, and 62% were affected by both. Whitebark pine trees that were selected as hosts by MPB exhibited significantly greater blister rust severity than trees that were not selected. Multiple logistic regression analyses identified a complex set of tree characteristics related to host selection by MPB; in addition to rust severity, stand type (mixed species or pure whitebark pine) and tree diameter were also significant predictors of selection. The interaction among MPB selection patterns, blister rust severity, tree diameter, and stand type quantified in this study will likely continue to influence the disturbance pattern and severity in whitebark pine ecosystems in the Greater Yellowstone Area. Understanding these patterns is critical to successful management of whitebark pine forests in this region.

Index terms: disturbance, Greater Yellowstone Ecosystem, mountain pine beetle, whitebark pine, white pine blister rust

INTRODUCTION

Whitebark pine (*Pinus albicaulis* Engelm.) is an important component of many high elevation ecosystems throughout the western United States and Canada, including the Greater Yellowstone Ecosystem (GYE). This keystone and foundation species plays a disproportionately large ecological role relative to its abundance, and it strongly defines ecosystem structure, function, and process (Tomback and Kendall 2001). Whitebark pine regulates soil development, facilitates plant succession, provides carbon storage, and captures and retains snow, thus increasing the quantity and duration of summer runoff (Arno and Hoff 1989). This protracted melting provides water to feed streams and riparian communities longer into the growing season, as well as producing a consistent flow to downstream water users. In addition, many wildlife species utilize the nutrient- and lipid-rich seeds of the whitebark pine, including many forest birds and rodents (Lorenz et al. 2008).

Large-scale outbreaks of mountain pine beetle (MPB; *Dendroctonus ponderosae* Hopkins), an insect native to coniferous forests of western North America, are not uncommon in many pine forests, particularly in lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm. Ex Wats.) ecosystems (Romme et al. 1986; Taylor and Carroll 2003). Dendrochronology records from subalpine forests indicate that these events are historically infrequent in whitebark pine ecosystems because winter temperatures were too cold for extensive episodes of MPB activity (Amman and Schmitz 1988; Perkins and Swetnam 1996; Hicke et al. 2006). The current MPB outbreak is intense, severe, and extensive both within its historic host range and in high elevation whitebark pine ecosystems, in part attributable to altered temperature and precipitation patterns (Logan and Powell 2001; Carroll et al. 2004; Bentz et al. 2010; Logan et al. 2010).

In contrast to MPB, white pine blister rust (WPBR) is caused by a non-native pathogen - *Cronartium ribicola* Fisch. - accidently introduced into the eastern United States as early as 1897, to western North America in approximately 1910, and which spread to the GYE by the 1940s (Geils et al. 2010). Spores of the fungus enter trees through leaf stomata, and the fungal mycelia grow through the living bark and cambial tissue. This destroys the trees' water and nutrient transport system, and forms cankers or spore-producing fruiting bodies on branches and the bole (Woo and Martin 1981). Not only can severe WPBR infections lead to the mortality of mature whitebark pine trees, the disease dramatically decreases recruitment by extensive damage to cone-bearing branches, seedlings, and saplings; and these impacts are not characteristic of most disturbance regimes in whitebark pine ecosystems (Tomback et al. 1995; McKinney et al. 2009). Blister rust incidence and severity continue to increase across the western United States and within the GYE (Schwartz et al. 2007; Bockino 2008; Bockino and McCloskey 2010; GYWPMWG 2010; Larson 2011).

Both MPB and WPBR are widespread in whitebark pine ecosystems in the GYE, yet an understanding of their interaction and subsequent impacts is limited, yet essential to successful management activities (Larson 2011). Two MPB events occurred during the 20th century in whitebark pine ecosystems; however, the extent and intensity of the current MPB outbreak combined with high incidence and severity of WPBR has resulted in historically unprecedented whitebark pine mortality (Bentz 2008; Macfarlane et al. 2009; Logan et al. 2010). In portions of the northern Rocky Mountains, mortality rates of whitebark pine trees are as high as 90% (Gibson et al. 2007), while in the Interior Columbia Basin whitebark pine populations have declined by at least 45% (Kendall and Keane 2001). Data from the 2009 Landscape Assessment aerial survey in the GYE indicate that approximately 90% of whitebark pine stands in the GYE contained some level of beetle activity, and 50% of these stands had experienced high levels of overstory whitebark pine mortality (Macfarlane et al. 2009). Depending on location, from 20% to 81% were infected with blister rust (Schwartz et al. 2007; Bockino 2008; Bockino and McCloskey 2010; GYWPMWG 2010). Interactions among MPB and WPBR, and tree- and stand-level responses in these ecosystems, will influence future ecosystem structure and function, energy and nutrient fluxes, and species diversity (Logan et al. 2010; Turner 2010; Larson 2011). The current conditions provide a timely opportunity for a deeper understanding of these interactions, which is fundamental to understanding population dynamics, species longevity, future status, and conservation.

This study aims to identify and describe potential or existing relationships among whitebark pine, WPBR, and host selection patterns of MPB. Our specific objectives included the quantification of: (1) the spatial extent and severity of MPB activity and WPBR infection in whitebark pine forests on our study sites in the southern the GYE during the summer of 2006; (2) the relationship between individual whitebark pine tree-level WPBR severity and selection as a host by the MPB; and (3) the influence of multiple tree- and stand-level predictor variables on the probability of selection of individual whitebark pine by MPB.

METHODS

Study Area

Our study was conducted in the Greater Yellowstone Ecosystem (GYE), which encompasses portions of southwestern Montana, northwestern Wyoming, and eastern Idaho. Two national parks, Grand Teton and Yellowstone, as well as portions of seven national forests, three National Wildlife Refuges, and Bureau of Land Management, state, and private properties lie within this extensive region. The climate, characterized by warm, dry summers and long, cold winters with continuous snow pack and mean temperatures below freezing are influenced by pacific, polar, and continental weather systems (Despain 1990). The growing season is two to three months in length at high elevation whitebark pine sites. The GYE represents one of the most extensive whitebark pine populations in the lower 48 states.

During the summer of 2006, we chose three study sites within the southern portion of the GYE (Figure 1; Table 1) that met the following criteria: (1) presence of current MPB activity in whitebark pine forested areas; (2) presence of WPBR symptoms; (3) overstory conifer species composition; and (4) absence of direct human manipulation of forest structure. Because of the large size of the GYE, a temporal range of MPB population phases existed among sites, based on the proportions of whitebark pine at each site that were either dead, red-needled, or green-needled. The approximate outbreak initiation on Teewinot was 2001, on Breccia Peak 2002, and 2003 on Mount Leidy, where MPB populations most recently transitioned to an epidemic phase. Because MPB selection patterns vary with outbreak phase and other factors, it should be noted that this study is a single spatial and temporal description of patterns in MPB activity in whitebark pine stands in the southern GYE.

Field Methods

At each of our study sites, we identified two stand types. The first stand type, referred to hereafter as PURE, was distinguished by whitebark pine as the dominant canopy species (≥ 90% of total stand basal area). The second stand type, referred to hereafter as MIX, was characterized by a canopy composition of whitebark pine mixed with subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) and/or Engelmann spruce (*Picea engelmannii* Parry ex Engelm.). In these stands, whitebark pine comprised at least 20%, but no greater than 80%, of the canopy tree total stand basal area. Within each stand type, we identified a polygon of relatively homogenous forest structure and species composition using digital vegetation maps and field observations. To minimize the influence of topography, elevation, and aspect on our dataset and final model, we targeted areas that were similar for these variables.

Twenty-four plots were sampled in each of the two stand types, PURE and MIX, at each of the three sites (Table 1; n = 144 plots). Within each site/stand type combination, we established a random starting point and transect azimuth. From the starting point, we identified the nearest whitebark pine tree along the transect with evidence of MPB presence - this tree served as the center of the first plot. Subsequent plots were placed along the transect based on the occurrence of a single whitebark pine with MPB activity, and were a minimum of 50 m apart. We used variable radius plot techniques to sample a minimum of 20 trees greater than 15 cm dbh in each plot (Bitterlich 1984).

For each sample tree, MPB activity was determined by the presence of: (1) pitch tubes, which are mixtures of tree resin and beetle-produced boring dust; (2) boring dust in bark crevices particularly around root collar of tree; (3) entrance holes with inconspicuous pitch tubes; (4) small (≈2

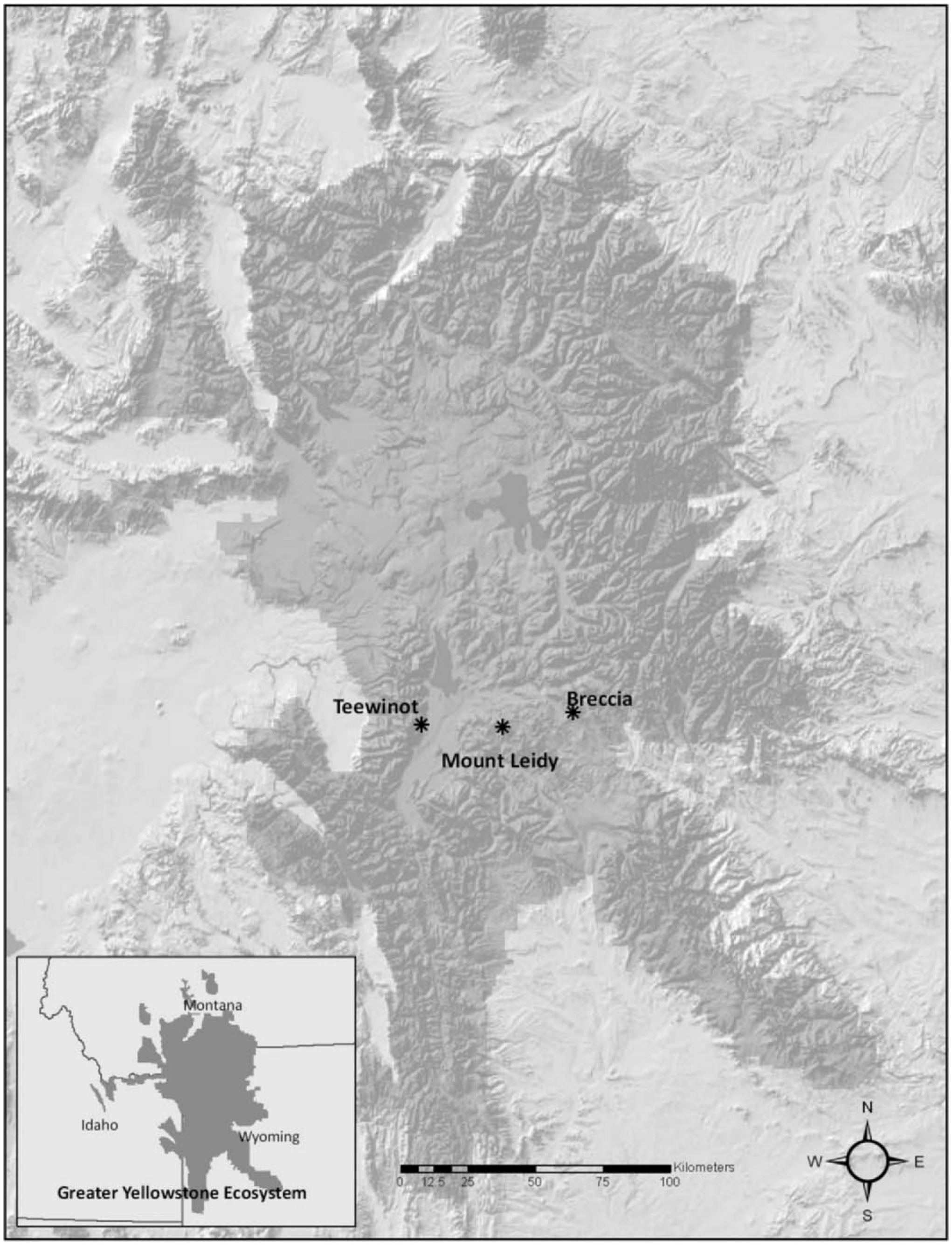

Figure 1. Study sites in the southern Greater Yellowstone Ecosystem.

mm diameter) emergence holes; or (5) beetles actively chewing into bark (Safranyik et al. 1974). Our work on National Park Service land prohibited destructive sampling or bark peeling; therefore, we could not verify MPB establishment or brood success. Hereafter, we refer to MPB activity within a tree as 'host selection.' We used crown needle color as an indicator of the temporal sequence of attack to determine host selection preferences. Crown needle color has been shown to be a valid and reliable index for the sequence of host tree selection, assuming that trees from the same location are compared to one another within a single time period (Wulder et al. 2006).

We evaluated WPBR severity using a condensed version of Six and Newcomb's (2005) severity rating system. Cankers

Table 1. Site attributes of sampled whitebark pine in the southern GYE. PURE stands have ≥ 80% whitebark pine; MIX stands are comprised of whitebark pine (< 80%) mixed with subalpine fir, and Engelmann spruce. Site order corresponds to the relative stage of the mountain pine beetle epidemic – the epidemic is oldest at Breccia Peak and most recent at Mount Leidy. Blister rust and mountain pine beetle were present at all sites. BTNF (Bridger-Teton National Forest) and GTNP (Grand Teton National Park) refer to management jurisdiction for each site.

Stand Type (by ite)	Number of Plots	Elevation (meter)	Aspect
Breccia Peak (BTNF)			
PUREk	24k	2981-3151k	160-270°k
MIXk	23k	2851-2990k	110-270°k
Teewinot (GTNP)			
PUREk	24k	2748-2984k	50-165°k
MIXk	24k	2568-2788k	50-145°k
Mount Leidy (BTNF)			
PUREk	24k	2815-2919k	150-260°k
MIXk	24k	2764-2887k	350-70°k

were confirmed by the identification of two or more of the following: (1) branch flagging; (2) rodent chewing; (3) roughened, dead bark; (4) thin, smooth, or swollen bark; or (5) old white aecial sacs or fresh orange aeciospores (Hoff 1992). Separate severity scores were given to the bole and crown of each tree. A score of 0 was assigned to the bole or crown when no cankers were detected, a score of 1 when there were 1 to 3 detectable cankers, and a score of 2 when there were > 3 cankers present. Whole tree blister rust severity ratings were calculated by adding the bole and crown scores, resulting in a severity range of 0 to 4. It has been suggested that high overall rust severity or more damaging bole infections contributes to greater disease related tree stress (Six and Adams 2007). This additive score accounts for this idea because a whitebark pine must have both bole and crown cankers to have a rust severity of 3 or 4.

Statistical Analyses

We used a series of analyses to test our null hypothesis that any individual whitebark pine greater than 15 cm dbh was equally likely to be selected as a host tree. Our primary assessment utilized one group t-tests to evaluate the differences in rust severity between whitebark pine selected by MPB and those not selected.

To further investigate the basic relationships identified with t-tests and to allow for more in-depth assessment of MPB host selection, we used plot-level Host Selection Ratios (HSRs). MPB patterns of spread exhibit a high degree of spatial autocorrelation, yet intensity is temporally variable, making assessment of beetle selection challenging (Macfarlane et al. 2009). HSRs can help quantify selection preference by comparing the availability of all the whitebark pine host trees to the availability of whitebark pine trees with a preferred characteristic - in this case, the presence of greater blister rust severity. HSRs account for plot-level stand density and rust severity and, therefore, provide a useful metric of relative host selection by MPB for each individual whitebark pine tree (Manly et al. 2002).

We defined two categories of host tree blister rust infection severity (Table 2): light (total rating of 0-1) and heavy (total rating of 2-4). Whole tree blister rust severity ratings were aggregated based on severity patterns reported in the literature (Kinloch 2003), observations in the field, and patterns identified by our data. We calculated HSRs for each plot by measuring the frequency of beetle selection of whitebark pine in the heavy rust category and comparing this to the total number of whitebark pine trees with heavy rust that were available for selection (Equation 1). For each of the three sites, we tested our sampled mean HSRs against selection ratios of non-preference (1.0) using one-group t-tests. We then plotted our calculated HSRs against the relative abundance of the preferred host and fitted a logarithmic curve to detect trends in host selection strength.

Table 2. Definitions of independent variables used to build logistic regression selection probability functions.

V ria le	V ria le Type	V lues	Description
Study Sitek	Categoricalk	1 – 3k	Breccia Pea , Mount Leidy, or Teewinot
Stand Typek	Bina yk	0 – 1k	MIX or PURE ovek kto y tree kp eciek compo ition
DBH	Continuou	10–130 cmk	Tkee diametek at breast height
Rust Sevekityk	Bina yk	0 – 1k	Whole tree ku t kevekityk (light ku t = 0,1; heavy ku t = 2-4)k

Equation 1: Host Selection Ratio =
(# whitebark with heavy rust selected by MPB ÷ total # whitebark selected by MPB) ÷ (# whitebark with heavy rust available ÷ total # whitebark available)

As a compliment to our HSR analysis, and to test the importance of additional plot variables, we used data from all sites to perform logistic regression to describe the probability of selection of an individual whitebark pine tree by the MPB. We regressed a binary, discrete response variable (either selected as host by MPB or not selected by MPB) against multiple tree- and stand-level predictor variables (Hosmer and Lemeshow 2000).

Independent variables used to develop this regression model were taken from PURE and MIX stand types at all three study sites: Breccia Peak, Mount Leidy, and Teewinot. We assigned categorical variables to study site, rust severity, and stand type. For dbh, we assigned each tree the midpoint of 10 cm diameter bins to display a continuous variable (Table 2).

RESULTS

Summary Data

For all whitebark pine trees sampled (n = 1787): 45% were dead; 83% were symptomatic for blister rust (81% had crown rust; 49% had bole rust); 67% were selected as a host by MPB; 62% were affected by both WPBR and MPB (Table 3). Individual whitebark pine trees with green needles and fresh MPB infestation account for the difference between the proportions of sampled whitebark that were dead and those selected by MPB. Among sites, whitebark pine mortality was lowest at Teewinot PURE (33%) and highest at Breccia Peak MIX (65%). The proportion of whitebark pine symptomatic for WPBR was highest at Teewinot MIX (92%) and lowest at Breccia PURE (76%). The proportion of whitebark pine selected as host trees by MPB was lowest at Teewinot PURE (50%) and highest at Breccia Peak PURE (82%).

Preferential Host Selection by Mountain Pine Beetle

Whole-tree blister rust severity for trees selected as hosts by MPB, regardless of site or stand type, was significantly greater than trees that were not selected by MPB (Table 4; p < 0.0001), and was also greater than whole tree rust, regardless of selection by MPB. For trees selected as hosts by MPB in all sites combined, mean whole-tree rust severity (2.39) was significantly greater and nearly twice as high as trees that were not selected (1.34; Table 4; t = 16.39; p < 0.0001). Among sites, whole-tree rust severity for trees selected as hosts by MPB was highest at Teewinot PURE (3.28) and lowest at Breccia PURE (1.69; Table 4), and crown rust severity was higher than bole severity in all sites. For all sites considered together, mean crown rust severity (1.32) was significantly greater than mean bole (0.73) severity (t = 31.37; p < 0.0001), and crown rust contributed 64 % (range 61% - 75%) toward the whole-tree rust severity rating (Table 4).

Directional one group t-tests indicated that mean HSRs were significantly greater than 1.0 for all sites and stand types (p < 0.001), with the strength of selection preference ranging from 1.109 to 1.452 (Table 5). Data pooled by stand type resulted in mean HSRs greater in PURE (1.334, SE = 0.09) than MIX (1.239, SE = 0.05) stands, yet both were significantly greater than 1.0 (p < 0.01). Pooled HSR data for all plots (n = 143) showed significant preferential host selection by MPB of whitebark pine with heavy WPBR (mean HSR = 1.287, SE = 0.05; Table 5). There was minor variability in HSRs among individual sites; at Breccia Peak and Teewinot mean, HSRs were greater in PURE stands. At Mount Leidy, the mean HSR was greater in MIX stands (Table 5).

Table 3. Summary conditions of whitebark pine stands as of summer 2006 field season, for study sites in the southern GYE. Values in bold are means.

Stand Type (by si e)	# Trees Sampled	Proportion of Whitebark Pine					
		Dead	Blis e r Rust Symptomatic	Crown Rust Presen	Bole Rust Presen	Selected by MPB	MPB & Rust
Breccia Peak							
PUREk	293	397k	6k	4	298k	2	67k
MIXk	226k	65	9k		5		5
Teewino							
PUREk	392	33	6k	5	45	50	4
MIXk	204	62	92	9k	3	66k	64
Mo n Leidy							
PUREk	3 5	45	9k	6k	51	4	63
MIXk	2	41	9k		52	61	5
Trees Sampled	**1787**	**45**	**83**	**81**	**49**	**67**	**62**

Table 4. Blister rust severity by site, location on individual tree, and in comparison to mountain pine beetle host selection. Maximum possible severity rating for crown or bole, separately is 2.0. Maximum whole tree severity rating is 4.0. Summary statistics are for all whitebark pine sampled, n = 1787. Subset of whitebark pine selected as host by beetle, n = 1203.

S and Type (by site) Peak	Crown	Bole	Whole Tree	Crown Rust: Whole Tree	Whole Tree (Selected as ost)	Whole Tree (Not-selected as ost)	Significance Between Whole Tree Rust - Selected/No Selected
PUREk	1.14	0.38	1.52	0.75	1. 9	0.79	t = -6. 3; p < 0.0001
MIXk	1.42	0.85	2.27	0. 3	2. 7	1.08	t = 9.31; p < 0.0001
Teewino							
PUREk	1.39	0. 5	2.04	0. 8	3.28	1. 8	t = -5.53; p < 0.0001
MIXk	1.52	1.18	2.7	0.	3.11	2.01	t = -5.49; p < 0.0001
Leidy							
PUREk	1.27	0.7	1.97	0. 5	2.28	1.11	t = -8.46; p < 0.0001
MIXk	1.25	0.81	2.06	0. 1	2.78	1.02	t = 12.16; p < 0.0001
All Sites	1.32	0.73	2.04	0. 4	2.39	1.34	t = 16.39; p < 0.0001

Scatter plots for all plots indicated a negative relationship between HSR and the relative abundance of trees with heavy rust available (Figure 2). The majority of HSRs were greater than 1.0 (HSR = 1.0 indicates no preferential selection); and HSR values were highest when fewer trees with heavy rust were available, demonstrating a preferential pattern of host selection for whitebark pine with heavy rust. HSR values decreased as the relative abundance of whitebark pine with heavy rust increases toward 100%. The highest HSR values represent plots wherein MPB selected all the whitebark pine available with heavy rust and, although available, none with light rust.

Our probability of selection model evaluated model plausibility from a biological perspective and Goodness-of-fit tests (G = 242.69; df = 6; $p < 0.0001$), and showed significant interactions among stand type, tree diameter, and rust severity (Table 6; Figure 3). Blister rust severity was the most

Table 5. Host selection ratios (HSRs) calculated for each plot to detect preferential habitat selection by mountain pine beetle. Host selection ratios in bold indicate significant deviation from 1.0 and preferential selection by MPB, assessed by a directional t-test (α = 0.05).

S and Type (by ite)	# Plo	Direc ional one group -te			
		Mean HSR*	SE of Mean	-value	Significance
Breccia Peak					
PURE	24k	**1.452**	0.25k	1.79	p = 0.04k
MIX	23k	**1.213**	0.07	2.72k	p = 0.01k
Teewino					
PURE	24k	**1.292**	0.08	3.28	p = 0.002k
MIX	24k	**1.109**	0.43k	2.49	p = 0.01k
Moun Leidy					
PURE	24k	**1.258**	0.12k	2.02k	p = 0.03k
MIX	24k	**1.395**	0.13k	2.87	p = 0.004k
All Plo	143k	**1.287**	0.05k	5.06	p < 0.0001k
PURE	72k	**1.334**	0.09	3.41k	p = 0.01k
MIX	71k	**1.239**	0.05k	4.20	p < 0.0001k

*N ll hypothesis: SR – 1.0 = 0.0 tested against alternate hypothesis: SR – 1.0 ≠ 0.0. R st severity is a binary habitat characteristic defined by whole tree r st severity: heavy r st (2-4) and light rust (0-1).

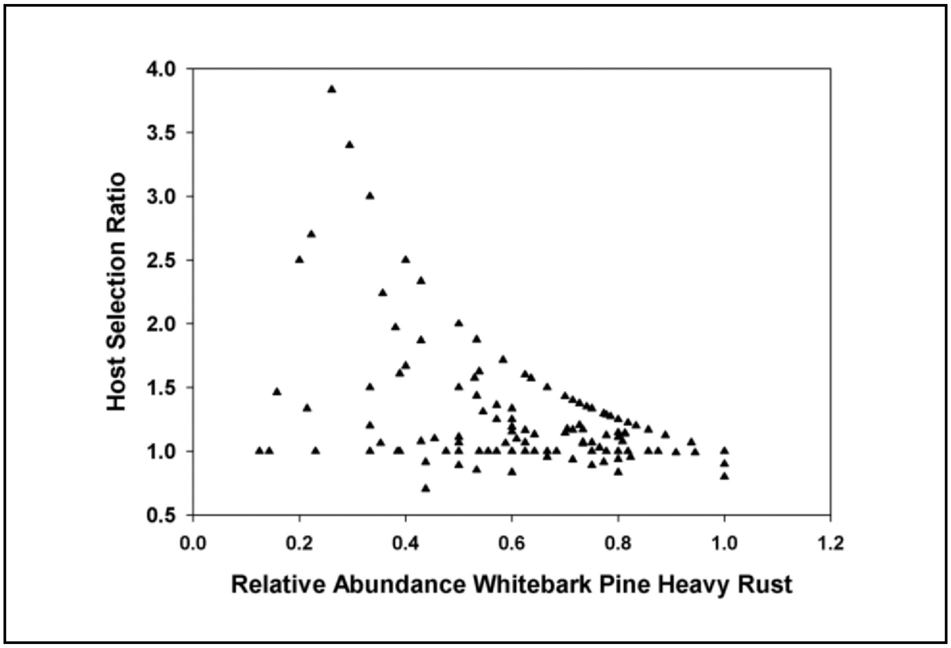

Figure 2. Host selection ratios plotted against the relative abundance of whitebark pine with heavy blister rust (whole tree rust severity 2-4) for all plots at Breccia Peak, Mount Leidy and Teewinot (total plots, n = 143).

significant variable, with the probability of selection as a host greatest for trees with heavy rust and lowest for those with light rust. The influence of tree diameter varied with stand type; at smaller diameters, host selection probability was greatest for trees in PURE stands. This relationship was reversed at larger tree diameters, where trees in MIX stands had greater probability of selection as a host to MPB. Probability of selection by MPB increased as tree diameter increases from 15 cm to approximately 65 to 85 cm and then decreased after 85 cm dbh (Figure 3).

DISCUSSION

Current Stand Conditions and the Influence of WPBR/MPB Interactions

It is evident that many whitebark pine forest systems in the western United States are in serious decline (Keane et al. 1994; Tomback and Kendall 2001; Zeglen 2002; Raffa et al. 2008; Smith et al. 2008; Tomback and Achuff 2010; this study). As anticipated, for whitebark pine stands within our study area, rates of mortality and WPBR infection are higher than prior surveys. Approximately one-half of all individual trees sampled were dead, excluding the most recently beetle-selected, green-needled whitebark pines which, when they die, will increase mortality to over two-thirds. Over 83% were symptomatic for WPBR, nearly two-thirds were afflicted with both MPB and WPBR (Table 3), and only ~50% of the trees were producing cones (data not shown). These data correspond with findings in other portions of the GYE (Macfarlane et al. 2009; GYWBPWG 2010) and are similar to, or slightly higher than, those reported from other areas in the western U.S. (Rochefort 2008; Smith et al. 2008; Larson 2011).

Our study identified a positive relationship between WPBR severity and MPB host selection for whitebark pine in our study sites in the southern GYE. Directional t-tests and HSR analysis both indicated that MPB preferentially selected whitebark pine with heavy blister rust infection over trees exhibiting less severe symptoms, regardless of their relative abundance in a stand. In fact, the mean rust severity scores of all whitebark pine selected as host trees by the beetle was nearly twice as high as that of trees not selected. Our probability of selection model further corroborated our HSR analysis, and suggests an interaction between MPB and WPBR is occurring.

Similar studies have also reported apparent interactions between WPBR and MPB. In Montana, Six and Adams (2007) also found that WPBR could be influencing the selection of whitebark pine trees by MPB, and they partially attributed this to a reduction in sapwood moisture content that may, in turn, lead to a reduction in tree defense capabilities. In a more recent study, Larson (2011) suggested that in whitebark pine stands where WPBR was severe prior to MPB outbreak, an interaction between MPB and WPBR could result in an amplification of the impacts of both disturbance types and increased losses of whitebark pine trees. Similarly, Ayres

Table 6. Global model parameters and fit statistics used in best subsets logistic regression procedure. Pearson's goodness of fit test: $\chi2$ = 26.40, df =26, p = 0.60. DBH2 term accounts for mountain pine beetle selection preference for mid-range tree diameters.

Variable	Coefficient (α)	SE Coefficient	Wal χ^2	Significan e
Constan1	-2.4181	0.351	-6.831	p < 0.0001
Rus1Severity	1.8721	0.181	9.981	p < 0.0001
Stland Type	1.5041	0.331	4.431	p < 0.0001
DB1	0.0691	0.01	5.141	p < 0.0001
DB1 [21]	01	0.0001	-2.971	p = 0.0031
Stland Type * DB1	-0.0221	0.0081	-2.71	p = 0.0071
S land Type * Rus1	-0.9581	0.231	-4.131	p < 0.0001

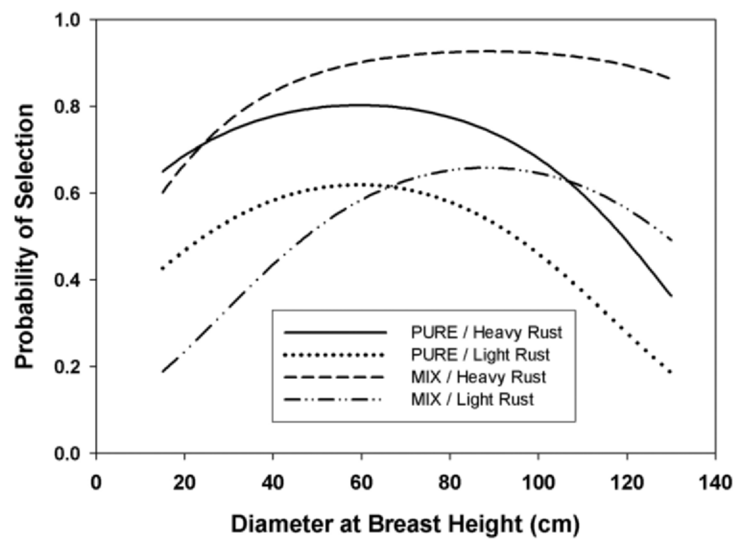

Figure 3. Probability of selection as a host by mountain pine beetle for an individual whitebark pine derived using a multiple logistic regression, represented as a function of diameter at breast height of tree.

and Lombardero (2000) suggested that widespread and severe WPBR infection rates may lead to increased availability of whitebark pine with decreased vigor on the landscape. However, in contrast to our findings, in northern Idaho, Schwandt and Kegley (2004) found that MPB seemed to prefer whitebark pine trees with little to no presence of WPBR, and suggested that at lower endemic levels, MPB may select whitebark pine trees with severe rust, but this selection pattern was reversed under epidemic population levels of MPB.

Multiple Whitebark Pine Characteristics Influence Beetle Selection

While the important role of WPBR in this ecosystem is illustrated by our findings (Figure 2), regression analyses also revealed complex relationships between other tree/stand characteristics and beetle selection. For example, while our findings partially support the conventional wisdom that mountain pine beetle host selection is based predominantly on tree dbh (Amman 1972; Amman and Schmitz 1988; Amman and Logan 1998), our results further suggest that the range of tree diameters preferred by the mountain pine beetle varies with both stand composition and blister rust severity, and that trees with smaller diameters may also be selected as a host by MPB (Figure 3). Larson's 2011 study in high-elevation whitebark pine stands also found that MPB selects trees of larger diameter, but that this selection may decline at the largest diameters, as our logistic regression model suggests. Notably, whitebark pines with larger dbh had lower selection probability in PURE stands than those in MIX stands. In these mixed stands, where the relative abundance of whitebark pine is lowest, trees with heavy blister rust have the greatest selection probability.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Our study quantifies that whitebark pine in our study sites that exhibit heavy blister rust infection are preferentially selected as hosts by MPB and that the interactions of WPBR and MPB will influence the patterns of intensity, severity, and extent of whitebark pine mortality. We also illustrate that due to interactions among variables, selection probability must be evaluated with multiple tree- or stand-characteristics. Specifically, combinations of tree diameter and stand type are significant indicators of host selection by MPB. In coming years and decades, these patterns will likely influence future stand structure, and could create a cascade of altered ecological functions, services, and processes, such as wildlife food resources, watershed quality, forest succession, and alpine vegetation biogeography and diversity that result from significant losses of whitebark pine ecosystems (Tomback et al. 2001; Logan et al. 2010). And, although we did not measure or quantify this, the interaction between MPB and WPBR identified in our study could contribute to the selective forces on whitebark pine and, in turn, the degree of rust resistance in future whitebark pine populations (Larson 2011). Identifying patterns of, and interactions among, disturbance agents such as MPB and WPBR will promote the appropriate assessment of these changes in ecosystem function and process, and inform management activities. Therefore, we suggest three management implications that have emerged from this study: (1) Losses of whitebark pine trees to MPB caused-mortality and blister rust infection and severity are high in the southern GYE, and continued monitoring of these trends is highly recommended; (2) During the beginning and middle portions of MPB outbreaks, whitebark pine with heavy blister rust infection are likely to be preferentially selected as hosts by MPB; and (3) When making predictions regarding the likelihood of tree selection by MPB, tree diameter measurements should be combined with additional stand characteristics, the presence and severity of WPBR, and MPB population levels.

SUGGESTIONS FOR FURTHER RESEARCH

It is important to note that the ecological relevance of our findings is limited to our study sites in the southern Greater Yellowstone. Variation in elevation, topography, soils, disturbance history, MPB outbreak phase, and climate patterns may limit this study's applicability. However, on an individual tree-level, the relationship between blister rust and beetle host selection patterns is likely universal within this region.

Although our research has quantified several relevant areas of whitebark pine ecology previously not well understood, we can explain only a portion of host tree selection patterns by MPB by the variables in this study; clearly, many areas of importance remain. We suggest future analyses that include more mechanistic properties in the following research areas: (1) phloem nutritional quality and quantity; (2) phenolic compounds available for pheromone production; (3) MPB productivity and survivorship – brood and individual beetle size and nitrogen composition; (4) host tree chemical defense composition; and (5) examination of the role of WPBR on MPB physiology and population dynamics. In addition, improving our understanding of the variation in successional pathways among different whitebark pine stand types, and describing the genetic composition of whitebark pine populations prior to and following MPB outbreaks, is equally important. Extensive evaluations of both historic and current disturbance patterns and subsequent whitebark pine ecosystem responses are vital to developing proper management strategies that ensure the sustainability of these foundation forest systems.

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