Project Title: Reciprocal interactions between bark beetles and wildfire in subalpine forests: landscape patterns and the risk of high-severity fire.

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ABSTRACT

The interactions of wildfire and bark beetle outbreaks and their reciprocal influences on fire behavior, bark beetle dynamics, and ecosystem structure are critical research issues in many coniferous forests of the Intermountain West. We combined field studies with new remote sensing methods to address three main questions regarding the recent bark beetle outbreak in the Greater Yellowstone Ecosystem (GYE): (1) What are the current patterns of beetle outbreaks in the GYE, and what broad- and fine-scale factors explain these patterns? (2) How do bark beetle outbreaks influence the probability and severity of wildfire, and how does post-disturbance biomass recovery differ between bark beetle outbreaks and wildfire? (3) How does the pattern of fire-damaged trees influence the pattern and severity of current and future MPB outbreaks?

For Question 1, our field studies revealed that in both lodgepole pine and whitebark pine stands, bark beetle damage was best explained by the ratio of large to small stems of host trees, with higher damage associated with a greater proportion of larger stems. In Engelmann spruce stands, beetle damage was negatively related to elevation, whereas in Douglas-fir stands, it was positively related to the proportion of host tree basal area in the stand. Remote sensing analyses indicated that approximately 55% of the area in mature conifer forest in the GYE showed evidence of tree mortality attributable to bark beetles: 10% of high-severity beetle kill (> 40% basal area killed), 17% of moderate-severity beetle damage (20% to 40% basal area killed, and about 27% of low-severity beetle kill (< 20% basal area killed). This substantial variation in severity of the beetle infestation severity created a spatially heterogeneous, fine-grained mosaic, with patches of high-severity beetle kill distributed widely across the landscape. The total area with moderate or high severity damage, while still considerable (27% of conifer forest cover), is nevertheless lower than popular perception, and still generally affects less than half the live basal area within the stand. Our analyses of fine-scale factors influencing mountain pine beetle activity in whitebark pine stands identified preferential host selection for whitebark pine that was symptomatic for white pine blister rust. Furthermore, whitebark pine trees were selected first by the mountain pine beetle and were selected in greater proportions than lodgepole pine. For whitebark pine, our findings do not support the conventional premise that mountain pine beetle host selection is based predominantly on tree DBH, but rather that the range of tree diameters preferred by the mountain pine beetle varies with both stand composition and blister rust severity.

For Question 2, fuels analyses in a chronosequence of sites that varied by time-since-beetle attack indicated that there was no difference in dead surface fuel loads of all size categories (1-hour to 1000-hour timelag fuels) between undisturbed, red-stage, and gray-stage stands, although forest floor needle litter in the red-stage sites (depth = 2.8 cm) was twice as deep as in the undisturbed sites (depth = 1.4 cm), with gray-stage sites having an intermediate value. Compared to undisturbed sites, red- and gray-stage sites had a lower canopy bulk density (0.065 kg/m^3, compared to 0.14 kg/m^3), a lower available canopy fuel load (8.7 tonnes/ha, compared to 15 tonnes/ha), and a lower canopy moisture content (78% compared to 100%). In older sites, coarse wood (1000-hour fuels) load doubled, from 40 to about 80 tonnes/ha, and needle litter and duff layers decreased by 50% and 60%, respectively. Simulation results suggested that in the short term, undisturbed, red, and gray stands were unlikely to allow transition of surface fires to tree crowns (torching) due to a lack of ladder fuels, and that the

ability to sustain an active crown fire (crowning) decreased from the undisturbed, to red and gray-stage stands, probably as a result of reduced canopy bulk density. Simulated fire behavior was little affected by forest structure when wind speed was either below 20 km/h or above 60 km/h. Under low wind speed conditions, most stands were predicted to have relatively slow moving surface fires, whereas at very high wind speeds, all stand types eventually achieved active crown fire. However, at intermediate wind speeds (about 40 to 60 km/h), fire hazard in the red and gray-stage stands was significantly lower than undisturbed stands, suggesting that beetle outbreaks may reduce probability of active crown fires in the short term (1-5 yrs). Preliminary results using a novel hybrid approach that combines a chronosequence and a time-series analysis to estimate biomass recovery following disturbance do not support the hypothesis that recovery was faster following beetle outbreak than after stand-replacing fire, which was surprising. Twenty years after fire or beetle outbreak, total biomass remained below pre-disturbance levels in both types of stands, and post-beetle stands typically contained more total biomass than burned stands; however, the slope of the curve relating biomass to time-since-disturbance was steeper for burned stands than for beetle-affected stands.

For Question 3, we found that mountain pine beetles were more likely to colonize lodgepole pine trees that had been injured by fire than those that had not. However, reproductive success was often lower in severely fired-injured trees due to interspecific competition incurred by mountain pine beetle intensifying with fire injury, indicating that fire injury was unlikely to trigger a bark beetle eruption. More trees that were highly scorched were colonized by wood borers and *Ips* sp. than were trees with moderate or low fire injury. Also, the population size of mountain pine beetles appeared to contribute to the colonization of fire-injured lodgepole pine trees. The ratios of fire-injured to non-fire-injured trees attacked were larger in sites where beetle populations were endemic than in sites where the beetle populations were epidemic.

Incorporating understanding of large and severe natural disturbances such as crown fires and bark beetle infestations into forest management continues to pose significant challenges for forest managers and the public. Because these disturbances kill many trees and cause rapid and extensive changes in the forests, there can be considerable pressure to “do something” to save the forests and minimize subsequent risks. Our results illustrate the highly complex nature of these disturbances, both individually and reciprocally, and that specific management prescriptions must be carefully considered and implemented at local scales, and then only when appropriate. A key conclusion from this and other studies is that although individual *trees* are killed, lodgepole pine *forests* in Greater Yellowstone have not been “destroyed” either by recent fires or bark beetle outbreaks. Our findings suggest that, in contrast to conventional wisdom, bark beetle infestations likely reduce the subsequent risk of active crown fire, and fire-damaged trees are unlikely to produce a subsequent bark beetle epidemic.

BACKGROUND AND PURPOSE

The interactions of wildfire and bark beetle outbreaks and their reciprocal influences on fire behavior, bark beetle dynamics, and ecosystem structure are critical research issues in many coniferous forests of the Intermountain West. Forest managers in the western US are now confronted with more fires and the most extensive bark beetle outbreaks recorded for the region. Changing disturbance regimes—especially fire and insect outbreaks—will have tremendous ecological and economic effects in western forests. Should current climate trends continue, the occurrence and severity of both fire and beetle epidemics may increase, highlighting the importance of increasing our understanding of how the reciprocal effects of these two disturbances interact.

Landscape-scale studies that identify spatial patterns of disturbance interactions between fire and insect outbreaks are relatively rare, but are receiving increasing attention (e.g., Knight 1987b; Parker and Stipe 1993;Veblen et al. 1994; Fleming et al. 2002; Bebi et al. 2003, Bigler et al. 2005; Page & Jenkins 2007a, 2007b, Jenkins et al. 2008). It is widely believed that insect outbreaks increase the probability for catastrophic wildfires because they create great quantities of dead fuels (e.g., Geiszler et al. 1980, Schmid and Amman 1992, McCullough et al. 1998, Parker et al. 2006). This idea has received surprisingly little rigorous testing, however, and results have been mixed among various beetle-host systems and time since beetle disturbance (McCullough et al. 1998, Knight 1987a, Simard et al. 2008a). Using spectral analysis, Fleming et al. (2002) reported an increased probability of fire 3-9 years after spruce budworm (*Choristoneura fumiferana*) outbreaks in central Canadian forests, but the probability of fire was not continuously elevated. Turner et al. (1999) found that the likelihood of crown fire in lodgepole pine forests of Yellowstone National Park (YNP), 5-17 years after mountain pine beetle (MPB; *Dendroctonus ponderosae*) outbreaks, was increased where beetle-caused mortality had been high, but was reduced where mortality was only moderate. Lynch and Moorcroft (2005) identified a small but significant interaction between the 1988 fires in Yellowstone National Park (YNP) and the beetle outbreaks of the 1970s. They found that locations affected by MPB in the 1970s were 11% more likely to have burned during the 1988 fires compared to areas not infested during that time. In spruce-fir forests of western Colorado, following a large fire in 2002, Bigler et al. (2005) found that stands affected by a spruce beetle (*D. rufipennis*) outbreak in ca. 1950 had an increased probability of burning in 2002 -- but the increase was slight, and was overshadowed by characteristics of stand structure unrelated to the beetle outbreak. Notably, there had been no large or severe fires in the stands affected by the ca. 1950 beetle outbreak until 2002, when fire weather conditions were extreme (Kulakowski et al. 2003, Bebi et al. 2003). Page and Jenkins (2007a) directly measured fuels distributions in lodgepole pine forests affected by mountain pine beetle, and found increased fine surface fuels ≤5 yrs after outbreak, and increased coarse woody fuels 20 yrs after outbreak. Subsequent modeling suggested that these changes in fuel loading would increase surface fire rate of spread, fireline intensity, and total heat release, but active crown fires would be reduced due to declines in aerial fuel continuity (Page and Jenkins 2007b; Jenkins et al. 2008). Derose and Long (2009) obtained similar modeling results for Engelmann spruce forests affected by spruce bark beetle, predicting a decline in the probability of active crown fire lasting up to 20 years.

Two key ideas emerged from the previous research. First, insect outbreaks appear to affect both the probability of fire occurrence and the severity of the fire when it occurs -- but these two parameters respond both to the severity of the insect outbreak and to ambient weather conditions when fire occurs. Second, the effects of an insect outbreak on subsequent fire occurrence and severity vary with time since the outbreak. Schmid and Amman (1992) proposed that there may be two periods when the probability of high-severity fire is increased: (1) during the first few years post-outbreak, while dead trees still retain flammable dead needles, and (2) approximately 50 years post-outbreak, when heavy surface fuels have accumulated through fall of beetle-killed trees and understory trees that survived the outbreak have reestablished a dense canopy. During the intervening period of several decades, the probability of severe fire actually may be reduced because of discontinuity of the canopy. Because active crown fires are the ones that burn the largest areas and are most hazardous to human values (e.g., homes) in lodgepole pine and similar coniferous forests (Johnson 1992, Turner and Romme 1994), managers urgently need a better understanding of how insect outbreaks actually affect the probability of these kinds of fires and of how that probability changes over time after an outbreak. Our research addressed these key knowledge gaps by quantifying beetle outbreaks in the Greater Yellowstone Ecosystem (GYE) and the subsequent probability of severe fires.

Opinions on whether fire-damaged trees are more likely to serve as hosts for beetle infestation also vary widely. Amman (1991a, b) reported that wildfire predisposes lodgepole pine trees to outbreaks of MPB. Conversely, Rasmussen et al. (1996), in their study of fire-injured trees in and near Yellowstone National Park, found that injury from the fires of 1988 did not result in higher beetle infestation rates, and that most delayed mortality of lodgepole pine was due to the injury sustained by the fires. At the stand level, controlled studies on whether bark beetle outbreaks occur after fires have yielded highly variable results that both support (Bradley and Tueller 2001, McHugh et al. 2003, Wallin et al. 2003) and fail to support this possibility (Santoro et al. 2001, Sullivan et al. 2003, Elkin and Reid 2004, Lombardero et al. 2006). There have also been numerous reports of bark beetle outbreaks following fires (reviewed by McCullough et al. 1998, Parker et al. 2006), but these were largely studies to detect insect damage. These reports generally suggest a relationship between fire and subsequent bark beetle outbreaks, but often do not provide the data necessary for comparing bark beetle damage between similar burned with unburned sites. Notably, we have found no studies that evaluate the differences in extent and severity of disturbance interactions that involve multiple species of beetles, as well as multiple tree species within the same landscape. The recent outbreak in the GYE involved multiple species of both beetles and trees, and provided an ideal opportunity to study broad-scale, complex disturbance interactions.

Recent advances in remote sensing make it possible to map important spatially explicit variables associated with insect dynamics, including: tree species composition (Townsend and Walsh 2001, Foster and Townsend 2004), age structure (Cohen et al. 1995, Cohen and Fiorella 1998, Cohen et al. 1998), and damage caused by outbreaks of pests (Goodwin et al. 2008). Although remote sensing has long been used to identify areas of land use change (e.g., Lambin and Strahler 1994, Lunetta and Elvidge 1998) and forest disturbance in general (e.g., Hall et al. 1991, Collins and Woodcock 1996), numerous recent studies have focused in particular upon the use of remote sensing imagery to map areas of change due to insect activity (Luther et al. 1997, Chalifoux et al. 1998, Allen and Kupfer 2000, 2001). Specifically, several studies have

demonstrated the capacity of Landsat imagery to map damage and mortality from mountain pine beetle attacks (Ahern 1988, Franklin et al. 2003, Skakun et al. 2003; Wulder et al. 2006a, 2006b, Goodwin et al. 2008). These techniques provided a foundation from which we developed new algorithms for mapping spatial patterns of the recent beetle outbreak in the GYE.

Our study addressed three main questions: **Question 1: What are the current patterns of beetle outbreaks in the GYE, and what factors explain these patterns?** We used field studies and new remote sensing methods to map the broad-scale patterns and time course of current beetle outbreaks in the GYE, and identify the biotic and abiotic factors that explain these patterns. In addition, we investigated how fine-scale variation in stand characteristics such as the occurrence of other pathogens and the presence of mixed conifer stands are influencing the susceptibility of trees to beetle infestation. **Question 2**: **How do MPB outbreaks influence the probability and severity of wildfire?** As stated earlier, it is widely believed that the probability of severe fire is elevated following beetle outbreaks and remains high until the next stand-replacing fire. We suggest that the increased probability of fire, if present, is transient, and the longer-term influence of tree mortality may reduce the likelihood of severe fires or at least create substantial variability in fire probability for an extended time. Also, we examined how disturbance type (fire vs. bark beetles) influences post-disturbance rates of vegetation biomass recovery in the GYE. **Question 3: How does the pattern of fire-damaged trees influence the pattern and severity of MPB outbreaks?** More specifically we asked, a) Are MPB more likely to colonize lodgepole pines that have been injured by fire?; and b) Among those trees that are colonized, what is the reproductive success of MPB in fire-injured vs. healthy trees?

STUDY DESCRIPTION AND LOCATION

Study description. Detailed descriptions for each of our primary objectives and questions are included below in the "Key Findings" section of this report.

Study area. Our study was conducted in the GYE, and focused especially on Yellowstone and Grand Teton National Parks and two National Forests bordering to the east—Shoshone NF and Bridger-Teton NF. The GYE is characterized by extensive subalpine forests dominated by lodgepole pine (*Pinus contorta* var. *latifolia*), but includes whitebark pine (*Pinus albicaulis*), subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmanii*) and Douglas-fir (*Pseudotsuga menziesii*). Fire has long played an important role in this landscape, with stand-replacing fires occurring at 100-500 yr intervals throughout the Holocene (Romme 1982, Millspaugh et al. 2000). Native phloem-eating insects, including mountain pine beetle, have also been a key element of this system. Insect outbreaks have been recorded since 1922 (Furniss and Renkin 2003). Recent fires (1988 through present) and the current insect infestation (1997 through present) set the stage for the studies described here.

KEY FINDINGS

Question 1: What are the current patterns of beetle outbreaks in the GYE, and what factors explain these patterns?

Rationale. Native bark beetles periodically affect the GYE's forests, and in the last five years, three species of bark beetles have been at high outbreak levels: the mountain pine beetle, which attacks both lodgepole pine and whitebark pine; the spruce beetle, which feeds on Engelmann spruce; and the Douglas-fir beetle (*D. pseudotsugae*), which is found on Douglas-fir. Although infestations primarily occur in mature stands, the complete suite of factors that explain the presence and severity of bark beetle damage are unknown. The current infestation offered a window of opportunity for quantifying and explaining the spatial-temporal patterns of beetle activity in the GYE. We determined the relative importance of these factors in explaining and predicting the current outbreak and characterized these patterns in the GYE at both broad (*Question 1a*) and fine (*Question 1b*) spatial scales.

(Q1a) *What are the* ***broad-scale*** *spatial distributions of current beetle outbreaks in the Yellowstone landscape, and what factors explain these distributions?*

The broad-scale patterns of beetle infestations may respond to a variety of factors, including tree community composition; stand density, basal area, tree size, age structure as generated by past fires; proximity to current beetle activity; and abiotic factors (e.g., elevation, slope, aspect, and substrate) that may influence drought stress on trees. We used field studies to determine the factors that explained the broad-scale patterns of damage and mortality caused by the three species of bark beetles and remotely sensed data to map the spatial distribution of bark beetle damage in the GYE.

Field studies

Methods. We used broad-scale surveys to select lodgepole pine, whitebark pine, Douglas-fir and Engelmann spruce stands that were either severely or lightly damaged by bark beetles (4 host species x 2 damage classes x 8 replicates = 64 stands; Figure 1). All selected stands were susceptible to beetle damage (i.e., > 100-yr-old and a high basal area of host species) and located in a relatively homogeneous area of at least 1 ha. In each stand, we established 0.25-ha plots in which we measured (1) forest attributes (tree composition, mortality, serotiny for lodgepole pine); (2) stand structure (tree dbh, diameter, and age); (3) bark beetle presence (galleries, pitch tubes, boring dust, etc.) and damage (red needles, beetle-caused mortality); (4) soil characteristics (organic layer depth, mineral soil texture and nutrient concentrations); and (5) site conditions (elevation, slope, aspect, Site Index, surficial deposits, etc.). All sites were sampled in summer 2006. From these data, we compiled absolute and relative basal area of host species and the ratio of large to small trees (cutoff = 25 cm) to represent the relative importance of large-diameter trees in the stands. We used logistic regression to relate bark beetle damage (low vs. high severity) to the explanatory variables for each species of beetles.

Results. Overall, severity of bark beetle damage (relative basal area beetle-killed) ranged from 0 to 26% in the lightly damaged stands, and from 45 to 98% in the high-severity stands. For each species, the average percent basal area beetle-killed was as follows: lodgepole pine, 4% (range = 0-12%) for low severity and 67% (range = 50-79%) for high severity; whitebark pine, 7% (range = 0-17%) for low severity and 78% (range = 65-91%); Engelmann spruce, 6% (range = 0-26%) for low severity and 88% (range = 73-98%) for high severity; and Douglas-fir,

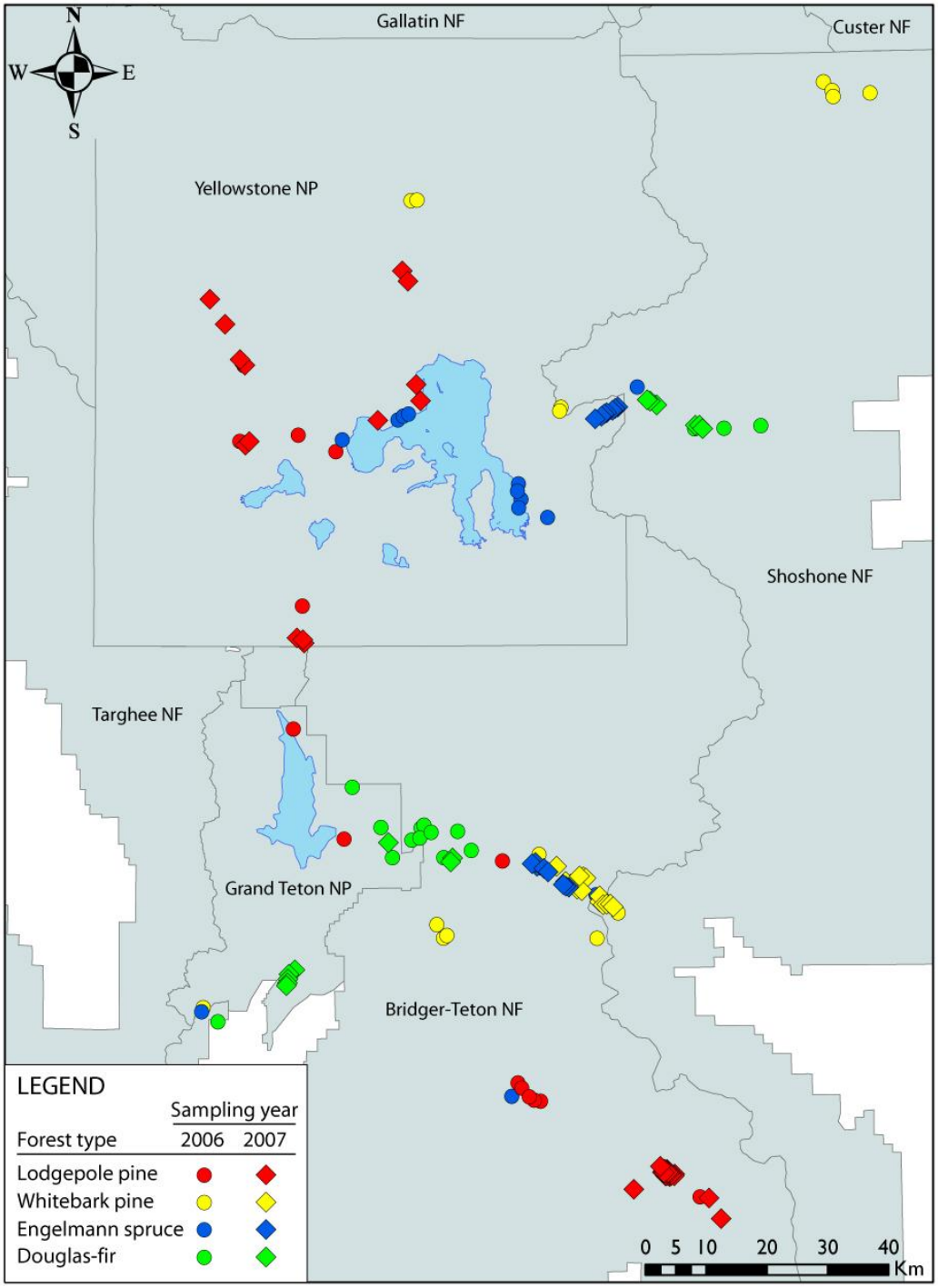

Figure 1. Location of sites sampled in 2006 (circles) and 2007 (squares) for Question 1A.

3% (range = 0-12%) for low severity and 73% (range = 45-86%) for high severity. Beetle damage in both lodgepole pine (P = 0.0105) and whitebark pine (P = 0.0112) stands was best explained by the ratio of large to small stems of host trees, with higher damage associated with a greater proportion of larger stems. In Engelmann spruce stands, beetle damage was negatively

related to elevation (P = 0.0092), whereas in Douglas-fir, it was positively related to the proportion of host tree basal area in the stand (P = 0.0199).

ADDENDUM: During the summer of 2007, we sampled an additional 56 sites (14 sites per host tree species; Figure 1), bringing the total number of sites to 120. We will re-analyze the data with these additional sites and add to the analysis variables that represent landscape context, i.e., the characteristics of the landscape surrounding the sampled stands. Potential landscape context variables (calculated for a certain radius around each site) include proportion of mature forest, proportion of area dominated by host species, proportion of mature host forest, etc.

Discussion. Our 2006 data indicate that in the pines and Douglas-fir forest types, beetle damage was proportional to the abundance and size of the host tree species. This is not surprising, as bark beetle reproductive success is related to the abundance of its food source, and large-diameter trees have a thicker phloem. In Engelmann spruce, beetle damage was lower at high elevations, which could be a direct effect of temperature on beetle development rate, or an indirect effect through the persistence of the snowpack in the spring. Unlike the Douglas-fir and mountain pine beetles, the spruce beetle overwinters in the forest floor and therefore is dependent on the timing of snowmelt for its emergence and development.

These statistical relationships could change, however, with inclusion of the additional sites sampled in 2007 and the landscape-level variables. We noted in the field that some lightly damaged stands were isolated from large tracts of susceptible forest, either because they were in a matrix of non-host species or surrounded by young forests. This was the case for lodgepole pine in Yellowstone National Park, where young stands that established after the 1988 fires are abundant and often surround unburned patches of susceptible forest. If this trend proved to be significant, it would mean that fire could reduce susceptibility of the remaining unburned forest to bark beetles not only by reducing the area of susceptible forest, but also by fragmenting it.

Remote Sensing Studies

Methods. To complement the plot-based field studies, we used remotely sensed data to map the magnitude, spatial patterns and temporal trend of the recent concurrent beetle outbreaks, including mountain pine beetle, spruce beetle and Douglas-fir beetle. A 9-year (1999-2007) time series of Landsat imagery (Table 1) was employed to estimate the probability that each pixel was disturbed on a yearly basis. The probability map for each year was developed from the difference image of Moisture Stress Index (MSI: Landsat band 5/band 4, (Hunt and Rock 1989) between a disturbance year and a base date (1999) using the normalized distribution of spectral data for the larger study area.

The specific analytical process involved calculation of vegetation indices related to disturbance followed by differencing of pre- and post-disturbance images, computation of a Z-score for the distribution of differences, and association of the resulting Z-score with its two-tailed probability of difference from the mean (P-value; Jin et al. in prep[*]) We initially tested several vegetation indices in addition to the MSI, including NDVI, the simple vegetation index, the normalized

[*] Draft complete. Submission expected for 28 September 2009.

difference moisture index (NDMI, Jin and Sader 2005), and the Disturbance Index (Healey et al. 2006). All indices performed moderately well, with MSI performing most consistently across images and across years (Jin et al., in prep). We detected the initial year of attack as the year in which an increased value of the MSI was sustained in subsequent years (Figure 2).

The MSI difference values (disturbance year minus base year) were related to field measurements of beetle damage collected during the summers on 2006 and 2007 to develop equations to map beetle damage on a continuous scale (Figure 3). Thus, an innovation of our approach is the ability to map the severity of the infestation, not simply whether there is beetle attack or not. There was a strong linear relationship between the MSI difference index and beetle-caused mortality represented by either absolute (m^2 ha^{-1}) or relative (%) basal area killed within a stand (Figure 3). This suggests that we can successfully map a continuous measure of beetle damage across the landscape.

Table 1. Characteristics of the Landsat imagery used to address Question 1(a).

Acquisition date	Day of year	Sun elevation (°)	Path / Rows (WRS-2)	Landsat sensor
9/15/1999	258	45.2	038 / 029-030	Landsat 7 ETM+
7/2/2001	183	61.74	038 / 029-030	Landsat 7 ETM+
7/29/2002	210	55.93	038 / 029-030	Landsat 5 TM
8/1/2003	213	55.67	038 / 029-030	Landsat 5 TM
7/21/2005	202	59.06	038 / 029-030	Landsat 5 TM
8/9/2006	221	55.92	038 / 029-030	Landsat 5 TM
8/28/2007	240	50.88	038 / 029-030	Landsat 5 TM

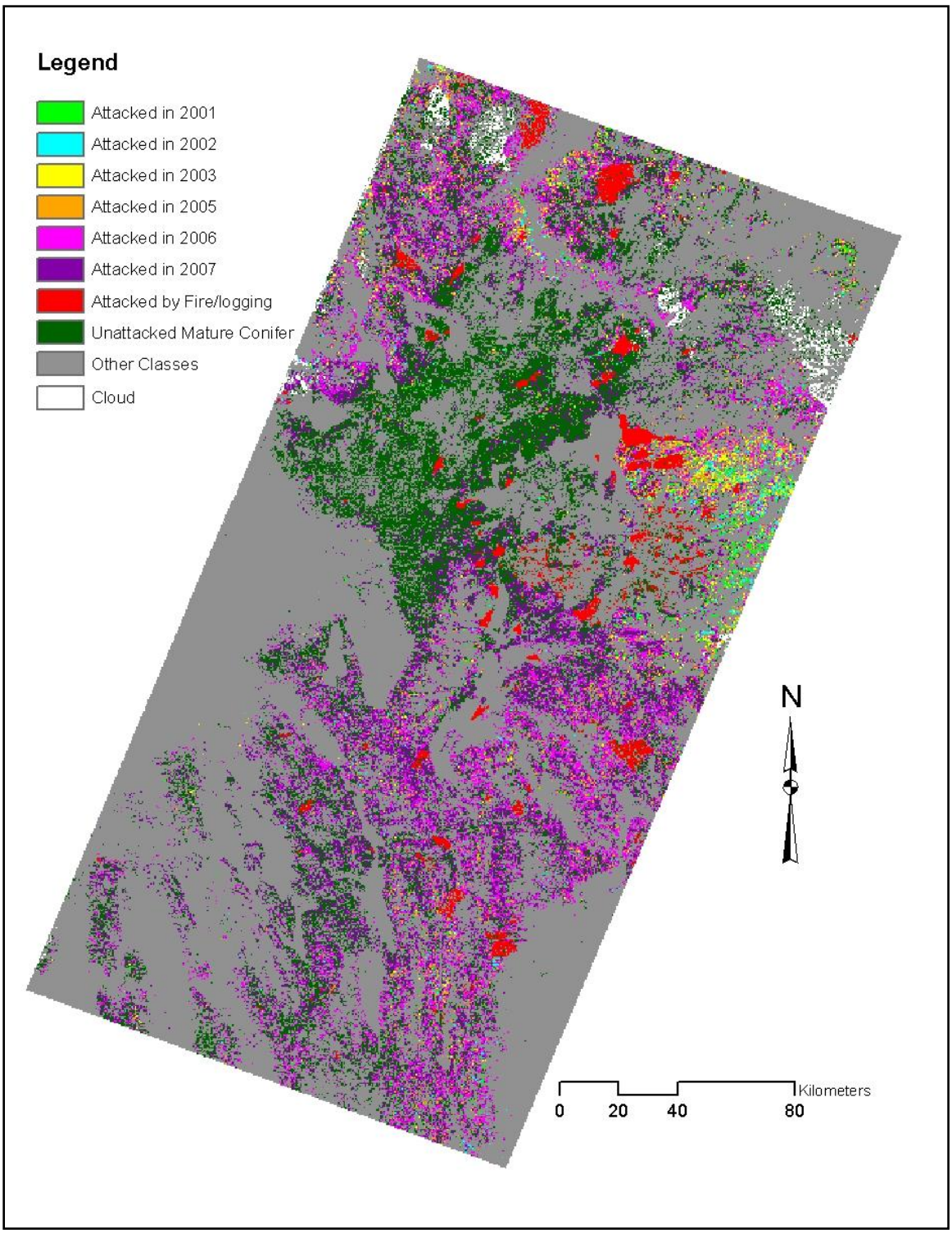

Figure 2. Temporal pattern of initial year of attack by bark beetles as determined from remotely sensed data. Dark green areas are unattacked forests (i.e., no increases in Moisture Stress Index, MSI). Note that some areas marked as attacked in 2006 and 2007 (magenta and red) are mapped as such because they exhibited increases in MSI. If those increases were not sustained in images from subsequent years, then those areas may switch to being mapped as not attacked (see also Figure 4.)

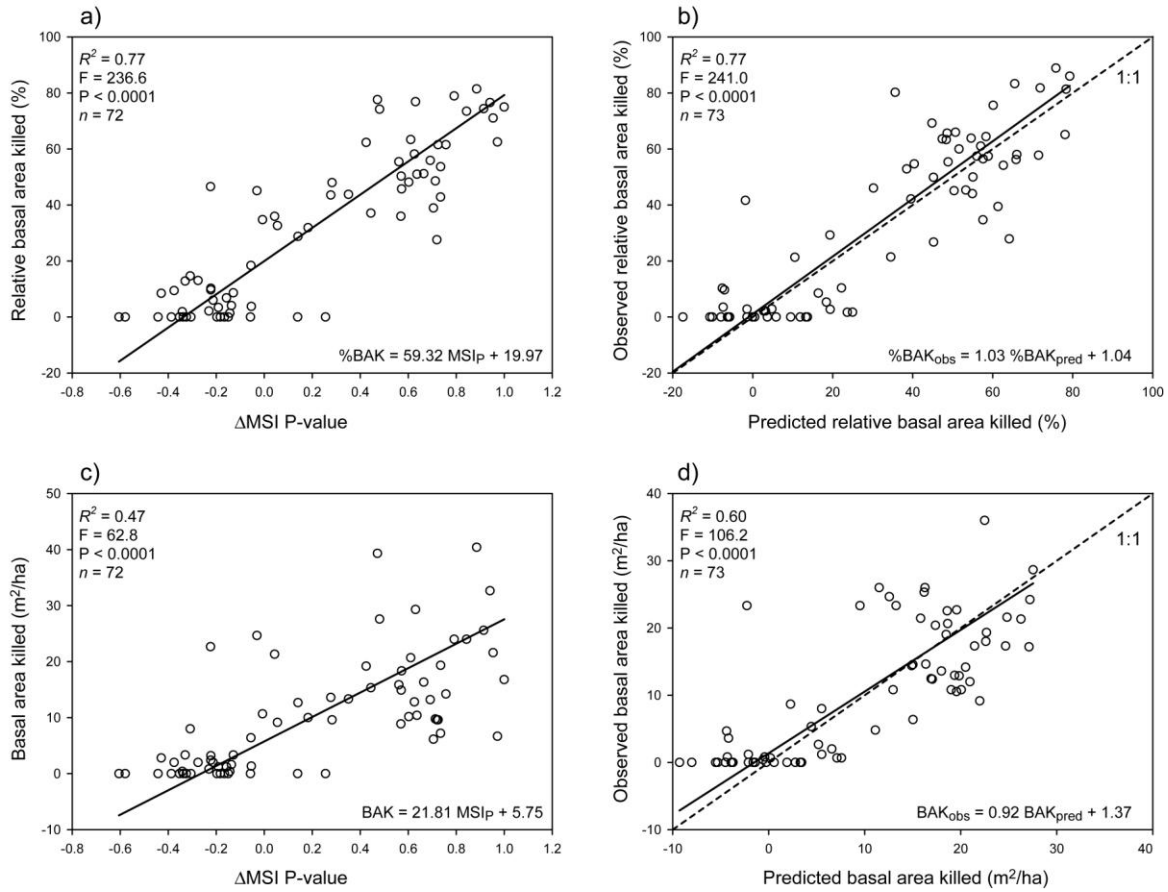

Figure 3. Relative basal area beetle-killed and total basal area beetle-killed (2007) showed linear relationships between field data and the remote sensing change index, ΔMSI (a, c). Validation using independent data held aside from model development (b, c) confirmed the strong relationships.

Before producing the final map of percent basal area of conifer forest killed by beetles, we removed from the Landsat images all known forest disturbances other than bark beetles that occurred between 1999 and 2007. We masked harvested areas using GIS layers from the US Forest Service, and forest fires were masked based on fire perimeter data from the National Park Service, US Forest Service, MODIS Active Fire products (USDA Forest Service 2008), and Landsat dNBR (differenced Normalized Burn Ratio, Key and Benson 2006) maps available online (NPS-USGS 2008) or produced by us (Figure 4). Cloud cover was also masked. Using relationships between MSI (from Landsat imagery) and field measurements, we mapped total percent beetle damage for the entire study area for 2007. The resulting final map for 2007 depicts the spatial pattern of beetle infestation throughout Greater Yellowstone (Figure 5).

Within the study landscape, our analyses indicated that mature conifer forests encompassed 2,340,387 ha (Table 2). Approximately 55% of the area in mature conifer forest showed evidence of tree mortality attributable to bark beetles: 10% of high-severity beetle kill (> 40% basal area killed), 17% of moderate-severity beetle damage (20% to 40% basal area killed, and about 27% of low-severity beetle kill (< 20% basal area killed; Table 2). Disturbance severity was spatially heterogeneous and appeared as a fine-grained mosaic, with patches of high-severity beetle kill distributed widely across the landscape (Figure 5). Our work provides a spatial

representation of the results from the plot-based field study. The total area with high severity damage, while still considerable (27% of conifer forest cover), is nevertheless lower than popular conception. However, with ongoing mortality (which our group will continue to map), we do expect the area or mortality to increase in the short term.

Discussion. The remote sensing work has provided considerable insight into the dynamics of mountain pine beetle infestation in the Greater Yellowstone Ecosystem. For the current infestation (starting in the late 1990's), the spread of forest damage has shown a distinct spatial pattern based on the onset of mortality within stands. Mortality from beetle attacks generally appeared first on east-facing and steep slopes, then expanded from the valleys upslope, i.e. from steep to moderate to gentle slopes. Mortality was highest in the east and southeast of the GYE, with considerably less mortality in the west, areas that were affected significantly by outbreaks in the 1970's and 1980's. In addition, the pace of mortality (i.e., extent and the level of damage) increased at a relatively constant rate in the early 2000's, with mortality expanding rapidly starting in 2005.

From our analyses, we can postulate a generalize landscape ecology of the current mountain beetle infestation in the GYE. It is clear that at a certain point, beetle populations are high enough that most forests with suitable host within an infestation zone will experience at least some mortality. Moreover, the forests that were previously attacked within the last 40 years (predominantly lodgepole pine forests) are less susceptible to beetle attack, probably because of reduced availability of large-diameter stems in previously attacked stands. Finally, the patterns of the spread in mortality are also informative. Mortality appears to occur first on east-facing and steeper slopes, presumably because of drier conditions and greater overall environmental stress on trees in such locations. Warmer temperatures in the valleys may also serve to keep a lower overwinter larval mortality compared to higher elevations. Once beetle populations reach infestation levels within stressed stands where the trees are least able to withstand mass attacks, the beetle populations may have expanded upslope into cooler climates and the gentler (more mesic) slope conditions where tree resistance to beetle attack may be higher because of lower environmental stresses. This would also suggest that by the time moderate and gentle slope areas show signs of mortality from beetles, the beetle populations have already reached the epidemic levels likely to lead to mass mortality. This work provides no insight into the effects of climate on the current outbreak, which is hypothesized to be related to warmer climate and ongoing drought. However, our results do support the hypotheses that landscape factors related to local climatic gradients do affect the timing and spread of beetle-related mortality.

The approach we have taken consists of a generalizable suite of methods that managers can implement using existing software and data to rapidly track beetle-related mortality using cost-efficient and spatially comprehensive data.

Table 2. Area of the Greater Yellowstone study in different classes of bark-beetle severity as mapped from Landsat imagery for 2007. See text for methods.

Class	Area (ha)	Percent of landscape	Percent of conifer forest only
Beetle damage ≤ 20%	633,614	10.1	27.1
Beetle damage, 21 to 40%	398,598	6.4	17.0
Beetle damage > 40%	243,910	3.9	10.4
High damage fire and logging*	119,488	1.9	5.1
Undamaged mature conifer forest	944,777	15.1	40.4
Subtotal conifer forest	2,340,087	--	100.0
Open water	89,652	1.4	--
Other forest types	239,2124	38.3	--
Other land-cover classes	143,0657	22.9	--
Total	6,252,821	100.0	--

*Total area logged was relatively small (3,061 ha) and was combined with fire when depicted in Figure 4.

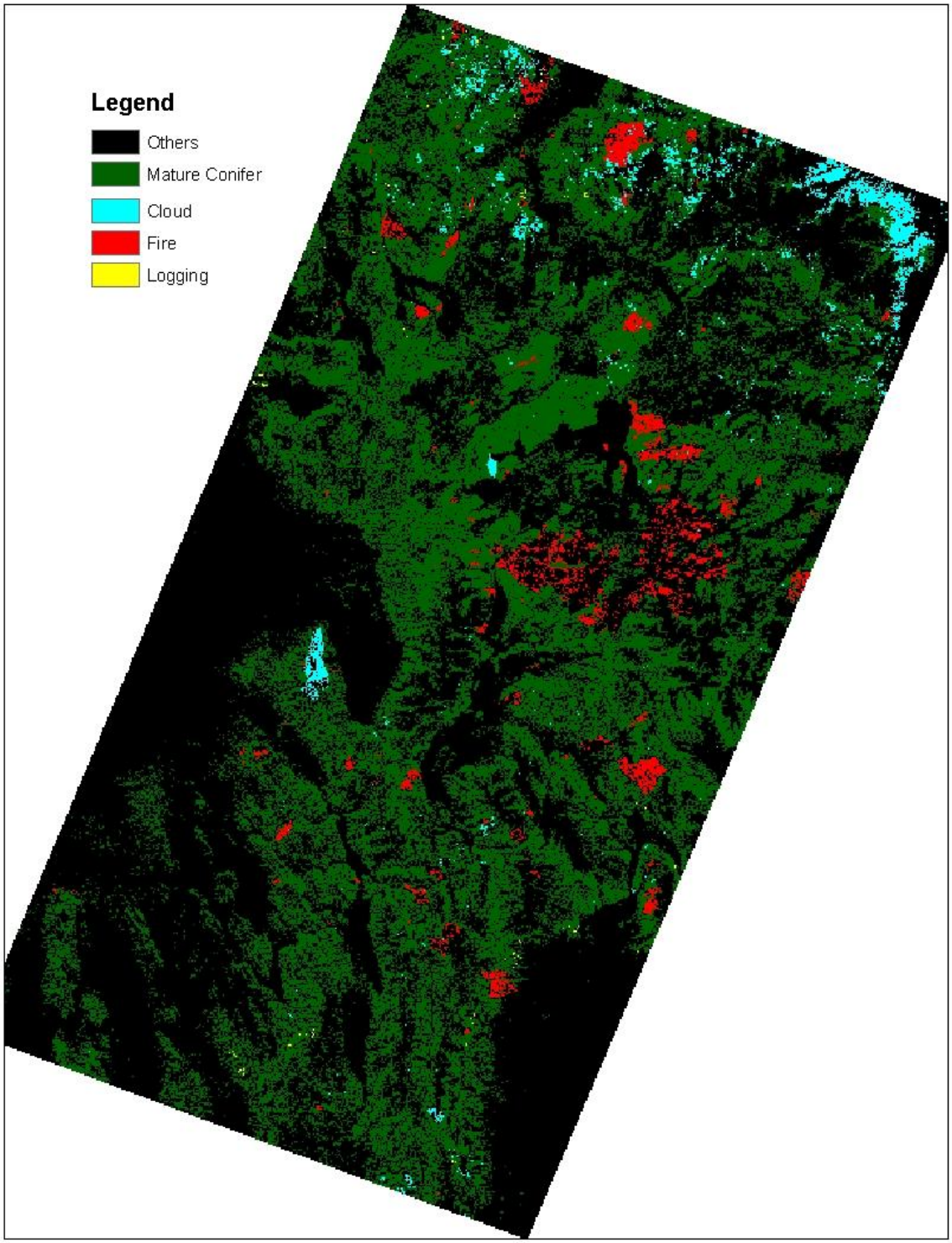

Figure 4. Cloud, burned and harvested area, and non-coniferous forest masks for the study area derived from Landsat imagery. Only the resulting mature conifer forest cover type was used for bark beetle damage analyses.

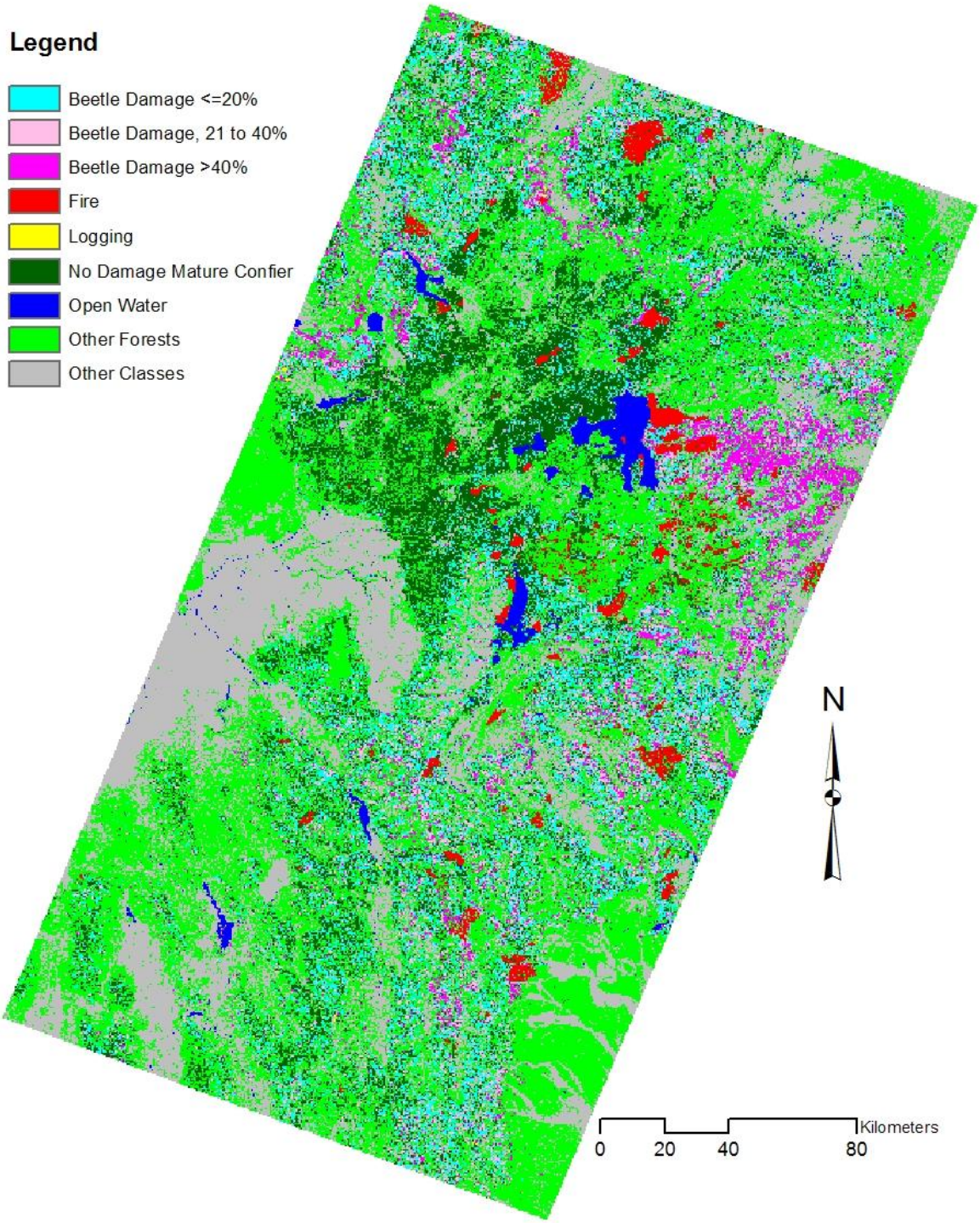

Figure 5. Spatial pattern of forest mortality attributed to bark beetles in conifer forests of Greater Yellowstone for 2007. Mortality that could be attributed to other known sources (e.g., fire and harvest) has been masked out.

(Q1b) *Within a zone of beetle infestation, how does* ***fine-scale*** *variation in tree characteristics influence tree susceptibility to MPB?*

Rationale. Numerous studies have identified aspects of tree size or physiology that influence susceptibility to MPB (e.g., Mitchell and Preisler 1991; Cole and Amman 1969), but few studies exist that relate fine-scale variation in stand characteristics to outbreaks of bark beetles. For example, many locations in the GYE include conifers other than lodgepole pine, yet whether mixed stands alter susceptibility to MPB is not known. Whitebark pine may be more vulnerable to MPB in mixed stands that are dominated by lodgepole pine, because of the common association of MPB with lodgepole pine. Similarly, whether multiple pathogens interact to increase susceptibility of trees to MPB is not known. Whitebark pine trees are also susceptible to the non-native white pine blister rust (WPBR; *Cronartium ribocila*), and trees that are symptomatic for WPBR may already be weakened and less resistant to beetle infestation than trees that are asymptomatic. Waring and Six (2005) studied the interaction of prescribed burning, WPBR, and beetle activity in whitebark pine, but low infestation rates prevented analysis of host selection for trees infected with WPBR. It should be noted, however, that beetle activity levels were not in outbreak proportions, but were more at endemic levels during their analysis period. In our current study, we have augmented this work by evaluating factors not previously studied. We tested whether susceptibility of whitebark pine trees to MPB infestation is higher in individual trees that are symptomatic for WPBR and/or in stands where whitebark pine is a minor component of a stand dominated by lodgepole pine.

Methods. To evaluate the relative importance of WPBR presence and the density of available whitebark pine host trees, we identified three study sites – Breccia Peak, Teewinot, and Mount Leidy – where whitebark pine was either dominant or co-dominant with other conifer non-MPB host species (e.g., Engelmann spruce or subalpine fir) and where WPBR was present. To address how the presence of an alternate host tree species influenced MPB selection of whitebark pine, we established a fourth site - Sylvan Pass - where no WPBR was present, but lodgepole pine, an alternate host for mountain pine beetle, was present or co-dominant with whitebark pine. At each site, we further delineated two stand types (PURE and MIX) based on overstory tree species composition, where PURE refers to a stand that contained only whitebark pine, and MIX refers to a stand containing both whitebark pine and one or more non-host conifer species. We examined 24 variable-radius plots in each of the two stand types at each site (n = 144 plots). Within each plot, we estimated mountain pine beetle activity by the presence of: *i*) pitch tubes, *ii*) boring dust in bark crevices particularly around root collar of tree; *iii*) entrance holes with inconspicuous pitch tubes; *iv*) small (≈2 mm diameter) emergence holes; or *v)* beetles actively chewing into bark (Safranyik et al. 1974). We used crown needle color as an indicator of the temporal sequence of attack to determine host selection preferences. White pine blister rust severity was estimated using Six and Newcomb's (2005) severity rating system. We calculated habitat use-availability selection ratios (HSR) for each plot by determining the frequency of beetle selection of whitebark pine with heavy rust compared to the total whitebark pine available, and for selection of whitebark pine compared to selection of lodgepole pine (Manly et al. 2002). For each site, we tested mean HSRs against selection ratios of non-preference (1.0) using one-group t-tests. We also used logistic regression to calculate the probability of selection of whitebark pine by MPB against multiple tree- and stand-level predictor variables.

Results. Pooled HSR data (*n* = 143) identified significant preferential host selection by mountain pine beetle of whitebark pine that was symptomatic for heavy rust (mean HSR = 1.287, SE = 0.05; Figure 6). Directional one group t-tests indicated that mean HSRs were significantly greater than 1.0 ($p < 0.001$), with the strength of selection preference ranging from 1.109 to 1.452 (Table 3). 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. 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.

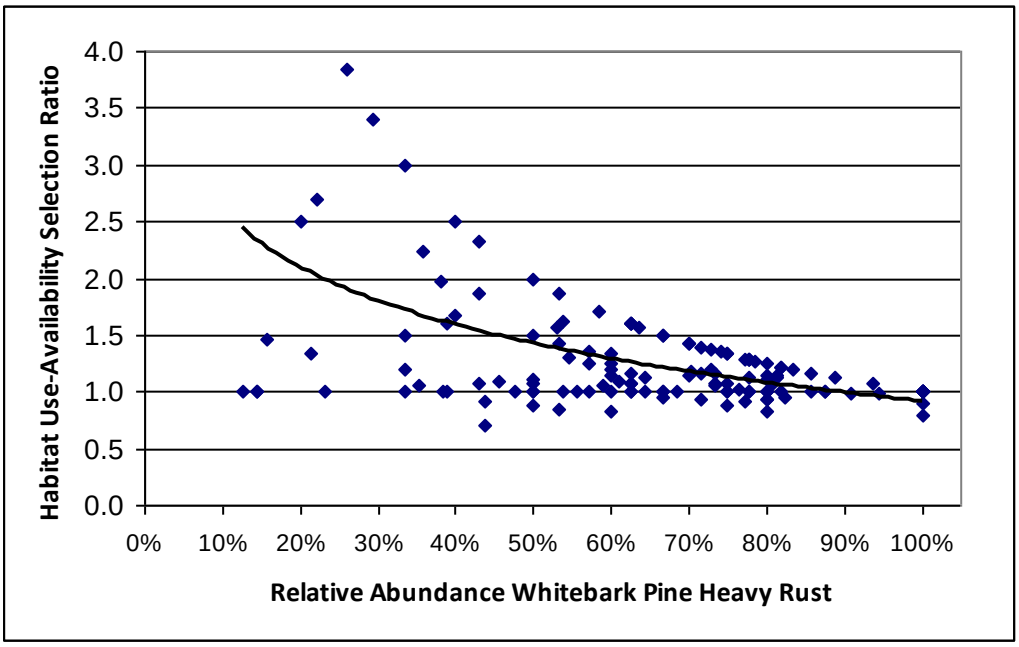

Figure 6. Habitat use-availability selection ratios for 'white pine blister rust' sites plotted against the relative abundance of whitebark pine with the preferred host/habitat characteristic of heavy blister rust (whole tree rust severity 2-4) for all plots at Breccia Peak, Mount Leidy and Teewinot (total plots, n = 143). HSR = 1.0 indicates no selectivity; increasing values >1.0 indicate progressively greater selectivity. Logarithmic curve overlaid to illustrate decrease in HSR strength with increase in the availability of preferred host/habitat.

Table 3. Habitat use-availability selection ratios (used habitat characteristic: available habitat characteristic) was calculated for each plot to detect preferential habitat selection by mountain pine beetle in whitebark pine forests of Greater Yellowstone. Habitat use-availability selection ratios (HSRs) in bold indicate significant deviation from 1.0 and preferential selection by MPB, assessed by a directional t-test (α = 0.05).

Stand Type (by site)	# Plots	Directional one group t-test					
		Host/Habitat Characteristic	Dichotomous Host Characteristic Categories	Mean HSR†	SE of Mean	t-value	Significance *
Sylvan Pass							
AHmix	24	Species	WB / LP	1.281	0.057	4.89	p< 0.0001
Breccia Peak							
PURE	24	Rust Severity	Light / Heavy	1.452	0.252	1.79	p=0.04
NHMIX	23	Rust Severity	Light / Heavy	1.213	0.078	2.72	p=0.01
Teewinot							
PURE	24	Rust Severity	Light / Heavy	1.292	0.088	3.28	p=0.002
NHMIX	24	Rust Severity	Light / Heavy	1.109	0.435	2.49	p=0.01
Mount Leidy							
PURE	24	Rust Severity	Light / Heavy	1.258	0.127	2.02	p=0.03
NHMIX	24	Rust Severity	Light / Heavy	1.395	0.139	2.87	p=0.004
All Plots With Rust	143	Rust Severity	Light / Heavy	1.287	0.056	5.06	p<0.0001
PURE	72	Rust Severity	Light / Heavy	1.334	0.097	3.41	p=0.01
NHMIX	71	Rust Severity	Light / Heavy	1.239	0.056	4.20	p<0.0001

†Ratios were calculated for each plot which calibrates the HSR to account for the host/habitat habitat composition at each plot.

*Null hypothesis: HSR – 1.0 = 0.0 tested against alternate hypothesis: HSR– 1.0 ≠ 0.0. Rust severity is a dichotomous habitat characteristic defined by whole tree rust severity: heavy rust (2-4) and light rust (0-1).

Data from the site at Sylvan Pass indicated that whitebark pine trees were selected by the mountain pine beetle first, and continue to be selected in greater proportions than lodgepole pine (Figure 7). Between both *Pinus* species that host the mountain pine beetle, proportionately more whitebark pine had red, yellow, or no needles compared to lodgepole pine. Conversely, proportionately more lodgepole pine were green-needled than were whitebark pine. HSR data also indicated that Whitebark pine was significantly and preferentially selected as a host tree over lodgepole pine (HSR = 1.281, SE = 0.06, p<0.001; Figure 8).

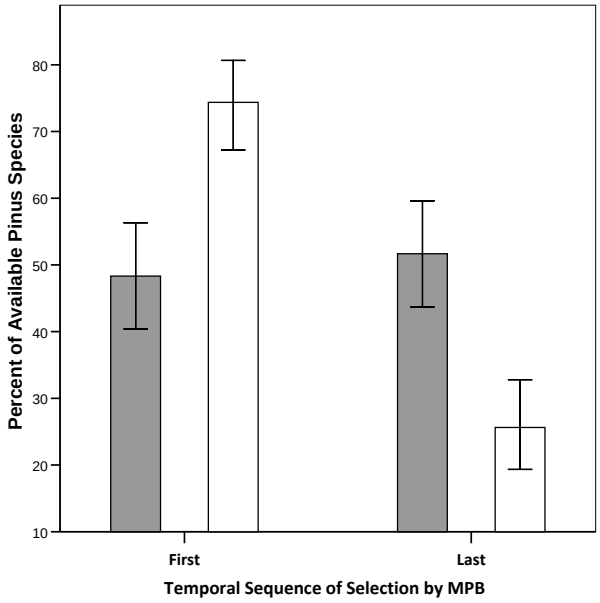

Figure 7. Temporal host selection by mountain pine beetle of percent available lodgepole pine and whitebark pine. We used crown needle color as a surrogate for time. Trees with red/yellow or no needles were selected as host trees first, and those with green needles were selected last or not at all. Error bars indicate a 95% confidence interval. Shaded bars are lodgepole pine, open whitebark pine.

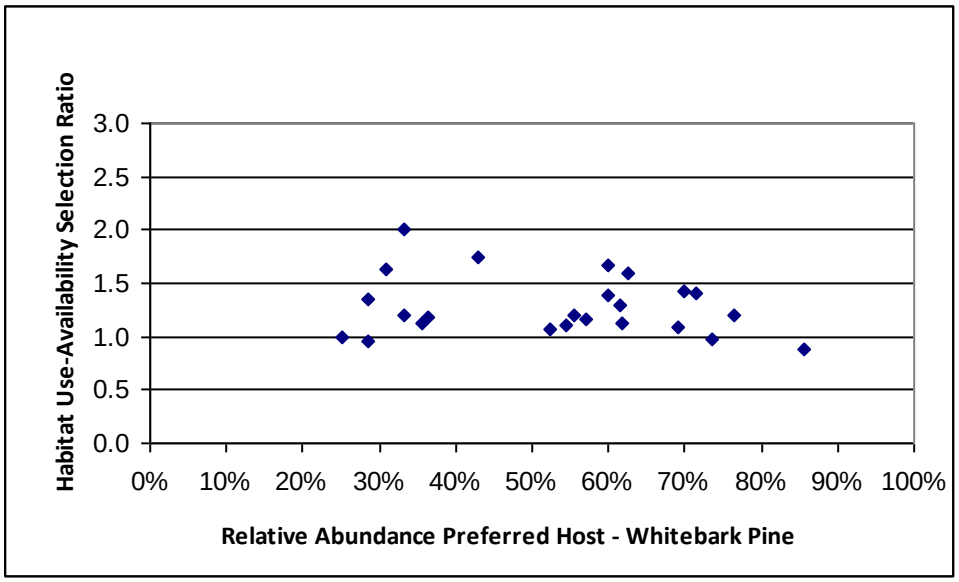

Figure 8. Habitat use-availability selection ratios for 'host species" sites of lodgepole pine compared to whitebark pine plotted against the relative abundance of whitebark pine. The preferred host/habitat tree identified by directional t-test (n = 24).

Our estimates of the probability of selection of whitebark pine by MPB against multiple tree- and stand-level predictor variables revealed significant interactions among stand type, DBH, and rust severity, illustrating the multifaceted and interactive nature of mountain pine beetle selection and the role of blister rust severity. Regardless of stand type or tree diameter, the probability of selection as a host was greater for whitebark pine with heavy rust than those with light rust (Figure 9). Host selection probability varied conversely with stand type; at smaller diameters, host selection probability was greatest for trees in PURE stands. This relationship switched at larger tree diameters, where trees in MIX stands had greater probability of selection as a host to mountain pine beetle.

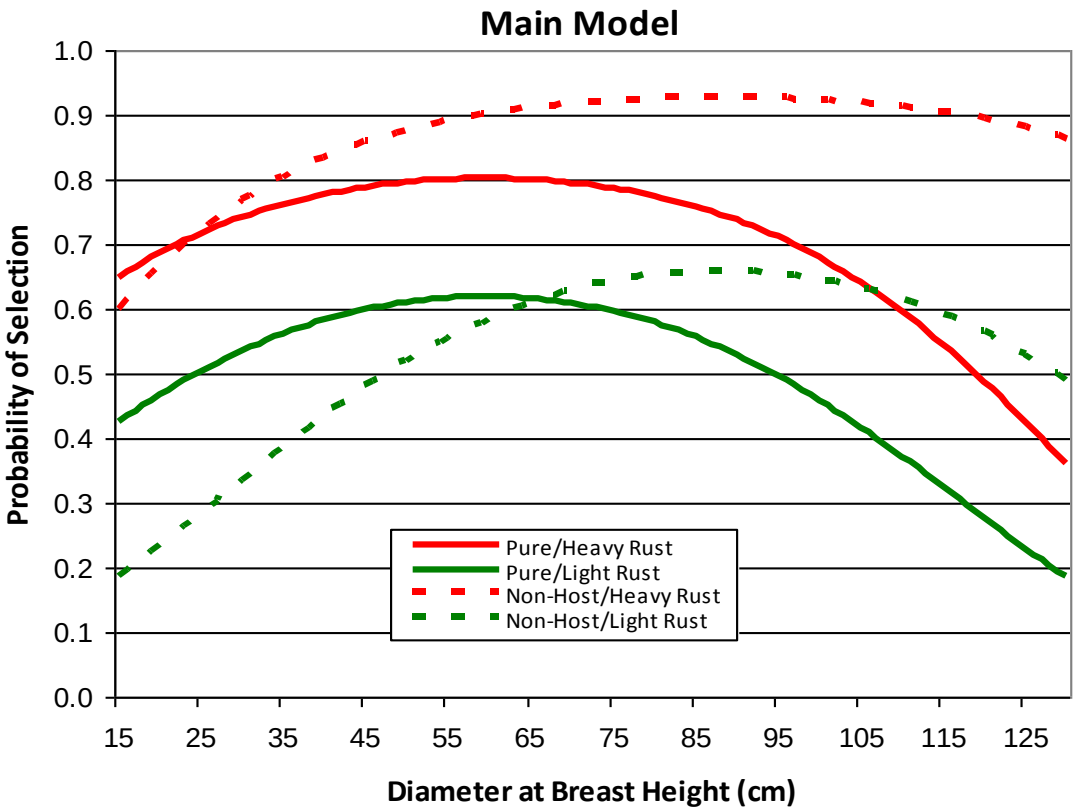

Figure 9. Main model – multiple logistic regression selection probability function derived using a manual, backward best subsets selection method based on the Wald statistic. Selection probability is for an individual whitebark pine with study site removed from model.

Discussion. Our results identified a positive relationship between blister rust severity and mountain pine beetle selection at both stand- and tree-levels for whitebark pine in our study area. These findings provide quantification of the interaction between the mountain pine beetle and white pine blister rust as agents of change within whitebark pine ecosystems. In addition, habitat use-availability selection ratio analyses illustrate that the mountain pine beetle preferentially selects whitebark pine with severe blister rust infection, regardless of relative abundance. The mean rust severity of all whitebark pine selected as host trees by the beetle was nearly twice as great as that of trees not selected. Previous research with which to compare our results is quite

limited. Our results complement a study in Montana, revealing a significant negative relationship between sapwood moisture content and blister rust severity, suggesting a reduction in tree defense capabilities (Six and Adams 2007). In another similar study, initial observations from a revisit survey also found beetles prefer whitebark pine with severe blister rust, although later observations were unclear (Schwandt and Kegley 2004).

Our findings regarding identification of specific tree characteristics that might influence host selection by MPB conflict with the conventional premise that mountain pine beetle host selection is based predominantly on tree DBH (Amman and Schmitz 1988). Our findings illustrate that the range of tree diameters preferred by the mountain pine beetle varies with both stand composition and blister rust severity. In addition, small diameter does not exclude individual whitebark pine from selection as a host.

We derived the models of selection probability presented in this study from data collected in the GYE. Site-specific models indicated that selection probability at Teewinot was slightly lower than Breccia Peak and Mount Leidy. This difference may be partially due to the similarity in abiotic context, specifically parent material origin, topography, aspect, and precipitation patterns between Breccia Peak and Mount Leidy compared to Teewinot. When we removed site from our analyses to produce our main model, common patterns among sites were evident and the initial relationships identified remained significant. The predictive ability of our model is limited to our study area; however, on an individual tree-level, the relationship between blister rust and beetle host selection patterns is likely universal. Variation in elevation, topography, soils, disturbance history, and climate patterns may limit this model's breadth of geographic applicability.

Question 2: How do MPB outbreaks influence the probability and severity of wildfire?

Rationale. It is often believed that widespread bark beetle outbreaks increase fire hazard because they create great quantities of dead and ladder fuels. On the other hand, it has also been proposed that bark beetle infestations may reduce the risk of crown fire by thinning the forests and reducing canopy fuel loads. Although there has been much progress in the last decade, surprisingly little empirical research has addressed this question (Simard et al. 2008), and results are ambivalent. This is especially true for lodgepole pine forests, which are among the most dynamic crown fire-dominated ecosystems in North America. Our goal was to document if and how fire hazard changed after severe MPB outbreak in lodgepole pine forests. Our general approach was to use a time-since-beetle outbreak chronosequence to quantify surface and canopy fuels, then simulate fire behavior in each stand for which fuels were quantified. However, we did not carry out the spatial analysis of historical maps exactly as originally proposed for two reasons. First, Lynch et al. (2006) published a study that was similar in scope (although not totally identical) to what we had proposed. Second, we wanted to take advantage of the opportunity presented by the newly acquired time series of Landsat imagery (Question 1), so we conducted a study (that was not originally proposed) to investigate more thoroughly the effects of bark beetles on forest ecosystems of the GYE (see 2b, below). However, a field-based spatial analysis of how recent fires have responded to the bark beetle mortality in the GYE will be carried out under a new 2009-2012 JFSP grant that we have just received.

(Q2a) *How do fuels and potential fire behavior change over time following a severe bark beetle outbreak in lodgepole pine forests?*

Methods.

Field sampling. In summer 2007, we selected 25 0.25-ha lodgepole pine-dominated sites that represented a time-since-beetle chronosequence, with five replicate stands in each of the following categories: undisturbed, red attack stage (1-2 years post-outbreak; beetle-killed trees bearing red needles), gray attack stage (3-5 years post-outbreak, beetle-killed trees needle-less), 25-year old attacks, and 35-year-old attacks. In all sites, we measured surface fuels using Brown's (1974) planar intersect method in ten 10-m long transects and estimated understory cover in twenty 0.25-m^2 circular quadrats. For each tree in three 200-m^2 quadrats, we recorded diameter at breast height (dbh; 1.4 m), species, status (live, dead standing, or dead downed), presence of MPB attack (pitch tubes for recent attacks [red and gray stages], and J-shaped beetle galleries in older attacks [25- and 35-yr-old]), canopy condition (green needles, 0-50% red needles, 50-100% red needles, or no needles), and crown base height (distance between the ground and lowest needles). In ¼ of each 200-m^2 quadrats, tree saplings and seedlings (< 1.4 m in height) were described using the same variables used for canopy trees, except that height (nearest 10 cm) was noted instead of dbh.

To determine soil texture, we sampled and composited 10 soil samples using 15-cm deep cores. To quantify the influence of MPB infestation on microscale meteorology (and with supplemental funding from the USFS Western Wildland Environmental Threat Assessment Center), we deployed temperature and relative humidity probes in three sites of each time-since-beetle class (n = 15 stands in total). At each of these sites, one probe was installed at 2 m from the ground to record air temperature and relative humidity, and three temperature-only probes were installed at the interface between the litter and duff layers. We used dendrochronology to determine stand age and time since beetle attack, and to verify that all stands had a similar basal area at time of infestation. In all 25- and 35-yr post-beetle stands, we sampled 50 increment cores from live trees, and 20 cross-sections on downed beetle-killed trees. In undisturbed, red-stage, and gray-stage sites, we only sampled 10 cores from live trees. The cores were mounted, cross-dated, and measured using a scanner and tree-ring measurement program.

Fire behavior modeling**.** Surface fuel loads were computed following standard methods (Brown 1974), and understory fuel loads were calculated using cover data and allometric relationships previously published (Turner et al. 2004) or developed for this study. We computed vertical canopy profiles of canopy bulk density (that included overstory trees and understory saplings/seedlings) following Reinhardt et al. (2006) from which we computed effective canopy base height, effective bulk density, and canopy fuel load (Scott and Reinhardt 2001).

We used the surface, understory, and canopy fuel measurements from the field to parameterize the fire modeling system NEXUS (Scott and Reinhardt 2001). To focus specifically on the effects of stand structure on fire behavior, we used the same slope (0%) and weather conditions (dry to very dry summer conditions: 5%, 6%, and 7% moisture content for the 1h, 10h, and 100h fuels; 70% and 100% moisture content for live herbaceous and live woody fuels, respectively) for all stands in all simulations. Canopy foliar moisture was computed as the average of the live

canopy biomass at 100% moisture content and of the red canopy biomass at 5% moisture content. Because wind is highly variable and has a qualitative effect on fire behavior, we simulated a range of wind speeds (0 to 100 km/h). To characterize fire behavior, we used the following variables: Torching Index, Crowning Index, fire type (surface, crown passive, crown active, and crown conditional), crown fraction burned, headfire rate of spread, heat per unit area, and fireline intensity.

Statistical analyses. We used two statistical approaches to analyze the fuels and the fire hazard index data. First, to test the short-term effects of beetle outbreak, we used ANOVA to compare fuels among the undisturbed, red, and gray stages of beetle infestation. Second, we used regression to assess long-term changes in fuel characteristics and fire hazard with time since beetle outbreak (as a continuous variable) in beetle-killed stands. Because fire behavior was analyzed with a range of wind speeds, we tested differences among time-since-beetle classes using ANOVA at four different wind speeds: 20, 40, 60, and 80 km/h. For all analyses, we used a significance level of 5%.

Results

Chronosequence. At time of sampling, undisturbed stands had a live basal area of 35 to 60 m^2/ha, which was significantly higher than that of beetle-killed stands, which ranged from 9 to 23 m^2/ha. However, according to tree-ring reconstructions, the five time-since-beetle classes did not differ in terms of (1) stand age at time of beetle infestation, (2) pre-outbreak basal area, and (3) infestation severity. Dendrochronology also confirmed timing of beetle attack in the oldest post-outbreak stands, and three stands that were originally classified as 35-yr-old attacks were reclassified as 25-yr old attacks.

Fuels, short-term (undisturbed to gray stage). Dead surface fuel loads of all size classes (1-hour to 1000-hour) did not change over the short term, with no significant differences between the undisturbed, red-stage, and gray-stage sites (Figure 10). Similarly, fuel bed depth and duff depth did not differ among these three classes. However, needle litter in the red-stage sites (depth = 2.8 cm) was twice as deep as in the undisturbed class (depth = 1.4 cm), with gray-stage sites having an intermediate value. Vertical profiles of canopy bulk density showed qualitative differences between time-since-beetle classes (Fig. 11). Compared to undisturbed sites, red- and gray-stage sites had a lower canopy bulk density (0.065 kg/m^3, compared to 0.14 kg/m^3), a lower available canopy fuel load (8.7 tonnes/ha, compared to 15 tonnes/ha), and a lower foliar moisture content (78% compared to 100%) (Figure 12). Canopy base height did not vary between the undisturbed, red, and gray sites, averaging 3.1 m (range = 0 – 6 m) (Figure 12).

Fuels, long-term (2- to 35-yr post-beetle). In the decades following beetle infestation, 1-hour fuels decreased from 1.7 tonnes/ha at 2 yrs to 1.2 tonnes/ha at 36 yrs post-beetle, but 10-hour fuels (average = 5.8 tonnes/ha), 100-hour fuels (average = 5.2 tonnes/ha), and fuel bed depth (average = 13 cm) did not change (Figure 10). During the same period, coarse wood (1000-hour fuels) load doubled, from 40 to about 80 tonnes/ha, and needle litter and duff layers decreased by 50% and 60%, respectively. Canopy base height was greatly reduced, from 3 to 0 m, and no change was observed for canopy fuel load and canopy bulk density (Figures 11 and 12).

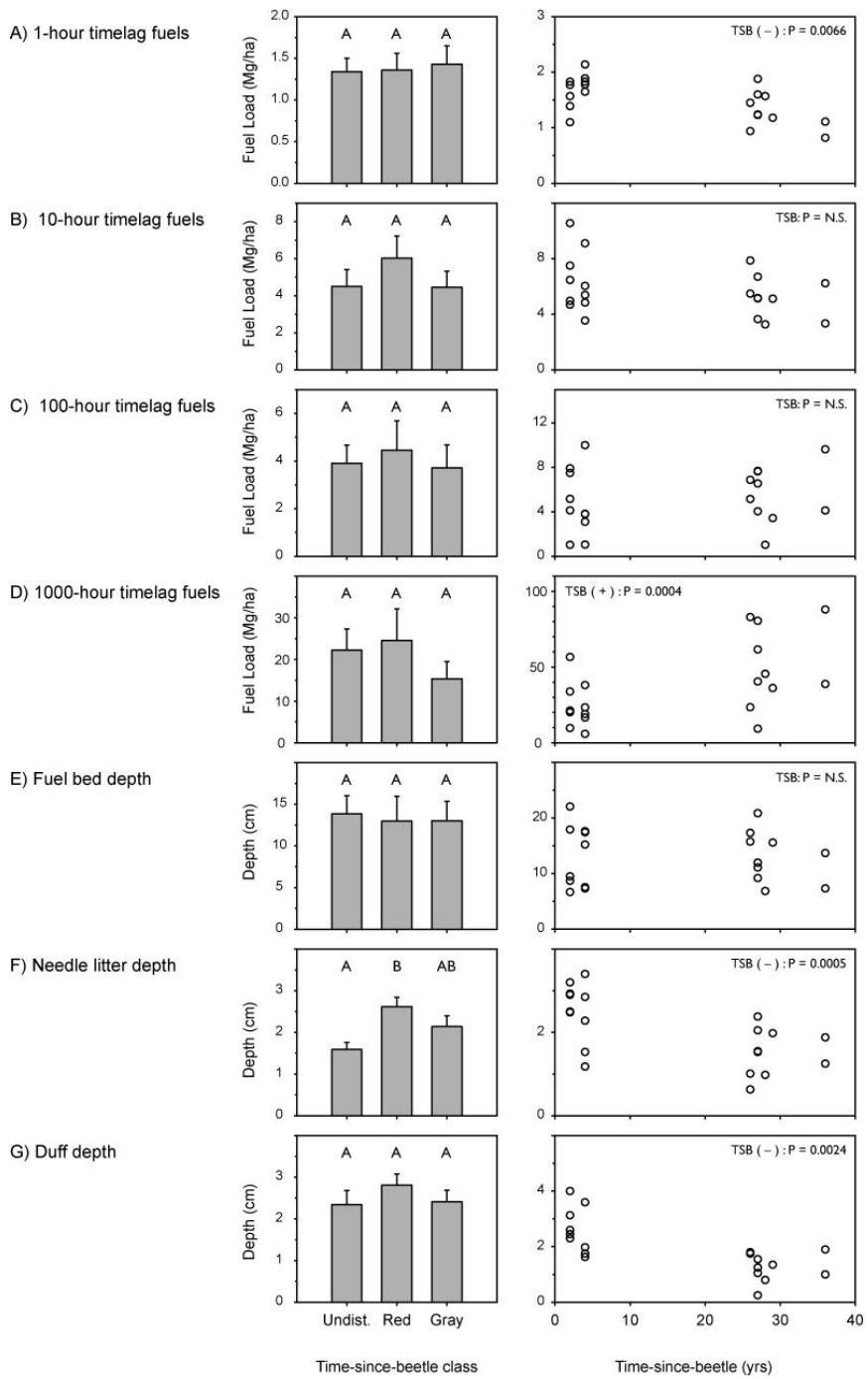

Figure 10 . (A-D) Fuel load of dead surface fuels in the 1-h to 1000-h size categories, and depth of (E) fuel bed, (F) needle litter layer, and (G) duff layer in the chronosequence sites. Left panels show short-term (< 5 years) means and standard error for the undisturbed, red-stage, and gray-stage stands only. Uppercase letters above each bar indicate ANOVA results testing differences in means among the three classes; means with different letters are significantly different (Duncan's multiple range test; alpha = 5%). Right panels show the long-term (2-35 years) relationship between each fuel category and time since beetle for beetle-killed sites only. P-values associated with TSB (time since beetle) effect are shown. The "(+)" or "(–)" symbols following TSB effect indicate the sign of the slope when significant (alpha = 5%).

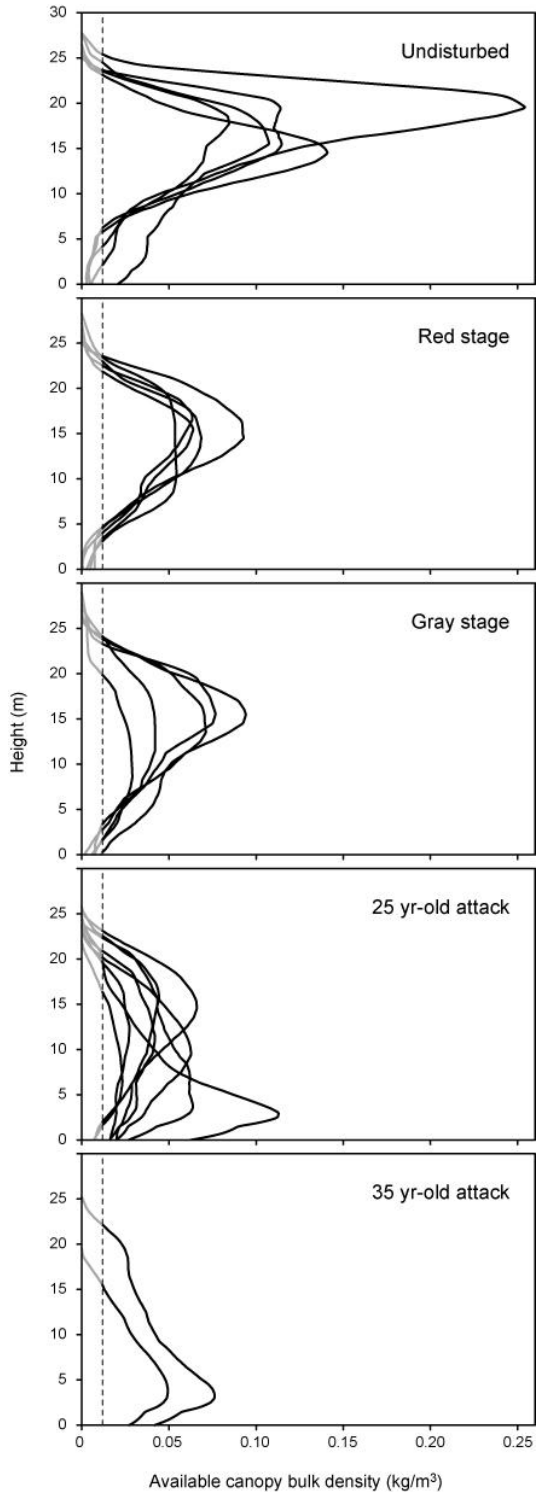

Figure 11. Vertical profiles of available canopy bulk density in the chronosequence sites (solid lines). The vertical dotted line represents the 0.011 kg/m^3 density threshold above which fire can propagate and that determines effective canopy base height.

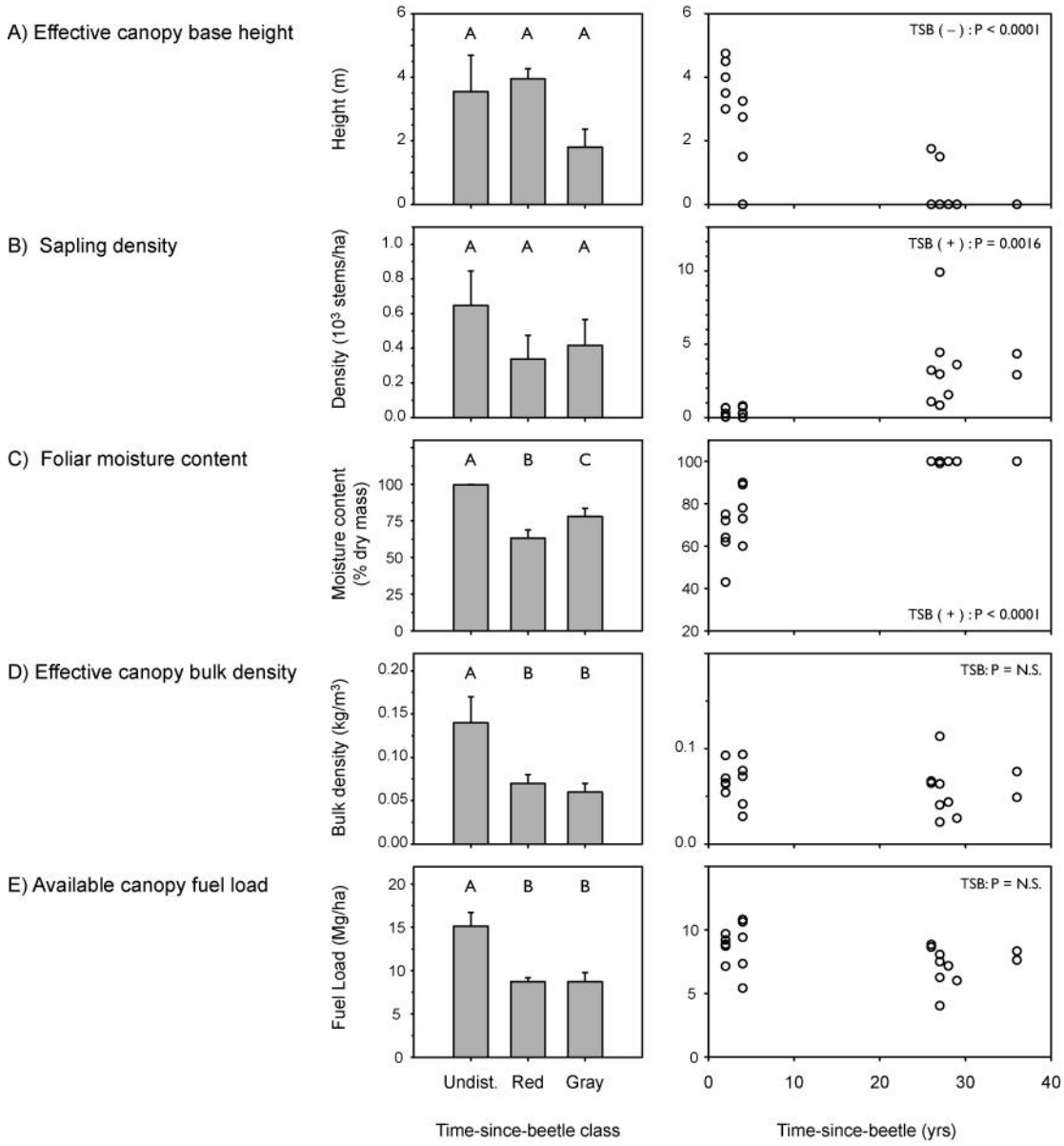

Figure 12. (A) Effective canopy base height, (B) density of saplings (0 cm < dbh < 7.5 cm), (C) canopy foliar moisture content, (D) effective canopy bulk density, and (E) available canopy fuel load in the chronosequence sites. Left panels show means and standard error for the undisturbed, red-stage, and gray-stage stands only. Uppercase letters above each bar indicate ANOVA results testing differences in means among the three classes; means with different letters are significantly different (Duncan's multiple range test; alpha = 5%). Right panels show the relationship between each canopy characteristic and time since beetle for beetle-killed sites only. P-values associated with TSB (time since beetle) effect are shown. The "(+)" or "(–)" symbols following TSB effect indicate the sign of the slope when significant (alpha = 5%). Superimposed data points are indicated with "n = ".

Microclimate**.** When expressed as a deviation from air temperature, daily mean temperature at the litter-duff interface was not significantly different from zero in the undisturbed sites but was 2 °C lower in the red and gray sites, and 2.5 °C warmer in the old beetle attacks. When only mid-afternoon temperatures were considered, the overall pattern remained but temperature differences were amplified in the old attacks, where litter and duff were about 11°C warmer than air.

Fire hazard. Simulation results suggested that in the short term, undisturbed, red, and gray stands were unlikely to torch, with Torching Index values (wind speed required to initiate torching) well above 100 km/h (Figure 13). In the long term (2- to 36-yrs post-outbreak), Torching Index was reduced to zero at 35 yrs post-beetle, suggesting that in these stands, passive crown fire could be initiated even without wind. Crowning Index (wind speed needed to sustain an active crown fire) was higher in gray-stage sites (71 km/h) than in undisturbed sites (39 km/h), with intermediate values in the red-stage sites (61 km/h), suggesting that the immediate effect of mountain pine beetle attack was to reduce the probability of active crown fire (Figure 12). In subsequent decades, Crowning Index did not change, with an average value of 71 km/h (Figure 13).

Fire behavior was qualitatively different among the time-since-beetle classes but these differences were sometimes overridden by the effect of wind speed (Figure 14). At wind speeds below 40 km/h, the undisturbed, red and gray stages, and 25-yr post-beetle stands were all predicted to have surface fires whereas the 35-yr post-beetle stands had passive crown fires. At these wind speeds, fire rate of spread and fireline intensity were low (> 0.25 km/h and < 1300 kW/m, respectively) in all time-since-beetle classes and heat per unit area was not different among the classes, with an average value of 7500 kJ/m^2.

For wind speeds between about 40 and 60 km/h, the overall effect of bark beetle outbreak was to reduce fire hazard in the short term (Fig. 14). Fire type switched from conditional crown fires in the undisturbed sites to surface fires in the red and gray sites, with a concomitant reduction of crown fraction burned from 0.58 to 0.06 (-90%), headfire rate of spread from 0.89 to 0.13 km/h (-85%), heat per unit area from 22,300 to 7,300 kJ/m2 (-67%), and fireline intensity from 8,300 to 600 kW/m (-93%) at 40 km/h (Fig. 14). The 25- and 35-yr post-beetle stands were predicted to display passive crown fires and had values of crown fraction burned, rate of spread, heat per unit area, and fireline intensity that were intermediate between the undisturbed and the red and gray classes. Consequently, for all fire behavior metrics, the long-term trend from undisturbed to 35-yr post-outbreak stands was a decline in fire hazard in the red stage followed by a gradual return to pre-outbreak values.

At very high wind speeds (> 60 km/h), most differences among time-since-beetle classes disappeared, with all classes having either conditional (undisturbed, red, and gray stands) or active (old attacks) crown fires, and having a similar crown fraction burned and headfire rate of spread. Heat per unit area and fireline intensity showed a trend similar to that observed between 40 and 60 km/h, with a decline in the red and gray stands followed by a return to pre-outbreak values (Figure 14).

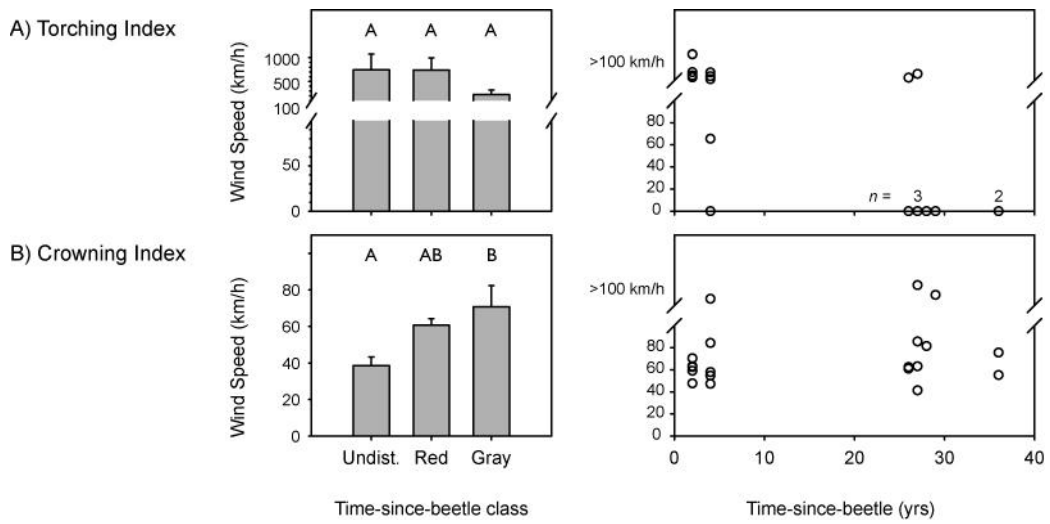

Figure 13. (A) Torching and (B) Crowning Index values in the chronosequence sites. Left panels show means and standard error for the undisturbed, red-stage, and gray-stage stands only (short term trends). Uppercase letters above each bar indicate ANOVA results testing differences in means among the three classes; means with different letters are significantly different (Duncan's multiple range test; alpha = 5%). Right panels show the long-term relationship between each Index and time since beetle for beetle-killed sites only. P-values associated with TSB (time since beetle) effect are shown. The "(–)" symbol following TSB effect indicate the sign of the slope when significant (alpha = 5%).

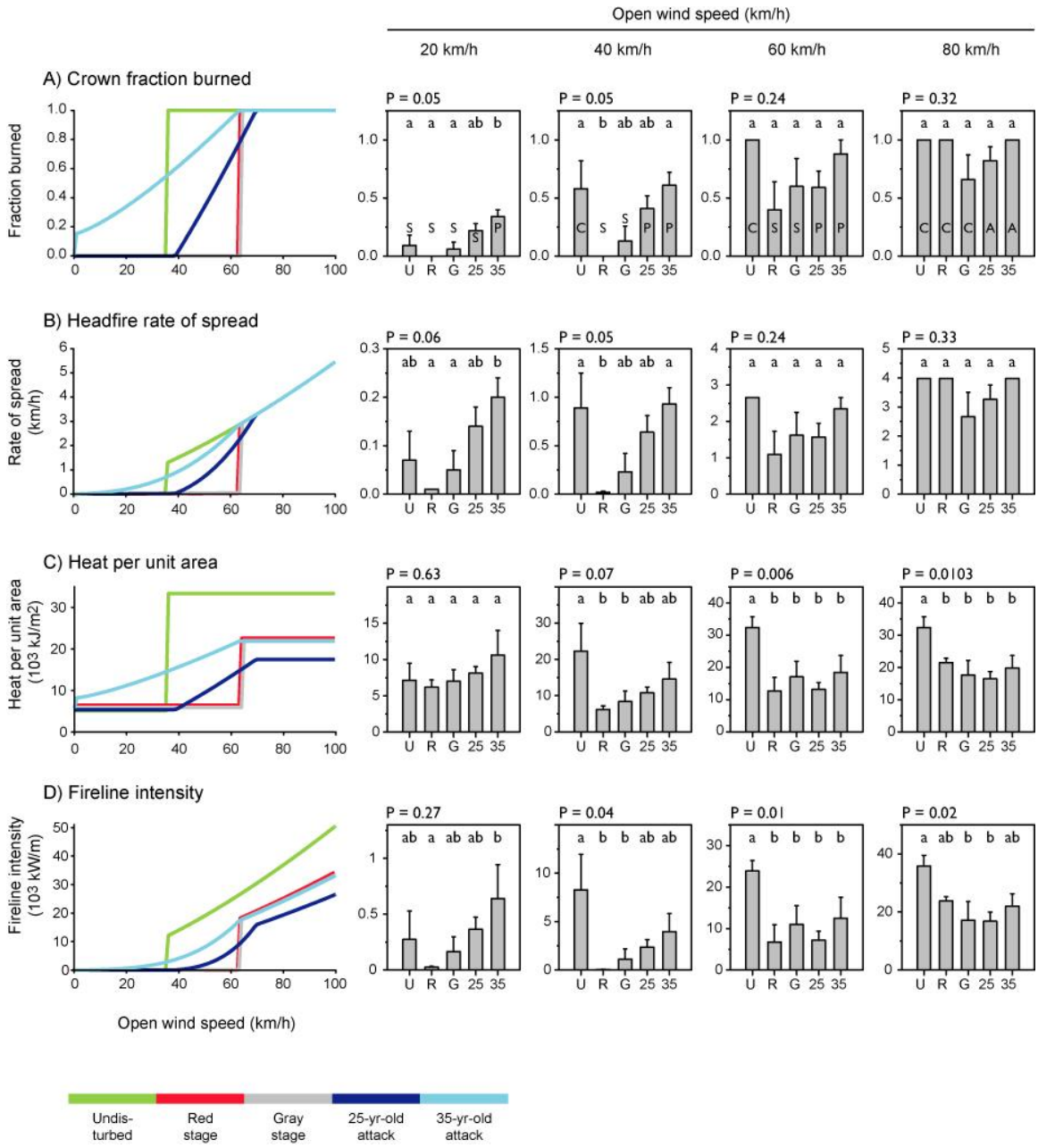

Figure 14. Fire behavior simulation results for the five TSB classes in the chronosequence sites. Left panels show change in fire behavior metrics with open wind speed for each TSB class (lines). Each line represents the result of one simulation using the average fuel loads for that class. Right panels show means and standard error of each fire behavior metric for each TSB class at 20, 40, 60, and 80 km/h wind speeds. Each bar represents the average of five simulations (one per site) per TSB class. Lowercase letters above each bar indicate ANOVA results testing differences in means among the TSB classes; means with different letters are significantly different (Duncan's multiple range test; alpha = 5%). P-values associated with the ANOVA are shown. For Crown Fraction Burned (A), uppercase letters on each bar indicate predicted fire type from simulation results in the left panel (S = surface fire, P = passive crown fire, A = active crown fire, C = conditional crown fire).

Discussion. Our data did not support the hypothesis that mountain pine beetle outbreak increased fire hazard in the short term (1 to 5 years post-outbreak). On the contrary, modeling results suggested that beetle outbreak may actually reduce the probability of active crown fire. Because canopy bulk density is the primary driver of crowning, post-outbreak reduction of canopy fuels would be the most likely mechanism that explains the reduction of fire hazard in red and gray stands. Torching Index went from 40 km/h in the undisturbed stands to about 70 km/h in the gray stands, suggesting that greater wind speeds would be needed for active crown fire to occur in theses stands. Most among-class differences in fire behavior occurred in a window of wind speed ranging from 30 to 60 km/h, where red- and gray-stage stands had lower crown fraction burned, headfire rate of spread, fireline intensity, and heat per unit area.

It is often thought that fire hazard is extreme in the red-needle stage because dead foliage is still in the canopy but is very dry. However, canopy bulk density of red-stage stands in our study was 50% lower than in undisturbed stands, and similar to that of the gray stands, suggesting that dead needle fall may already occur in the red-needle stage. This is supported by field observations that mortality in these stands occurred over a number of years, and that all stands had a mixture of red-needle, bare, and live trees in different proportions. Thus, although canopy foliar moisture during the red-needle stage was reduced to about 78% of its pre-outbreak value, we did not observe increased torching or crowning in the fire modeling results, probably because of the overriding effect of canopy bulk density.

In the decades that followed the infestation, the growth of understory saplings greatly reduced canopy base height, providing ladder fuels that facilitated torching. Thirty-five years after the outbreak, effective canopy base height was down to 0 m, suggesting that torching could potentially occur even in the absence of wind. Canopy bulk density however was still low and did not allow crowning, and thus only passive fires were predicted.

To focus specifically on the effects of stand structural changes on fire behavior, we purposefully did not use the temperature data gathered in the chronosequence stands as inputs for the simulations. However, a qualitative assessment of these data reveals that micro-scale temperature could possibly strengthen the observed trends in potential fire behavior. Compared to undisturbed sites, temperature at the interface of the litter and duff layers was lower in the red- and gray-stage sites, and higher in the old attacks. These trends were likely caused by the insulating effect of thicker litter layer in the red and gray sites, and by increased solar radiation in stands that were attacked 25 to 35 years ago and that are now very open. Lower soil surface temperatures in the red and gray stands were probably associated with higher moisture content although we did not measure it. We speculate that moister surface fuels in the red and gray-stage stands may reduce surface fire intensity and rate of spread, and that dryer fuels in the old attacks would have the opposite effect.

Fire behavior was little affected by forest structure when wind speed was either below 20 km/h or above 60 km/h. Under low wind speed conditions, most stands were predicted to have surface fires, whereas at very high wind speeds, all stand types eventually achieved crowning. This suggests that beetle outbreaks may influence fire behavior only under certain intermediate weather conditions. This scenario is somehow analogous to the situation that occurred during the 1988 fires in Yellowstone National Park, when forest type greatly influenced the spread of early

season, low-intensity fires, whereas it had little to no effects during the late-summer fires that burned under extreme conditions (Renkin and Despain 1992). So when does stand structure in general, and bark beetle damage in particular, really matter? The relative importance of fuels and weather in explaining fire activity is variable across ecosystems, but the evidence points toward strong climatic control of wildfire area burned in subalpine forests (Littell et al 2009, Bessie and Johnson 1995). Still, it is unclear how important fuel conditions are compared to climate during a year of moderately severe fire weather. Future research on bark beetle-fire interactions should concentrate on the actual probability within a given fire year that beetle-killed stands have an influence on fire behavior, and on the potential consequences of these interactions on wildfire area burned.

(Q2b) *Disturbance severity and post-disturbance biomass recovery in western subalpine forests: how do bark beetle outbreaks and wildfires differ?*

Rationale. Forested landscapes throughout the West are periodically affected by fires and bark beetle outbreaks of different severity, extent, and spatial configuration. Rates of vegetation biomass recovery can influence important ecological processes like ecosystem carbon balance but are typically difficult to assess because of a lack of long-term data over large areas. We analyzed multi-year remote sensing data in a chronosequence framework to address the following question: how does disturbance type (fire vs. bark beetles) influence post-disturbance rates of vegetation biomass recovery in the Greater Yellowstone Ecosystem? Because post-beetle stands have more residual vegetation than post-fire sites, we hypothesized that biomass recovery rates would be higher following mountain pine beetle outbreak than after stand-replacing fire.

Methods. To determine post-disturbance recovery rates across the landscape, we combined a time series analysis approach, where multiple years of satellite imagery were used to follow post-disturbance vegetation development, and a chronosequence approach, where historical disturbance maps were used to sample forest areas of the landscape at different stages of post-disturbance recovery. We did not use remote sensing to detect disturbance events because the spectral information of the satellite imagery was used as our response variable. Instead, we used fire and insect disturbance maps that were derived independently from aerial flight surveys, and created a time-since-last disturbance template that was used to sample the imagery.

Satellite imagery**.** We used Landsat TM and ETM imagery acquired in the summer or fall of 1987, 1989, 1994, 1999, and 2006 (two scenes for each year: path 38, rows 29 and 30). Raw images were converted to top of atmosphere reflectance, mosaicked, and georectified using the 1999 image as a reference. To correct for year-to-year variations in reflectance that are caused by changes in atmospheric conditions at the time of image acquisition, we normalized the images to the 1999 scene using bright (e.g., treeless geothermal areas) and dark (small dark lakes) pseudo-invariant features (Schott et al., 1988). Moisture Stress Index (MSI; Landsat TM5 / TM4; Hunt and Rock 1989) was calculated for each scene as a proxy for live vegetation cover. The final images, masked for clouds and non-forest cover type, were then used as base images to be sampled using historical fire and insect disturbance maps.

Canopy burn map. To identify forest stands that sustained high severity crown fires, we mapped fire severity using the differenced normalized burn ratio (dNBR; Key and Benson 2006). For our

preliminary analysis, we only mapped the 1988 fire, using the 1987 and 1989 Landsat images for pre- and post-fire conditions. We created a map that only contained high-severity canopy burns (dNBR > 660) in lodgepole pine stands (using a cover type map), and masked areas that were attacked by bark beetles previous to the fire. The resulting canopy burn map was then used to sample the Landsat images younger than the fire (1989, 1994, 1999, and 2006) using 50 windows of 3 x 3 pixels (90 m x 90 m, averaged).

Mountain pine beetle damage map**.** Aerial detection survey GIS layers that cover the whole GYE from 2000 to 2006 were obtained from the US Forest Service, and were supplemented by historical insect survey data available for Yellowstone National Park from 1962 to 1986 (Despain 1990, Lynch et al. 2006). Both datasets were subsetted, keeping only polygons that represented very heavy mountain pine beetle damage (> 50 beetle-killed trees/ha) in lodgepole pine-dominated stands. Yearly layers of bark beetle damage were then combined into a single vector layer, keeping only the most recent attack when polygons of multiple attack years overlapped over a given area. A historical map of fire perimeters in Yellowstone (1880-2007; YNP archives) was then used to mask areas that burned after being infested by the mountain pine beetle. For each infestation year, we determined 50 randomly placed windows of 3 x 3 pixels that were used to sample the satellite imagery.

Field sampling. To determine the relationship between MSI and forest biomass, we used data from 55 survey plots that were sampled in 2006 and 2007 for question 1a and 2a of this project and that were located in the area covered by the satellite imagery. Live tree basal area (5 to 40 m^2/ha) was related to MSI using linear regression.

Results. Moisture Stress Index was strongly and negatively related to live tree basal area (R^2_{adj} = 0.51;F = 58.95; P < 0.0001), suggesting that this index can reliably represent post-disturbance recovery of disturbed stands. MSI values increased (lower live biomass) drastically after stand-replacing fire, with a drop of 1.4 units (Figure 15). This was followed by a rapid recovery of 1 unit MSI within the first 20 years, accounting for 70% of the initial change. In contrast, MSI of stands that were attacked by bark beetles only increased by 0.2 units and recovered at a much slower rate over the following decades. There was a very strong agreement among the different time series used to quantify post-beetle recovery patterns, with the three outbreak years having the same slope (no TSB*outbreak year interaction). For both disturbance types, the best regression model that fit the post-disturbance recovery data was a logarithmic function, suggesting a diminishing rate of recovery with time since disturbance. The relationship between the recovery phase of MSI and time since disturbance was, for the two disturbance types:

$$\ln(MSI) = 0.6996 - 0.0428*TSF$$

for post-fire recovery (R^2 = 0.80; P < 0.0001; n = 200), and

$$\ln(MSI) = -0.0586 - 0.0106*TSB$$

for post-beetle recovery (R^2 = 0.37; P < 0.0001; n = 450), where TSF stands for time since fire, and TSB stands for time since beetle. Rate of recovery was greater in post-fire than in post-beetle stands, but post-beetle biomass, as estimated with MSI, was always greater than post-fire

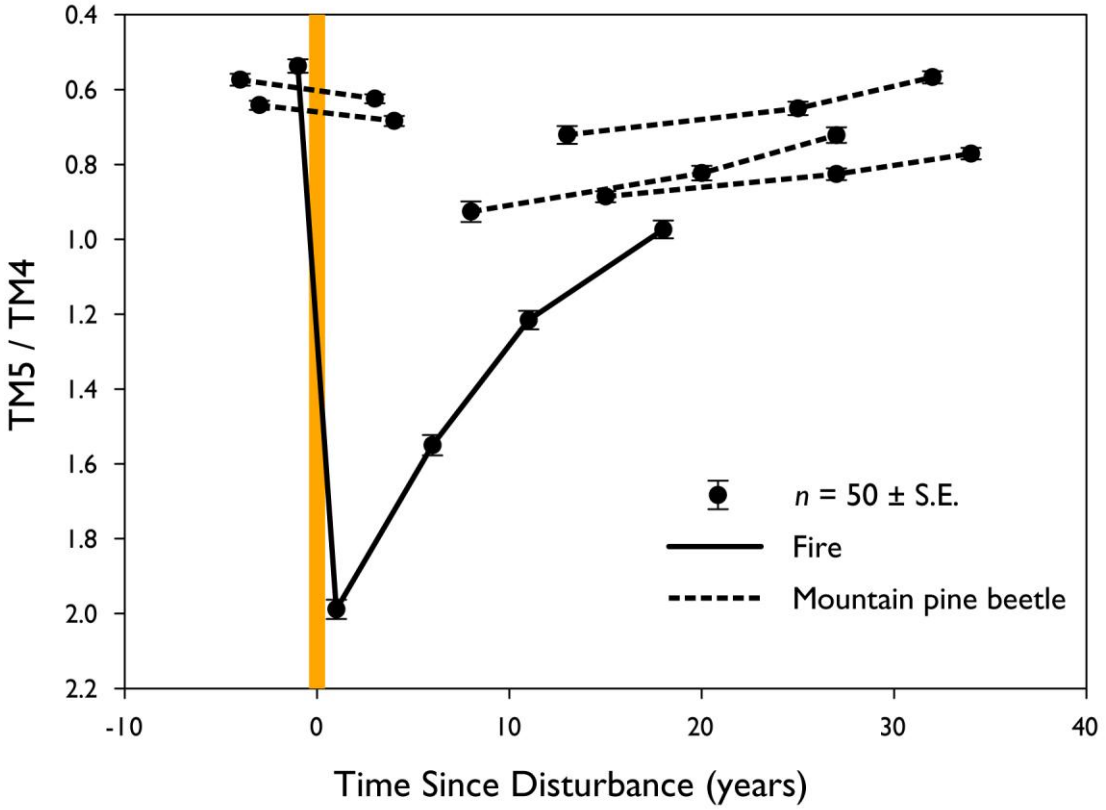

Figure 15. Change in Moisture Stress Index (MSI) with time since disturbance for post-fire (solid line) and mountain pine beetle (dashed lines) disturbances. Each line represents a different disturbance year, and symbols linked by a line represent time series for the same locations. Only the 1988 fire was used in this preliminary analysis. The vertical orange line represents year of disturbance.

biomass for a given time since disturbance (Figure 15).

Discussion. Although we were only able to test our method on a limited number of fires (one) and bark beetle outbreak years (five) in this preliminary analysis, this new approach is promising. Post-outbreak recovery time series were very consistent among each other, even though they represented infested areas that were spatially and temporally separated. The three post-beetle time series had significantly different intercepts, suggesting different infestation severities among outbreak years, but the rate of recovery was similar, with no TSB*outbreak year interaction. Results from the chronosequence analysis, which allowed post-disturbance recovery over a period of 35 years to be estimated, were confirmed by use of time series, which by themselves covered a period of only 20 years. To our knowledge, this is the first time that chronosequence and time series analyses have been combined in a hybrid approach that reduces the limitations and builds on the strengths of both methods. We plan to refine this preliminary analysis by adding more fire and outbreak years, and by optimizing the length of the chronosequence and the time series.

Results thus far do not support the hypothesis that recovery was faster following beetle outbreak than after stand-replacing fire. This is surprising because compared to fire, bark beetle

disturbance leaves more vegetation that could contribute to post-disturbance recovery. There are two main mechanisms of post-beetle recovery. First, because not all mature trees are killed by the outbreak, growth of surviving canopy trees is enhanced by the sudden increase in resources (light, nutrients) that are usually limiting tree growth. Second, when an understory of tree seedlings, shrubs, and/or grasses is present, these plants also take advantage of increased resources by filling gaps created by the infestation. In contrast, most of the biomass recovery following severe stand-replacing crown fire is through establishment of tree seedlings from surviving canopy seed banks. These results however only hold if the linear relationship between MSI and basal area, which was only tested between MSI values of 0.5 and 1.2, still holds in the whole range covered by the disturbance events that were studied, i.e., 0.5 – 2.0. Further development of the method will address this question.

Question 3: How does the pattern of fire-damaged trees influence the pattern and severity of MPB outbreaks?

Rationale: In lodgepole pine forests of the Greater Yellowstone Ecosystem, the interaction between two major agents of disturbance, fire and mountain pine beetle (MPB) is of particular concern to forest managers. First, there is the potential that MPB-caused mortality will lead to an increase in stand replacing fires. Our findings for question #2 suggest that beetle outbreaks do not increase the likelihood of large severe fires in lodgepole pine forests. Reciprocally, and the focus of this portion of the research, it is hypothesized that fire-caused injury to trees may make them more susceptible to subsequent MPB attack.

At low population, or endemic, densities, MPB is limited to colonizing stressed trees. At larger population, or epidemic, densities, the ability of these beetles to engage in mass-attacks enables them to overwhelm healthy host defenses. Given the large number of fire-injured trees at a burn site, there is concern that MPB will reproduce within these trees, leading to increased populations that attack healthy trees in subsequent years. We asked a) Are MPB more likely to colonize lodgepole pines that have been injured by fire? b) Among those trees that are colonized, what is the reproductive success of MPB in fire-injured vs. healthy trees?

This work was jointly funded by JFSP, the University of Wisconsin College of Agricultural and Life Sciences through a grant from McIntire-Stennis, and the University of Wisconsin Graduate School through a Hilldale Undergraduate Research Fellowship.

Methods: Eight burns of lodgepole pine forest within the GYE were sampled during the summers of 2007 and 2008. Four burns occurred during the summer of 2006 and were sampled during the summer of 2007. The remaining four occurred during the summer of 2007 and were sampled during the summer of 2008. We established four 5m x 100m belt transects at the edge of each burn. Each lodgepole pine tree was determined to be of "Low", "Moderate", or "High" fire injury and was also sampled for the presence of various bark beetle and wood borer species and for the presence of pathogens, e.g. Dwarf mistletoe and Comandra blister rust. The fire injury categories were differentiated by the amount of charring at the base, the bole, and the canopy of each tree, as well as by the rate of cambium kill. "Low" trees had 0-10% charring of the base and bole, 0% charring of the canopy, and a cambium kill rate of 0 or 1. "Moderate" trees had 11-49% charring of the base and bole, 0-10% charring of the canopy, and a cambium

kill rate of 1 or 2. "High" trees had a 50-100% charring of the base and bole, 11-100% charring of the canopy, and a cambium kill rate of 3 or 4.

Baited Lindgren Multiple Funnel traps were set along the edge of each burn. At each burn three traps were baited with *trans*-verbenol, myrcene, and *exo*-brevcomin for the attraction of MPB, three traps were baited with ipsdienol and lanierone for the attraction of *Ips* sp., and three traps were baited with ethanol and alpha-pinene for the attraction of wood boring beetles (Cerambycidae).

Results: Trends in MPB colonization were consistent across both years of sampling, 2007 and 2008. We found that MPB is more likely to colonize lodgepole pine trees that have been injured by fire than those that have not, and the beetles appear to first colonize trees of the "Moderate" category, followed by trees of the "Low" category, and lastly trees of the "High" category. Interspecific competition incurred by MPB intensifies with fire injury. More trees of the "High" category are colonized by wood borers and *Ips* sp. than are trees of the "Moderate" and "Low" categories. Therefore the reproductive success of MPB in those trees it did successfully attack was often lower in severely fire-injured than non-injured lodgepole pines.
The population size of MPB appears to contribute to the colonization of fire-injured lodgepole pine trees. The ratios of fire-injured to non-fire-injured trees attacked were larger in sites where beetle populations are endemic than in sites where the beetle populations are epidemic.

The species of beetles present in the baited Lindgren Multiple Funnel traps were fairly consistent across the 8 burns. The majority of beetles captured were MPB, *Ips pini*, and *Monochamus scutellatus*. Elateridae (Coleoptera), Siricidae (Hymenoptera), and parasitoid wasps were also captured but in much smaller numbers. The number of mountain pine beetles captured in the baited traps differed among burn sites. Sites with epidemic MPB populations averaged 4000 beetles per trap, and sites with endemic MPB populations averaged 700 beetles per trap.

Discussion. Our results reinforce the view that the population dynamics of tree-killing bark beetles are highly complex, and that simple extrapolations from increased numbers of killed trees to projected likelihoods of stand- or landscape- scale outbreaks are not valid. Specifically, our results indicate that MPB is more likely to colonize fire-injured than healthy lodgepole pines, but their reproductive success is often lower in severely fired-injured trees due to higher interspecific competition and perhaps reduced substrate quality within them. MPB population eruptions are dependent on several tree- and stand-level drivers, such as host susceptibility, host substrate quality, insect competition, and regional beetle dynamics (Raffa et al. 2008). Our results suggest that fire injury can improve the favorability of one driver while decreasing the favorability of another. This hypothesis will be examined in depth from population and tree physiological data collected during the summers of 2008 and 2009, in work supported by additional funding sources.

Presentation of Results and Future Directions: The above preliminary results were presented at three meetings during 2008: a student presentation was given at the annual conference for the International Association of Landscape Ecology in May, 2008, a field trip was co-led with Martin Simard and Jacob Griffin for the International Association of Wildland Fire in September, 2008, and a student presentation was given at the annual conference for the

Entomological Society of America in November, 2008. This work also contributed to the training of one graduate student and two undergraduate students (see below).

The preliminary results were also used to support a competitive proposal to the NSF Ecology program. This proposal was successful, and awarded in 2008 to Drs. Kenneth Raffa and Phillip Townsend. This NSF funded project will investigate the physiological and biochemical mechanisms of tree defense affected by fire-injury, mechanisms of competitive interactions between 'secondary' insects and mountain pine beetle, effects of fire injury on the nutritional quality (particularly nitrogen content) of lodgepole pine for MPB larvae, effects of fire injury on the microbial symbionts of MPB, and population-level responses of MPB to stands with varying numbers and severities of fire-injured trees.

MANAGEMENT IMPLICATIONS

(1) Our findings suggest that mountain pine beetle infestation in lodgepole pine does not increase the subsequent risk of active crown fire, and that fire does not necessarily cause an epidemic of mountain pine beetle in nearby lodgepole pine.

Rather than elevating subsequent risk of severe fire, our findings suggest that bark beetle infestation may reduce the likelihood of active crown fire for up to 30 years. Our results showed no evidence of an increased crown fire risk, counter to perceptions that seem to be widespread; in essence, the beetles are thinning the forest. However, probability of passive crown fires was greater 25 to 35 years after beetle outbreak compared to undisturbed stands. Similarly, our results show no evidence that fire damage initiates beetle outbreak in areas with low, endemic beetle populations. Notably, severe fires and bark beetle infestations are both more likely during drought conditions, and thus these natural disturbances can occur together. However, this co-occurrence does not appear to be a "cause-effect" relationship, but rather a response to the same drivers.

(2) Our findings indicated that mountain pine beetles preferred whitebark pine relative to lodgepole pine. Furthermore, mountain pine beetles were more likely to select whitebark pine trees that were infected by white pine blister rust.

Climatic warming appears to be associated with the expansion of mountain pine beetles to habitats that previously had only rarely been affected and into habitats with new (naïve) species associations. In Greater Yellowstone, whitebark pine forests were not often subjected to MPB infestation in the past presumably because cold temperatures at the higher elevations limited distribution and reproduction of the beetles. Whitebark pine lacks defensive adaptations to bark beetles and is experiencing elevated mortality in the current outbreak. White pine blister rust also appears to increase susceptibility of the trees to subsequent beetle attack. Thus, whitebark pine communities are likely to be at greater risk of extreme tree mortality or even local extirpation compared to other conifers. Unfortunately, there may be relatively little that managers can do to prevent infestation and extensive mortality in whitebark pine forests.

(3) Even within high-severity bark beetle infestations, all lodgepole pine trees were not killed. These forests generally remain well stocked, with density of young trees sufficient to replace individuals lost during the current epidemic.

In our study, basal area killed in lodgepole pine ranged from 60 to 80%, but the number of trees killed ranged from only 40 to 60%. Beetles were limited to mature lodgepole pine, whereas advance regeneration (younger or suppressed lodgepole pines, and other species such as Engelmann spruce and subalpine fir) generally was not affected. With reduced competition, these surviving trees are likely to grow rapidly in response to increased light, soil moisture and nutrient availability (Romme et al. 1986). The associated increase in herbaceous and understory vegetation may also benefit wildlife species. Thus, although it is visually striking, the MPB infestation in lodgepole pine forests of the GYE is not catastrophic and is unlikely to have a long-term detrimental effect on the forests (Rocca and Romme 2009).

(4) Post-disturbance management of stands affected by bark beetles <u>for the purpose of reducing fire hazard</u> is probably not needed in beetle-killed lodgepole pine forests of Greater Yellowstone.

Management activities such as salvage harvest are sometimes conducted to minimize the perceived risk of subsequent fire because an increase in fuels or flammability is often assumed. Our study found neither an increase in total fuel quantity nor potential for torching or crowning following beetle infestation in lodgepole pine. Salvage operations may be conducted to meet other goals, e.g., for eliminating tree-fall risks along roads and power-lines or obtaining marketable timber and fuel-wood, but the goal of reducing fire risk is not supported by our findings. Large, intense fires will occur in the future in beetle-affected areas, whether treated or not, but the behavior and effects of those fires likely will not exceed the historical behavior or effects of fire in this ecosystem, which is naturally characterized by episodic severe fire.

(5) Our findings support the need for forest managers to take a long-term and broad-scale view of timber and disturbance dynamics.

Incorporating understanding of large and severe natural disturbances into forest management continues to pose significant challenges for forest managers and the public. Because such disturbances, which include crown fires and bark beetle infestations, kill many trees and cause rapid and extensive changes in the forests, there can be considerable pressure to "do something" to save the forests and minimize subsequent risks. With respect to bark beetles and lodgepole pine, our data indicate that restocking will occur naturally in almost every affected stand. Forest canopies that have been severely thinned by beetles will fill in again primarily though growth of pre-existing advance regeneration rather than requiring new seedling recruitment. Stand-level productivity does decline initially, but growth of surviving plants accelerates. A key conclusion from this and other studies is that although individual *trees* are killed, lodgepole pine *forests* in Greater Yellowstone have not been "destroyed" either by recent fires or bark beetle outbreaks. Lodgepole pine forests will continue to be a dominant component of this landscape into the foreseeable future. However, many lodgepole pine forests will be composed of younger and smaller trees for the next several decades.

(6) Because climate drivers are so important for both fire and insect disturbances, forest managers may be very limited in their ability to change or stop these disturbances.

The set of conditions that produce bark beetle epidemics is complex and requires crossing a series of biological thresholds related to host entry, aggregation, establishment, reproduction, stand-level eruption, and finally landscape-level eruption (see Raffa et al. 2008 for a full discussion). Management will only be effective if it is targeted to the appropriate stage in development of the outbreak, and only if it prevents the next threshold from being exceeded. Once large-scale eruptions are underway, no known feasible management option can stop the eruption. The eruptions generally continue until the supply of suitable hosts is exhausted or until unseasonably cold temperatures occur over large areas. The perceived need "to do something" in response to these large, severe disturbances should be balanced by an understanding of the conditions under which management can be effective, and also by recognition of the natural role of episodic severe disturbances within the long-term dynamics of lodgepole pine ecosystems. The current mountain pine beetle outbreak has reached a level at which managers probably can do nothing to stop its continued spread across the landscape, although actions can be taken to preserve individual trees of special value at very local scales (e.g., around home sites or campgrounds). Fortunately, no action appears necessary to "save" the lodgepole pine forest ecosystem at a landscape scale, although local mitigation actions may be warranted, e.g., fuel reduction near homes and removal of dead trees near roads and power-lines. In contrast to the general resilience of lodgepole pine forests, the situation appears graver in whitebark pine forests, where the trees have little or no innate defensive capability against bark beetle attacks and where a non-native pathogen (blister rust) is further increasing the susceptibility of the trees to beetle-caused mortality. Unfortunately, there appears to be little that managers can do at this time to mitigate losses in whitebark pine forests of Greater Yellowstone.

RELATIONSHIP TO OTHER FINDINGS AND ONGOING WORK

We initiated and are conducting several other studies in Greater Yellowstone that directly complement this JFSP project. All of these studies were possible, in part, because of the research conducted as part of this project, and collectively, they will provide a more comprehensive understanding of disturbance interactions involving fire. First, Turner and Raffa, with graduate students Simard, Griffin and Powell, established a Joint Venture Agreement (JVA) with the USFS Western Wildland Environmental Threat Assessment Center (WWETAC) to provide input to forest managers regarding the interactions between fire and bark beetles and to study the ecological consequences of salvage harvest following mountain pine beetle infestations in lodgepole pine on the Bridger-Teton National Forest. Following a bark beetle outbreak, forest managers may conduct a salvage harvest to extract economically valuable timber and/or to reduce perceived risk of subsequent disturbance. However, the ecological consequences of post-beetle salvage harvest are largely unknown. Under the JVA with WWETAC, we summarized published literature on reciprocal interactions between fire and bark beetles to make this available for managers, and field studies of post-beetle salvage are ongoing. For additional information or to download the annotated bibliography, see http://www.fs.fed.us/wwetac/projects/turner.html. In addition, two years of pre-treatment data were obtained from 10 pairs of study plots in beetle-killed lodgepole pine, and salvage operations in half the plots (one plot of each pair) are in progress during summer/fall 2009. We

will evaluate changes in fuel characteristics and profiles following salvage, and compare regeneration, microclimate and nutrient availability between salvage and un-salvaged plots.

Second, based on the initial field season for Question 3 (see above), Raffa and Townsend, with graduate student Powell, received funding from the National Science Foundation to conduct a more comprehensive study of how fire damage may affect the vulnerability of lodgepole pine trees to insect attack. Fire is being evaluated within the set of conditions that can release eruptive population dynamics, to explicitly test the effects of fire on key processes affecting the herbivore's reproductive success, and to test its consequences to herbivore populations at broader scales. The study is addressing four major objectives. (i) Determine the relationship between fire injury and colonization by mountain pine beetle. (ii) Compare mountain pine beetle reproductive success in fire-injured versus non-injured trees. (iii) Quantify the likelihood that proximity to fire-injured trees will affect subsequent colonization of healthy trees by mountain pine beetles, and how this relationship is influenced by regional patterns of infestation. (iv) Determine how components of host resistance and host quality important to mountain pine beetle reproductive success are affected by fire injury. This study will produce new understanding of the effects of fire on bark beetles by taking a more mechanistic approach to the work that was part of the current JFSP project.

Third, building upon the present study, Turner, Romme and Townsend, with Renkin as federal cooperator, are beginning a new JFSP-funded study designed (i) to extend our studies in lodgepole pine of how fuel profiles and fire hazard change following bark beetle infestation to Douglas-fir forests, (ii) to determine how actual spatial variation of fire severity across the landscape was related to pre-fire beetle infestation by sampling in recently burned forests in Greater Yellowstone, and (iii) to model the effects of a wide range of common forest management practices (e.g., thinning, removal of beetle killed trees or remaining small trees, slash management, etc.) in beetle-killed lodgepole pine and Douglas-fir forests on future fire hazard. Study sites will be located on both the Bridger-Teton and Shoshone National Forests, and we will be able to test directly (using recent fires) the effects of recent beetle infestation on fire.

In addition to our ongoing related studies, we are also communicating with other research groups in the Rocky Mountains who are also studying bark beetle-fire interactions. This has included informal contacts by email to discuss findings and discussion at professional conferences and regional meetings.

FUTURE WORK NEEDED

Future work should include empirical studies of fire frequency and severity in the full range of western forest types that have and have not been affected by bark beetles while accounting for the influences of forest type, time-since-beetle outbreak and climatic conditions. The conditions under which variation in fuels is and is not important to fire spread and severity should be identified, particularly given anticipated climate change. Because post-disturbance management can affect subsequent fire hazard, there is also a need for future work on the consequences of salvage harvest and other post-disturbance treatments for stand regeneration and fire hazard. Fire hazard must be balanced against a wider array of ecosystem services, and forest disturbance

dynamics must be considered over long time periods and across large landscapes. The prognosis for future fire regimes and bark beetle infestations must consider the effects of global climate change. Therefore, we suggest that additional research address the effects of natural disturbances and an array of potential post-disturbance treatments on a range of ecosystem services in western forests, and that the sustainability of forests be considered over the long term. Effective methods to inform forest managers and the public about current scientific understanding – particularly if the data contradict perceptions or "conventional wisdom" – are also needed.

DELIVERABLES CROSSWALK

Deliverable	**Description**	**Delivery Dates**	**Status**
Annual maps of tree mortality from bark beetles	Annual maps of percent dead basal area for current infestation of MPB in GYE (*Will be available on appropriate institutional/agency websites*)	2007-09	Maps now available on Townsend lab website at University of Wisconsin. https://mywebspace.wisc.edu/ptownsend/public/Yellowstone/
Journal article	Influence of fine-scale factors on MPB infestation (**Bockino and Tinker**) (*Forest Ecology and Management*)	2007	Thesis completed; Revised manuscript to be resubmitted Oct. 2009 to *Forest Ecology and Management*.
Imagery Algorithms/Journal article	New algorithms based on Landsat imagery that can be applied in other lodgepole-pine dominated landscapes to quantify and map beetle infestation (**Townsend and Jin**) (*International Journal of Remote Sensing*)	2008	Manuscript in preparation to be submitted to *Remote Sensing of Environment*.
Journal article	Factors explaining broad-scale patterns of MPB infestation (**Simard et al.**) (*Global Ecology and Biogeography*)	2009	Manuscript to be submitted November 2009
Journal article	Simard, M., W.H. Romme, J.M. Griffin, and M.G. Turner. Do mountain pine beetle outbreaks change fire hazard in lodgepole pine forests?	2009	To be submitted October 2009 to *Ecological Monographs*.
Journal article	Bark beetle/wildfire interactions in the Greater Yellowstone Ecosystem (**Romme**) (*Yellowstone Science*)	2009	Article to reach regional managers and those interested in Greater Yellowstone; paper may be led by **Erinn Powell** and will be developed after primary data papers are completed.
Journal article	Influence of MPB on fuel	2009	For managers, read by foresters; needs to be based on

	accumulations in forests of the GYE (**Turner**) (*Journal of Forestry*)		the previous papers.
Technical Report	Wildfire/bark beetle interactions: forest effects and management guidelines (**Tinker**) (*General Technical Report*)	2009-2010	Will be written based on our final report during 2010.
Final Report	Final Scientific Report to JFSP (**Tinker and others**)	2009	Final Report submitted Sept. 30, 2009
Workshop	Workshop or seminar presenting results of study to interagency managers	2009-10	A field trip for participants at the 2008 Fire Conference (Jackson, WY) was led by Simard, Powell and Griffin
Synthesis paper	Integrative peer-reviewed journal article summarizing proposed study (**Tinker, Romme, Turner, Townsend**) (*Frontiers in Ecology and the Environment*)	2009-10	To be written during 2010.
Websites	Project results, maps, etc. available on appropriate institutional/agency websites	2008-09	Synopsis of project is on Turner lab web site. Will also be added to Tinker lab website in 2009.

PUBLICATIONS

Published or in press:

Raffa, K. F., B. H. Aukema, B. J. Bentz, A. L. Carroll, J. A. Hicke, M. G. Turner and W. H. Romme. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. BioScience 58:501-517.

Manuscripts in preparation:

Jin, S., P. Townsend, M. Simard, J. Griffin and M. Turner, in prep. Mapping the severity of bark beetle outbreaks across years using image statistical properties. Complete manuscript (9/29/09), to be submitted to *Remote Sensing of Environment*.

Theses and dissertations:

Bockino, N. K. Interactions of white pine blister rust, host species, and mountain pine beetle in whitebark pine ecosystems in the Greater Yellowstone. MS Thesis, Department of Botany, University of Wyoming. May 2008

Simard, M. Bark beetle–fire–forest interactions in the Greater Yellowstone Ecosystem (tentative title). PhD Dissertation, Department of Zoology, University of Wisconsin-Madison. Anticipated completion in 2009.

Powell, E. N. Interactions between disturbance agents in conifer forests: fire-scorched trees as a potential reservoir of and suboptimal resource for endemic mountain pine beetles (tentative title). Department of Entomology, University of Wisconsin-Madison. Anticipated completion in 2010.

Outreach to managers:

Simard, M., E. N. Powell, J. M. Griffin, K. F. Raffa and M. G. Turner. 2008. Annotated bibliography for forest managers on fire-bark beetle interactions. US Forest Service, Western Wildland Environmental Threat Assessment Center. http://www.fs.fed.us/wwetac/publications.html.

Simard, M., J.M. Griffin, & E.N. Powell, in collaboration with M.G. Turner, K.F. Raffa, P.A. Townsend, D.B. Tinker, & W.H. Romme. 2008. Reciprocal interactions between bark beetle outbreaks and wildfires in subalpine lodgepole pine forests. Field guide for an excursion organized for the conference “The ‘88 Fires: Yellowstone and Beyond” and 9th Biennial Scientific Conference on the Greater Yellowstone Ecosystem, Jackson, WY,September 26. 45 p.

Field Trips:

Simard, M., Griffin, J.M., Powell, E.N. 2008. Reciprocal interactions between bark beetle outbreaks and wildfires in subalpine lodgepole pine forests. September 22-27, 2008. International Association of Wildland Fire Annual Conference: The '88 Fires Yellowstone and Beyond. Jackson, WY.

Conference Presentations:

Simard, M., W. H Romme, J. M Griffin, D. B Tinker and M. G Turner. 2009. Do mountain pine beetle outbreaks reduce the risk of active crown fires in the Greater Yellowstone Ecosystem? Annual Meeting of the Ecological Society of America, Albuquerque, NM.

Simard, M., W.H. Romme, J.M. Griffin D.B. Tinker, and M.G. Turner. 2008. Do bark beetle outbreaks increase fire risk in the western US? A synthesis of current knowledge and fuel dynamics in the Greater Yellowstone Ecosystem."The '88 Fires: Yellowstone and Beyond" and 9th Biennial Scientific Conference on the Greater Yellowstone Ecosystem, Jackson, WY, September 22-25.

Simard, M., J.M. Griffin, P.A. Townsend, and S. Jin. 2008. Disturbance severity and post-disturbance biomass recovery in western subalpine forests: a comparison of bark beetle outbreaks and wildfires. 23rd Annual Meeting of the International Association for Landscape Ecology, US chapter (US-IALE), Madison (WI), April 6-10.

Simard, M. and M.G. Turner. 2006. Explaining broad-scale patterns of infestation of three bark beetle species in the Greater Yellowstone Ecosystem. 3rd International Fire Ecology and Management Congress, San Diego (CA). November 13-17.

Bockino, N, and D.B. Tinker. 2006. Blister rust and mountain pine beetle interactions in whitebark pine ecosystems in the Greater Yellowstone Ecosystem. Grand Teton National Park Resource Information Exchange, September.

Bockino, N, and D.B. Tinker. 2006. Blister rust and mountain pine beetle interactions in whitebark pine ecosystems in the Greater Yellowstone Ecosystem. 3rd International Fire Ecology and Management Congress, San Diego, CA, November 13-17.

Bockino, N, and D.B. Tinker. 2006. Blister rust and mountain pine beetle interactions in whitebark pine ecosystems in the Greater Yellowstone Ecosystem. Jackson Hole Wildlife Symposium, Jackson, WY, December.

Bockino, N, and D.B. Tinker. 2007. Blister rust and mountain pine beetle interactions in whitebark pine ecosystems in the Greater Yellowstone Ecosystem. University of Wyoming Graduate Student Research Symposium, Laramie, WY, April.

Bockino, N, and D.B. Tinker. 2007. Blister rust and mountain pine beetle interactions in whitebark pine ecosystems in the Greater Yellowstone Ecosystem. Front Range Graduate Student Ecology Symposium, Ft. Collins, CO, April.

Bockino, N, and D.B. Tinker. 2007. Blister rust and mountain pine beetle interactions in whitebark pine ecosystems in the Greater Yellowstone Ecosystem. Annual Meeting of the Ecological Society of America, San Jose, CA.

Bockino, N, and D.B. Tinker. 2007. Blister rust and mountain pine beetle interactions in whitebark pine ecosystems in the Greater Yellowstone Ecosystem. Greater Yellowstone Whitebark Pine Coordinating Committee Resource Information Exchange, Bozeman, MT, October.

Bockino, N, and D.B. Tinker. 2008. Blister rust and mountain pine beetle interactions in whitebark pine ecosystems in the Greater Yellowstone Ecosystem. Grand Teton Fire Ecology Symposium, Jackson, WY, February .

Bockino, N, and D.B. Tinker. 2008. Blister rust and mountain pine beetle interactions in whitebark pine ecosystems in the Greater Yellowstone Ecosystem. Whitebark Ecosystem Foundation, Annual Meeting, Driggs, ID.

Bockino, N, and D.B. Tinker. 2009. Blister rust and mountain pine beetle interactions in whitebark pine ecosystems in the Greater Yellowstone Ecosystem. North American Forest Ecology Workshop, Logan, UT, June.

Jin, S., P.A. Townsend, M. Simard and J. Griffin. 2008. Spatial patterns of bark beetle disturbance in the Greater Yellowstone Ecosystem. US-IALE 2008 Symposium (Madison).

Powell, E., and Raffa, K.F. Fire injury increases both host susceptibility and competitor load for the mountain pine beetle (Dendroctonus ponderosae Hopkins): Implications to population dynamics and outbreaks. Student Competition Presentation. Entomological Society of America. Reno, NV. November 2008.

Powell, E., and Raffa, K.F. Interactions between disturbance agents in conifer forests: fire-injured lodgepole pine as a potential reservoir for mountain pine beetles (Dendroctonus ponderosae Hopkins). Student Presentation. International Association of Landscape Ecology. Madison, WI. April 2008.

Romme, W,H., and M. Simard. 2008. Bark beetle outbreaks and fire hazard in Rocky Mountain coniferous forests: the status of our knowledge. Invited presentation to Colorado bark beetle cooperative, Denver, CO, 11/17/09.

REFERENCES CITED

Ahern, F.J. 1988. The effects of bark beetle stress on the foliar spectral reflectance of lodgepole pine. International Journal of Remote Sensing 9:1451-1468.

Allen, T. R., and J. A. Kupfer. 2000. Application of spherical statistics to change vector analysis of Landsat data: Southern Appalachian spruce-fir forests. Remote Sensing of Environment 74:482-493.

Allen, T. R., and J. A. Kupfer. 2001. Spectral response and spatial pattern of Fraser fir mortality and regeneration, Great Smoky Mountains, USA. Plant Ecology 156:59-74.

Amman, G.D. 1991a. Insect infestation of fire-injured trees in the Greater Yellowstone area. Gen. Tech. Rep. INT-398. USDA For. Serv. Intermt. Res. Stn. 9 pp.

Amman, G.D. 1991b. Bark beetle-fire associations in the greater Yellowstone area. In Fire and the Environment: Ecological and cultural perspectives, Proc. Int. Symp. Gen. Tech. Rep. SE-69, pp. 313-320. USDA For. Serv. Southeast. For. Exp. Stn.

Amman, G.D. & Schmitz, R.F. 1988. Mountain pine beetle – lodgepole pine interactions and strategies for reducing tree losses. Am. Bio. 17: 62-68.

Bebi, P., D. Kulakowski, and T.T. Veblen. 2003. Interactions between fire and spruce beetles in a subalpine Rocky Mountain forest landscape. Ecology 84: 362-371.

Bessie, W. C., and E. A. Johnson. 1995. The relative importance of fuels and weather on fire behavior in sub-alpine forests. Ecology **76**:747-762.

Bigler, C., D. Kulakowski, and T. T. Veblen. 2005. Multiple disturbance interactions and drought influence fire severity in Rocky Mountain subalpine forests. Ecology 86:3018-3029.

Bradley, T., and P. Tueller. 2001. Effects of fire on bark beetle presence on Jeffrey pine in the Lake Tahoe Basin. Forest Ecology and Management **142**:205-214.

Brown, J. K. 1974. Handbook for inventorying downed woody material. Gen. Tech. Rep. INT-16, USDA For. Serv., Interm. For. Rang. Exp. Stn, Ogden, UT.

Chalifoux, S., F. Cavayas, and J. T. Gray. 1998. Map-guided approach for the automatic detection on Landsat TM images of forest stands damaged by the spruce budworm. Photogrammetric Engineering and Remote Sensing 64:629-635.

Cohen, W. B., T. A. Spies, and M. Fiorella. 1995. Estimating the age and structure of forests in a multi- ownership landscape of western Oregon, USA. International Journal of Remote Sensing 16:721-746.

Cohen, W. B., and M. Fiorella. 1998. Comparison of methods for detecting conifer forest change with thematic mapper imagery. Pages 89-102 in R. S. Lunetta and C. D. Elvidge, editors. Remote Sensing Change Detection: Environmental Monitoring Methods and Applications. Ann Arbor Press, Chelsea, MI.

Cohen, W. B., M. Fiorella, J. Gray, E. Helmer, and K. Anderson. 1998. An efficient and accurate method for mapping forest clearcuts in the Pacific Northwest using Landsat imagery. Photogrammetric Engineering and Remote Sensing 64:293-300.

Cole, W.E. & Amman, G.D. 1969. Mountain pine beetle infestations in relation to lodgepole pine diameters. USDA Forest Service, Intermountain Forest and Range Experiment Station, Research Paper INT-96.

Collins, J. B., and C. E. Woodcock. 1996. An assessment of several linear change detection techniques for mapping forest mortality using multitemporal Landsat TM data. Remote Sensing of Environment 56:66-77.

Derose, R. J., and J. N. Long. 2009. Wildfire and spruce beetle outbreak: Simulation of interacting disturbances in the central Rocky Mountains. Ecoscience **16**:28-38.

Despain, D. G. 1990. Yellowstone vegetation: consequences of environment and history in a natural setting. Rinehart Publishers, Boulder, CO.

Elkin, C. M., and M. L. Reid. 2004. Attack and reproductive success of mountain pine beetles (Coleoptera : Scolytidae) in fire-damaged lodgepole pines. Environmental Entomology **33**:1070-1080.

Fleming, R.A., J. Candau, and R.S. McAlpine. 2002. Landscape-scale analysis of interactions between insect defoliation and forest fire in central Canada. Climatic Change 55: 251-272.

Foster, J. R., and P. A. Townsend. 2004. Linking hyperspectral imagery and forest inventories for forest assessment in the Central Appalachians. in Proceedings of the 14th Central Hardwood Conference, March 17-19, 2004. USDA Forest Service General Technical Report.

Franklin, S. E., M. A. Wulder, R. S. Skakun, and A. L. Carroll. 2003. Mountain pine beetle red-attack forest damage classification using stratified Landsat TM data in British Columbia, Canada. Photogrammetric Engineering and Remote Sensing 69:283-288.

Furniss, M. M. and R. Renkin. 2003. Forest entomology in Yellowstone National Park, 1923-1957: a time of discovery and learning to let live. American Entomologist 49:199-209.

Geiszler, D. R., R. I. Gara, C. H. Driver, V. F. Gallucci, and R. E. Martin. 1980. Fire, fungi, and beetle influences on a lodgepole pine ecosystem of south-central Oregon. Oecologia 46:239-243.

Goodwin, N. R., N. C. Coops, M. A. Wulder, S. Gillanders, T. A. Schroeder, and T. Nelson. 2008. Estimation of insect infestation dynamics using a temporal sequence of Landsat data. Remote Sensing of Environment **112**:3680-3689.

Hall, F. G., D. B. Botkin, D. B. Strebel, K. D. Woods, and S. J. Goetz. 1991. Large-scale patterns of forest succession as determined by remote sensing. Ecology 72:628-640.

Healey, S.P., Yang, Z.Q., Cohen, W.B., & Pierce, D.J. (2006). Application of two regression-based methods to estimate the effects of partial harvest on forest structure using Landsat data. *Remote Sensing of Environment, 101*, 115-126.

Hunt, E.R., & Rock, B.N. 1989. Detection of changes in leaf water content using near-infrared and middle-infrared reflectances. *Remote Sensing of Environment, 30*, 43-54.

Jenkins, M.J., E. Hebertson, W. Page, and C.A. Jorgensen. 2008. Bark beetles, fuels, fires, and implications for forest management in the Intermountain West. Forest Ecology and Management 254: 16-34.

Jin, S.M., & Sader, S.A. (2005). Comparison of time series tasseled cap wetness and the normalized difference moisture index in detecting forest disturbances. *Remote Sensing of Environment, 94*, 364-372.

Johnson, E. A. 1992. Fire and vegetation dynamics: Studies from the North American boreal forest. Cambridge Studies in Ecology. Cambridge University Press.

Key, C.H., and Benson, N.C. (2006). Landscape assessment: sampling and analysis methods. In D.C. Lutes, R.E. Keane, J.F. Caratti, N.C. Benson, S. Sutherland & L.J. Gangi (Eds.), *FIREMON: Fire effects monitoring and inventory system* (pp. LA1-LA51). Fort Collins, Co: Gen. Tech. Rep. RMRS-GTR-164-CD, USDA For. Serv., Rocky Mtn Res. Stn.

Knight, D. H. 1987a. Ecosystem studies in the subalpine coniferous forests of Wyoming. Pages 235-242 in: Troendle, C. A., M. R. Kaufmann, R. H. Hamre, and R. P. Winokur

(technical coordinators), Management of subalpine forests: building on 50 years of research. USDA Forest Service General Technical Report RM-149.
Knight, D. H. 1987b. Parasites, lightning and the vegetation mosaic in wilderness landscapes. Pages 59-83 in: M. G. Turner, editor. Landscape heterogeneity and disturbance. Springer-Verlag, New York.
Kulakowski, D., T. T. Veblen, and P. Bebi. 2003. Effects of fire and spruce beetle outbreak legacies on the disturbance regime of a subalpine forest in Colorado. Journal of Biogeography 30:1445-1456.
Lambin, E. F., and A. H. Strahler. 1994. Change-vector analysis in multitemporal space - a tool to detect and categorize land-cover change processes using high temporal-resolution satellite data. Remote Sensing of Environment 48:231-244.
Littell, J. S., D. McKenzie, D. L. Peterson, and A. L. Westerling. 2009. Climate and wildfire area burned in western U. S. ecoprovinces, 1916-2003. Ecological Applications **19**:1003-1021.
Lombardero, M. J., M. P. Ayres, and B. D. Ayres. 2006. Effects of fire and mechanical wounding on Pinus resinosa resin defenses, beetle attacks, and pathogens. Forest Ecology and Management **225**:349-358.
Lunetta, R. S., and C. D. Elvidge, editors. 1998. Remote Sensing Change Detection: Environmental Monitoring Methods and Applications. Ann Arbor Press, Chelsea, Mich.
Luther, J. E., S. E. Franklin, J. Hudak, and J. P. Meades. 1997. Forecasting the susceptibility and vulnerability of balsam fir stands to insect defoliation with Landsat Thematic Mapper data. Remote Sensing of Environment 59:77-91.
Lynch, H.J., and P.R. Moorcroft. 2005. Spatiotemporal dynamics of insect-fire interactions. Abstract and oral presentation, 90th Annual meeting of the Ecological Society of America, Montreal, Canada.
Lynch, H.J., R.A. Renkin, R.L. Crabtree, and P.R. Moorcroft. 2006. The influence of previous mountain pine beetle (*Dendroctonus ponderosae*) activity on the 1988 Yellowstone fires. Ecosystems 9: 1318-1327.
Manly, B.F., McDonald, T.L. & Erickson, W. 2002. Resource selection by animals: statistical design and analysis for field studies. 2nd ed. Kluwer Press, New York, NY.
McCullough, D.G., R.A. Werner, and D. Neumann. 1998. Fire and insects in northern and boreal forest ecosystems of North America. Annual Review of Entomology 43: 107-127.
McHugh, C. W., T. E. Kolb, and J. L. Wilson. 2003. Bark beetle attacks on ponderosa pine following fire in northern Arizona. Environmental Entomology **32**:510-522.
Millspaugh, S.H., C. Whitlock, and P.J. Bartlein. 2000. Variations in fire frequency and climate over the past 17000 years in Yellowstone National Park. Geology 28: 211-214.
Mitchell, R.G., and H.K. Preisler. 1991. Analysis of spatial patterns of lodgepole pine attacked by outbreak populations of the mountain pine beetle. For. Sci. 37: 1390-1408.
NPS-USGS. 2008. National Burn Severity Mapping project. Accessed online December 20, 2008: http://burnseverity.cr.usgs.gov
Page, W. G., and M. J. Jenkins. 2007a. Mountain pine beetle-induced changes to selected lodgepole pine fuel complexes within the intermountain region. Forest Science 53:507-518.
Page, W., and M. J. Jenkins. 2007b. Predicted fire behavior in selected mountain pine beetle-infested lodgepole pine. Forest Science 53:662-674.

Parker, D. L., and L. E. Stipe. 1993. A sequence of destruction: mountain pine beetle and wildfire. USDA Forest Service, Albuquerque, NM.

Parker, T. J., K. M. Clancy, and R. L. Mathiasen. 2006. Interactions among fire, insects and pathogens in coniferous forests of the interior western United States and Canada. Agricultural and Forest Entomology 8:167-189.

Raffa, K.F. and A.A. Berryman. 1987. Interacting selective pressures in conifer-bark beetle systems: a basis for reciprocal interactions? American Naturalist 129:234-262.

Rasmussen, L. A., G. D. Amman, J. C. Vandygriff, R. D. Oakes, A. S. Munson, and K. E. Gibson. 1996. Bark beetle and wood borer infestation in the Greater Yellowstone Area during four postfire years. USDA Forest Service Research Paper INT-RP-487. Intermountain Research Station. Ogden, Utah, USA.

Reinhardt, E., J. Scott, K. Gray, and R. Keane. 2006. Estimating canopy fuel characteristics in five conifer stands in the western United States using tree and stand measurements. Canadian Journal of Forest Research **36**:2803-2814.

Renkin, R. A., and D. G. Despain. 1992. Fuel moisture, forest type, and lightning-caused fire in Yellowstone National Park. Canadian Journal of Forest Research **22**:37-45.

Rocca, M. E., and W. H. Romme. 2009. Beetle-infested forests are not "destroyed". Frontiers in Ecology and the Environment **7**:71-72.

Romme, W.H. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. Ecological Monographs 52: 199-221.

Romme, W.H., D.H. Knight, and J.B. Yavitt. 1986. Mountain pine beetle outbreaks in the Rocky Mountains: Regulators of primary productivity? American Naturalist 127:484-494.

Safranyik, L., Shrimpton, D.M., & Whitney, H.S. 1974. Management of lodgepole pine to reduce losses from the mountain pine beetle. Canadian Forest Service, Technical Report 1. 24 p.

Santoro, A. E., M. J. Lombardero, M. P. Ayres, and J. J. Ruel. 2001. Interactions between fire and bark beetles in an old growth pine forest. Forest Ecology and Management **144**:245-254.

Schmid, J. M., and G. D. Amman. 1992. Dendroctonus beetles and old-growth forests in the Rockies. Pages 51-59 in: Kaufmann, M. R., W. H. Moir, and R. L. Bassett (technical coordinators), Old-growth forests of the southwest and Rocky Mountain regions: proceedings of a workshop. USDA Forest Service General Technical Report RM-213.

Schott, J. R., C. Salvaggio, and W. J. Volchok. 1988. Radiometric Scene Normalization Using Pseudoinvariant Features. Remote Sensing of Environment 26:1-16.

Schwandt, J.W. & Kegley, S. 2004. Mountain pine beetle, blister rust, and their interaction on whitebark pine at Trout Lake and Fischer Peak in northern Idaho from 2001-2003. USDA Forest Service, R-1, FHP 04-9.

Scott, J. H., and E. D. Reinhardt. 2001. Assessing crown fire potential by linking models of surface and crown behavior. Res. Pap. RMRS-RP-29, USDA For. Serv., Rocky Mtn Res. Stn, Ogden, UT.

Skakun, R. S., M. A. Wulder, and S. E. Franklin. 2003. Sensitivity of the thematic mapper enhanced wetness difference index to detect mountain pine beetle red-attack damage. Remote Sensing of Environment 86:433-443.

Simard, M., Powell, E.N., Griffin, J.M., Turner, M.G. 2008. Annotated bibliography for forest managers on fire-bark beetle interactions. Prepared for the Western Wildlands

Environmental Threat Assessment Center, Jan 18, 2008. 14 p. URL: http://www.fs.fed.us/wwetac/publications/WWETAC_Fire-BB_InterX_25Feb2008.pdf

Six, D.L., and Adams, J.C. 2007. Relationships between white pine blister rust and the selection of individual whitebark pine by the mountain pine beetle. J. Ento. Sci. 42: 345-353.

Six, D.L. & Newcomb, M. 2005. A rapid rating system for rating white pine blister rust incidence, severity, and within-tree distribution in whitebark pine. Northwest Science. 79(2/3):189-195.

Sullivan, B. T., C. J. Fettig, W. J. Otrosina, M. J. Dalusky, and C. W. Berisford. 2003. Association between severity of prescribed burns and subsequent activity of conifer-infesting beetles in stands of longleaf pine. Forest Ecology and Management **185**:327-340.

Townsend, P. A., and S. J. Walsh. 2001. Remote sensing of forested wetlands: application of multitemporal and multispectral satellite imagery to determine plant community composition and structure in Southeastern USA. Plant Ecology 157:129-149.

Turner, .G., and W.H. Romme. 1994. Landscape dynamics in crown fire ecosystems. Landscape Ecology 9:59-77.

Turner, M. G., W. H. Romme, and R. H. Gardner. 1999. Prefire heterogeneity, fire severity, and early postfire plant reestablishment in subalpine forests of Yellowstone National Park, Wyoming. International Journal of Wildland Fire 9: 21-36.

Turner, M.G., D.B. Tinker, W.H. Romme, D.M. Kashian, and C.M. Litton. 2004. Landscape patterns of sapling density, leaf area, and aboveground primary production in postfire lodgepole pine forests, Yellowstone National Park. Ecosystems 7: 751-775.

USDA Forest Service (2008). MODIS Active Fire Mapping Program. Accessed online December 15, 2008: http://activefiremaps.fs.fed.us/.

Veblen, T.T., K.S. Hadley, E.M. Nel, T. Kitzberger, M.Reid, and R. Villalba. 1994. Disturbance regime and disturbance interactions in a Rocky Mountain subalpine forest. Journal of Ecology 82: 125-135.

Wallin, K. F., T. E. Kolb, K. R. Skov, and M. R. Wagner. 2003. Effects of crown scorch on ponderosa pine resistance to bark beetles in northern Arizona. Environmental Entomology **32**:652-661.

Waring, K.M., and D.L. Six. 2005. Distribution of bark beetle attacks after whitebark pine restoration treatments: a case study. Western Journal of Applied Forestry 20: 110-116.

Wulder, M. A., C. C. Dymond, J. C. White, and B. J. Erickson. 2006a. Detection, mapping, and monitoring of the mountain pine beetle. Pages 123-154 *in* L. Safranyik and B. Wilson, editors. The mountain pine beetle: A synthesis of biology, management, and impacts on lodgepole pine. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, B.C.

Wulder, M. A., C. C. Dymond, J. C. White, D. G. Leckie, and A. L. Carroll. 2006b. Surveying mountain pine beetle damage of forests: A review of remote sensing opportunities. Forest Ecology and Management **221**:27-41.