

Annotated Bibliography for Forest Managers on Fire-Bark Beetle Interactions

Prepared for USFS Western Wildlands Environmental Threats Assessment Center

January 18, 2008

Revised February 25, 2008

Martin Simard¹, Erinn N. Powell^{2,3}, Jacob M. Griffin¹,
Kenneth F. Raffa^{2,3}, and Monica G. Turner^{1,4}

¹Department of Zoology, ²Department of Forest and Wildlife Ecology,

³Department of Entomology

University of Wisconsin

Madison, WI 53706

⁴Email contact: turnermg@wisc.edu

In a nutshell

- *Forest managers in the western US are facing more fires and the most extensive bark beetle outbreaks recorded for the region.*
- *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 western coniferous forests.*
- *For the effects of bark beetles on fire:*
 - *There is increasing evidence that spruce beetle outbreaks **have no effect** on the occurrence and severity of stand-replacing fires in spruce-fir forests.*
 - *The effect of mountain pine beetle infestations on fire occurrence and severity in lodgepole pine forests **are unclear**; research results are ambivalent.*
 - *Effect of bark beetle outbreaks on fire in other forest types are unknown (ponderosa pine, pinyon-juniper) or need more research (Douglas-fir).*
 - *Time-since-beetle outbreak is an important factor to consider in the relationship between bark beetle outbreaks and fire risk because fuels change over time.*
- *For the effects of fire on bark beetle outbreaks:*
 - *There is increasing evidence that Douglas-fir beetle attack rates **are higher** on fire-injured Douglas-fir trees.*
 - *The evidence regarding effects of fire injury in lodgepole pine on mountain pine beetle attack rates **is inconclusive**, and whether attacks on fire-injured trees lead to subsequent attacks on healthy trees and/or outbreaks is not known.*
 - *Effects of fire injury on attack rates of tree-killing bark beetles in other systems (spruce beetle-Engelmann spruce, mountain pine beetle-ponderosa pine, Jeffrey pine beetle-Jeffrey pine) need more research.*
 - *Non-aggressive bark beetles such as Ips and wood borers have higher attack rates on fire-injured trees.*
 - *More studies are needed to test whether the above trends in attack rates result in changes in bark beetle reproductive success.*

Abbreviations: **DFB**, Douglas-fir beetle; **JPB**, Jeffrey pine beetle; **MPB**, Mountain pine beetle; **SB**, Spruce beetle;

I. Current trends in fire and bark beetle activity in western forests

Context: 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; understanding these effects is crucial for wise stewardship of these landscapes.

Fire: Fire is a natural component of western conifer forests, although fire regimes vary substantially across the region by forest type (Schoennagel et al. 2004). Fire seasons during the past two decades have been among the most severe and expensive on record, and widespread media attention on wildfire has elevated public awareness and catalyzed management and policy responses (Allen et al. 2002, Stephens and Ruth 2005). The number of large fires in the northern Rocky Mountains has increased in association with warmer temperatures, earlier snowmelt, and longer fire seasons (Westerling et al. 2006), and this trend is likely to continue with global warming (Whitlock et al. 2003, Tymstra et al. 2007).

The distinction between natural understory fire regimes and stand-replacing fire regimes is particularly important in western forests (Brown 2000, Schoennagel et al. 2004). Understory fires burn at relatively low intensity and are typically characterized by short return intervals (for example, years to several decades). These surface fires burn along the ground, consuming woody fuels and understory vegetation, reducing tree regeneration, and maintaining an open forest structure. Historically, understory fire regimes dominated the open ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) forests of the West. In contrast, subalpine conifer forests are typically characterized by infrequent, high-severity fires that kill most of the canopy either via intense surface fire or fire spread through the crowns of the trees (active crown fires). Fire return intervals are long, ranging from 60 years or so in jack pine (*Pinus banksiana*) to several centuries in some spruce-fir (*Picea-Abies*) communities. Stand-replacing fire regimes dominate the extensive boreal forests and many forests of the Northern Rocky Mountains, including Yellowstone National Park (Turner and Romme 1994, Schoennagel et al. 2006). Climate, particularly severe regional drought, sets the stage for occasional years of extensive conflagrations, and it is these few large fires that account for most of the cumulative area burned over a long period of time (Johnson 1992, Johnson and Wowchuck 1993, Bessie and Johnson 1995, Flannigan and Wotton 2001).

Bark beetles: Insect outbreaks are also a significant component of the natural disturbance regime in western forests, affecting a larger area than fire each year (Kurz and Apps 1999, Dale et al. 2001). The severity of epidemics by some species has increased in recent years, and insects have expanded their ranges to new geographic areas and previously unaffected plant communities (Raffa et al. in press). Several species of native bark beetles (Curculionidae: Scolytinae) such as the mountain pine beetle (MPB; *Dendroctonus ponderosae*), Douglas-fir beetle (DFB; *Dendroctonus pseudotsugae*), and spruce beetle (SB; *Dendroctonus rufipennis*) are currently in outbreak phase in the Rocky Mountains, affecting millions of hectares of forest. As with fire, warming climate has been implicated in the increasing extent and severity of bark beetle outbreaks (Logan et al. 2003, Hicke et al. 2006).

An important distinction exists between bark beetle species that can kill live trees during outbreaks and the non-aggressive beetle species that mainly feed on dead or highly stressed trees. Most bark beetle species of the genus *Ips*, as well as wood borers (such as cerambycids, which are also called longhorned or roundheaded beetles, and buprestids which are also called flatheaded beetles) exclusively feed on weakened or dead trees, and their populations never or only rarely reach outbreak levels. On the other hand, several species of the genus *Dendroctonus*, such as the MPB, the DFB, the SB, and the Jeffrey pine beetle (JPB; *Dendroctonus jeffreyi*), undergo extensive outbreaks in which they kill large numbers of healthy trees.

Fire-beetle interactions: 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. Indeed, a recent review of federal forest-fire policy in the United States (Stephens and Ruth 2005) underscored the relative paucity of scientific information pertinent to regional issues regarding wildfire, noting that this lack of information “...cripples efforts to respond appropriately to accumulated fuels and high fire hazards.” Enhanced understanding of the influence of insect infestations on fire risk would allow land managers to focus their efforts in areas where risk is indeed elevated.

II. Beetle effects on fire activity

The potential effect of bark beetle outbreaks on fire risk has been discussed for a long time (reviewed by McCullough et al. 1998, Parker et al. 2006, Lynch 2006), but only recently have studies presented empirical data to detect and quantify this relationship. Some authors have claimed that beetle outbreaks set the stage for catastrophic wildfires (Hopkins 1909, Brown 1975, Geiszler et al. 1980, Parker and Stipe 1993), whereas others have stressed the importance of time since beetle outbreak (Gara et al. 1985, Schmid and Amman 1992, Romme et al. 2006) and theorized that crown fire risk might be increased only during the first year or two after an infestation because of dead needles still on the trees. After the dead needles fall to the ground, the risk of crown fire might actually be lower than pre-outbreak conditions because of reduced canopy continuity and bulk density, two important predictors of crown fire rate of spread. One to several decades after the outbreak, when beetle-killed snags fall on the ground and understory tree growth creates ladder fuels, the risk of crown fire may again be increased (Gara et al. 1985, Romme et al. 2006).

Recently published empirical studies have used two approaches to quantify the effect of bark beetle outbreaks on fire risk. Some studies have used a retrospective approach, comparing observed to expected patterns of area burned in a landscape that was previously affected by bark beetle outbreaks, whereas others have looked at potential fire behavior based on fire behavior models and fuel loadings sampled in the field (Table 1). Retrospective studies were done in spruce-fir (*Picea engelmannii*-*Abies lasiocarpa*) forests in Colorado (Bebi et al. 2003, Kulakowski et al. 2003, Bigler et al. 2005, Kulakowski and Veblen 2007) and in lodgepole pine (*Pinus contorta* var. *latifolia*) forests in Wyoming (Turner et al. 1999; Lynch et al. 2006), and looked at the change in fire occurrence and/or severity. **The majority of the studies undertaken in the spruce-fir forests did not support the hypothesized increase in fire occurrence, extent, or severity following SB or MPB outbreaks** at any of the time-since-beetle intervals

(range = 0-60 years) that were studied (Bebi et al., 2003, Kulakowski et al, 2003, Kulakowski and Veblen, 2007). One study (Bigler et al. 2005) found a slightly elevated probability of high-severity burns 60 years after a SB outbreak. However stand structure was by far a better predictor of fire severity than occurrence of previous beetle outbreaks *per se*, suggesting that stand structure, not tree mortality, was the driver of fire severity (Bigler et al. 2005). This result emphasizes the importance of considering time since beetle outbreak because bark beetle effects can be delayed through changes in forest structure. **Results for the lodgepole pine-dominated forests are less clear.** Turner et al. (1999) found that probability of severe fire increased with severe MPB damage and in late-successional stands, whereas it decreased with light or moderate beetle damage and in mid-successional stands; however beetle damage occurs in late-successional stands, and because these two variables were analyzed independently, it is not possible to untangle the respective effects of each. Using historical data in Yellowstone National Park, Lynch et al. (2006) found that the 1988 fires were slightly more likely (+11%) to occur in areas that were damaged by the mountain pine beetle in the 1970s, but there was no change in fire risk associated with the outbreaks of the 1980s. Lynch considered presence or absence of fire and not fire severity, which might explain why successional stage was not a significant variable in her analyses, contrary to the findings of other researchers (Renkin and Despain 1992, Turner et al 1999).

Studies that have looked at potential fire behavior (Page and Jenkins 2007a, 2007b; Jenkins et al. 2008) have compared undamaged stands to stands that were damaged recently (0-5 years post-outbreak) or decades ago (5-60 years post-outbreak) in three beetle/forest systems: DFB/Douglas-fir, MPB/lodgepole pine, and SB/Engelmann spruce (Table 1). These studies have found a consistent increase in *surface* fire intensity (fireline intensity and rate of surface fire spread) in 0-5 years post-outbreak stands (caused by a pulse of surface fine fuels from dead trees) and in 5-60 years post-outbreak stands (caused by an increase in wind speed in the more open stands). Probability of *crowning* (that is, the probability that a surface fire ignites tree crowns) was not tested in 0-5 years post-outbreak stands but was predicted to increase in 5-60 years post-outbreak stands because of lower crown base heights (that is, more ladder fuels allowing fuel continuity between forest floor and forest canopy) and higher surface fire intensity. However, *rate of crown fire spread* was reduced in 5-60 years post-outbreak stands because the density of the canopy (which needs to be above a certain threshold to allow active crown fires) was reduced by the beetles, which thinned the forest. This predicted reduction (or at least lack of increase) in active crown fire risk in post-outbreak stands support retrospective studies (see above) that have shown no effect of bark beetle outbreaks on occurrence of stand-replacing fires.

Collectively, studies to date have shown that time-since-beetle outbreak is critical in understanding the relationship between beetle outbreaks, stand structure, fuel dynamics and fire risk. Nonetheless, empirical studies remain relatively few.

Table 1. Published empirical studies on bark beetle effects on fire activity. N.A., not applicable.

Reference	Type of study	State	Forest type	Bark beetle species (1)	Time since beetle (yrs)	Effect of bark beetle outbreaks on	
						Fire occurrence or extent	Fire severity or behavior
Kulakowski and Veblen 2007	Retrospective	CO	Spruce-fir	SB, MPB	5	No effect	No effect
Bebi et al. 2003	Retrospective	CO	Spruce-fir	SB	0-50	No effect	N.A.
Kulakowski et al. 2003	Retrospective	CO	Spruce-fir	SB	0-50	No effect	N.A.
Bigler et al. 2005	Retrospective	CO	Spruce-fir	SB	60	N.A.	Minor increase in severity †
Lynch et al. 2006	Retrospective	WY	Lodgepole pine	MPB	7, 15	7 = No effect; 15 = Minor increase	N.A.
Turner et al. 1999	Retrospective	WY	Lodgepole pine	MPB	7-15	N.A.	Increase in severity †
Page and Jenkins 2007a, 2007b	Fuel sampling + potential fire behavior modeling	UT, ID	Lodgepole pine	MPB	5, 20	N.A.	5 = increased surface fire intensity and rate of spread; crowning and crown rate of spread not tested; 20 = increased surface fire intensity and rate of spread; increased risk of crowning; reduced crown rate of spread
Jenkins et al. 2008	Fuel sampling + potential fire behavior modeling	UT, ID	Douglas-fir, Lodgepole pine, Spruce-fir	DFB, MPB, SB	0-5, 5-60	N.A.	0-5 = increased surface fire intensity and rate of spread; crowning and crown rate of spread not tested 5-60 = increased surface fire intensity and rate of spread; increased risk of crowning ‡; reduced crown rate of spread ‡

(1) DFB, Douglas-fir beetle, *Dendroctonus pseudotsugae*; MPB, Mountain pine beetle, *Dendroctonus ponderosae*; SB, Spruce beetle, *Dendroctonus rufipennis*;

† Possible confounding effect of stand age / successional stage

‡ Data not shown in paper

III. Fire effects on beetle activity

Whether or not fire injury to trees facilitates beetle attack and outbreak has also been of concern to forest managers. In terms of host tree availability, fire strongly affects the species composition and structure of forests, which establishes the template on which beetles must find and colonize hosts (Bebi et al. 2003, Kulakowski et al. 2003, Barclay et al. 2005, Lynch 2006). At very broad spatial scales and over a long period of time, stand-replacing fires may reduce the risk of infestation by bark beetles (Veblen et al. 1994, Bebi et al. 2003, Kulakowski et al. 2003) because most tree-killing beetle species (such as MPB, SB, and DFB) have their highest rates of population increase when they develop in large-diameter trees with thick phloem (Reynolds and Holsten 1994, Negron 1998, Shore et al. 2000, Perkins and Roberts 2003, Negron and Popp 2004). However short-term (1-3 yrs) effects of fire injury on beetle dynamics raise more concerns among forest managers than long-term effects, so the rest of the text focuses on these more immediate effects. We consider effects at both the stand and tree scales.

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.

At the level of trees, some physiological responses of trees to fire injury appear common, but we do not have enough data to extrapolate from these responses to their effects on bark beetle reproduction and population dynamics. For example, crown scorch altered resin flow in ponderosa pine, and this was followed by variable but generally increased activity by *Dendroctonus* and *Ips* species (Wallin et al. 2003). Fire scorching of red pine (*Pinus resinosa*) also altered patterns of resin flow (Lombardero et al. 2006), but this had variable effects on the local abundance of different species of *Ips* beetles (Santoro et al. 2001). Furthermore, fire did not result in increased beetle-caused mortality of non-injured trees. Controlled burns of Jeffrey pine (*Pinus jeffreyi*) increased the incidence of colonization by Jeffrey pine beetle, red turpentine beetle (*D. valens*), and *Ips* spp. However, this colonization did not lead to increased attack of unburned trees near the burned area (Bradley and Tueller 1999). Thus, there is much uncertainty about the influence of fire on the susceptibility of scorched and nearby unburned trees to bark beetle attack.

Fire may also facilitate attack by other organisms that may weaken the trees and subsequently predispose them to bark beetles (Parker et al. 2006). For example, fire injury may increase tree susceptibility to root pathogens, which in turn can reduce stem defenses against bark beetles (Geiszler et al. 1980, 1984; Gara 1995). Likewise, Bradley and Tueller (2001) reported that attacks by the tree-killing Jeffrey pine beetle coincided with attacks by the red turpentine beetle, which does not kill trees, but vectors *Leptographium* fungi into roots and so predisposes trees to stem-colonizing bark beetle attack (Klepzig et al. 1991). Little is known about how fire injury affects the quality of the substrate for the development of bark beetle larvae. For example,

severely burned trees may have too little remaining utilizable phloem for larval development (White et al. 1992).

When all the above reports and studies are considered together, some trends seem to emerge in the response of tree-killing *Dendroctonus* beetles to fire (Table 2), although these trends should be interpreted with caution because of the high variability in the methods used. **All studies reviewed here found increased DFB attack rates in Douglas-fir trees that were moderately and/or highly injured by fire** (Furniss 1965, Amman and Ryan 1991, Rasmussen et al. 1996, Cunningham et al. 2005, Hood and Bentz 2007). On the other hand, **none of the studies that looked at fire injuries to lodgepole pine found increased MPB attack rates on severely fire-injured trees** (Geiszler et al. 1984, Amman and Ryan 1991, Rasmussen et al. 1996, Elkin and Reid 2004). Information on other species of tree-killing beetles is too scarce to draw conclusions, but suggest that both SB and JPB attack rates increase in fire-injured Engelmann spruce (Ammann and Ryan 1991, Rasmussen et al. 1996) and Jeffrey pine (Bradley and Tueller 2001), respectively. It should be noted that these trends only relate to bark beetle attack rates, which do not translate directly to reproductive success. Elkin and Reid (2004) examined MPB reproductive success in lodgepole pine with varying degrees of fire injury, and found that the number of offspring produced in moderately fire-injured trees increased when the local population density of the MPB was low. Very few other studies actually looked at beetle reproductive success in fire-injured vs. uninjured trees, which is a necessary step to determine if fires lead to increased tree-killing bark beetle populations in healthy forests. Many species of Cerambycidae, Buprestidae, Siricidae and secondary bark beetles that do not typically cause outbreaks are attracted to fire-injured trees (Table 2) (Evans 1964, 1966, Ross 1960, Wickman 1964). These insects can be important competitors of tree-killing bark beetles when both are present on weakened trees (Gara et al. 1995).

Table 2. Published empirical studies on fire effects on bark beetle activity. Only studies dealing with short-term effects (1-3 years after fire) are included. N.A., not applicable.

Reference	Type of study	State	Tree species (1)	Beetle species (2)	Effect of fire injury on	
					Attack incidence	Reproductive success
Hood and Bentz 2007	Field observation, wildfire	MT	Douglas-fir	DFB	Increased in moderate burn severity	N.A.
Cunningham et al. 2005	Field observation, wildfire	UT	Douglas-fir	DFB	Increased in moderate burn severity	Increased in moderate burn severity
Rasmussen et al. 1996	Field observation, wildfire	WY	Douglas-fir	DFB	Increased in high burn severity	N.A.
Amman and Ryan 1991	Field observation, wildfire	WY	Douglas-fir	DFB	Increased in moderate and high burn severity	N.A.
Furniss 1965	Field observation, wildfire	ID	Douglas-fir	DFB	Increased in moderate burn severity	N.A.
Elkin and Reid 2004	Field experiment	AB, BC	Lodgepole pine (<i>lat.</i>)	MPB	No effect	No effect at high beetle density; Increased at low beetle density
Rasmussen et al. 1996	Field observation, wildfire	WY	Lodgepole pine (<i>lat.</i>)	MPB	Inconclusive	N.A.
Amman and Ryan 1991	Field observation, wildfire	WY	Lodgepole pine (<i>lat.</i>)	MPB	Inconclusive	N.A.
Geiszler et al. 1984	Field observation, wildfire	OR	Lodgepole pine (<i>mur.</i>)	MPB	Increased in lightly injured trees	N.A.
Rasmussen et al. 1996	Field observation, wildfire	WY	Engelmann spruce	SB	Increased in moderate burn severity	N.A.
Amman and Ryan 1991	Field observation, wildfire	WY	Engelmann spruce	SB	Increased in high burn severity	N.A.
Bradley and Tueller 2001	Field observation, prescribed burn	NV	Jeffrey pine	JPB	Increased in fire-injured trees	N.A.
Wallin et al. 2003	Field observation, prescribed burn	AZ	Ponderosa pine	<i>Ips</i> spp. + <i>Dendroctonus</i> spp.	Increased in fire-injured trees	N.A.
McHugh et al. 2003	Field observation, wildfire and prescribed burn	AZ	Ponderosa pine	MPB + <i>Ips</i> spp.	No effect	N.A.
Geiszler et al. 1984	Field observation, wildfire	OR	Lodgepole pine (<i>mur.</i>)	<i>Ips</i> spp.	Increased with increasing burn severity	N.A.
Amman and Ryan 1991	Field observation, wildfire	WY	Lodgepole pine (<i>lat.</i>)	<i>Ips pini</i>	Increased in high burn severity	N.A.
Rasmussen et al. 1996	Field observation, wildfire	WY	Lodgepole pine (<i>lat.</i>)	<i>Ips pini</i>	Increased in high burn severity	N.A.
Santoro et al. 2001	Field observation, prescribed burn	MN	Red pine	<i>Ips pini</i>	Increased briefly in burned plots	N.A.
Santoro et al. 2001	Field observation, prescribed burn	MN	Red pine	<i>Ips grandicollis</i> , <i>Ips perrotti</i>	No effect	N.A.
Lombardero et al. 2006	Field experiment	WI	Red pine	<i>Ips grandicollis</i> + <i>Ips pini</i>	Increased in fire-injured trees	Null in fire-injured trees
Hanula et al. 2002	Field observation, wildfire	FL	Longleaf pine + Slash pine	<i>Ips grandicollis</i>	Reduced in fire-injured trees	N.A.
Hanula et al. 2002	Field observation, wildfire	FL	Longleaf pine + Slash pine	<i>Dendroctonus terebrans</i>	Reduced in fire-injured trees	N.A.
Hanula et al. 2002	Field observation, wildfire	FL	Longleaf pine + Slash pine	<i>Hylastes salebrosus</i>	Reduced in fire-injured trees	N.A.
Hanula et al. 2002	Field observation, wildfire	FL	Longleaf pine + Slash pine	<i>Hyloborus</i> spp.	Increased with increasing burn severity	N.A.
Sullivan et al. 2003	Field observation, prescribed burn	SC	Longleaf pine	<i>Ips grandicollis</i>	Increased in fire-injured trees	N.A.
Sullivan et al. 2003	Field observation, prescribed burn	SC	Longleaf pine	<i>Dendroctonus terebrans</i>	Increased in fire-injured trees	N.A.
Bradley and Tueller 2001	Field observation, prescribed burn	NV	Jeffrey pine	<i>Ips</i> spp.	Increased in fire-injured trees	N.A.
Bradley and Tueller 2001	Field observation, prescribed burn	NV	Jeffrey pine	Red turpentine beetle	Increased in fire-injured trees	N.A.
Amman and Ryan 1991	Field observation, wildfire	WY	Subalpine fir	Buprestids, Cerambycids	Increased in high burn severity	N.A.
McHugh et al. 2003	Field observation, wildfire and prescribed burn	AZ	Ponderosa pine	Buprestids, Cerambycids	Increased in high burn severity	N.A.

(1) Douglas-fir, *Pseudotsuga menziesii*; Engelmann spruce, *Picea engelmannii*; Jeffrey pine, *Pinus jeffreyi*; Lodgepole pine (*lat.*), *Pinus contorta* var. *latifolia*; Lodgepole pine (*mur.*), *Pinus contorta* var. *murrayana*; Longleaf pine, *Pinus palustris*; Ponderosa pine, *Pinus ponderosa*; Red pine, *Pinus resinosa*; Slash pine, *Pinus elliotii*; Subalpine fir, *Abies lasiocarpa*;

(2) DFB, Douglas-fir beetle, *Dendroctonus pseudotsugae*; JPB, Jeffrey pine beetle, *Dendroctonus jeffreyi*; MPB, Mountain pine beetle, *Dendroctonus ponderosae*; SB, Spruce beetle, *Dendroctonus rufipennis*; Pine engraver, *Ips pini*; Southern pine engraver, *Ips grandicollis*; Black turpentine beetle, *Dendroctonus terebrans*; Red turpentine beetle, *Dendroctonus valens*;

Bibliography for part I. Current trends in fire and bark-beetle activity in western forests

- Allen, C. D., M. Savage, D. A. Falk, K. F. Suckling, T. W. Swetnam, T. Schulke, P. B. Stacey, P. Morgan, M. Hoffman, and J. T. Klingel. 2002. Ecological restoration of southwestern ponderosa pine ecosystems: A broad perspective. *Ecological Applications* **12**:1418-1433.
- 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.
- Brown, J. K. 2000. Introduction and fire regimes. Pages 1-7 in J. K. Brown and J. K. Smith, editors. *Wildland fire in ecosystems: effects of fire on flora*. USDA Forest Service General Technical Report RMRS-GTR-42 volume 2, Ogden, UT. URL: http://www.fs.fed.us/rm/pubs/rmrs_gtr42_2.html
- Dale, V. H., L. A. Joyce, S. McNulty, R. P. Neilson, M. P. Ayres, M. D. Flannigan, P. J. Hanson, L. C. Irland, A. E. Lugo, C. J. Peterson, D. Simberloff, F. J. Swanson, B. J. Stocks, and B. M. Wotton. 2001. Climate change and forest disturbances. *BioScience* **51**:723-734.
- Flannigan, M. D., and B. M. Wotton. 2001. Climate, weather and area burned. Pages 351-373 in E. A. Johnson and K. Miyanishi, editors. *Forest fires*. Academic Press, New York.
- Hicke, J. A., J. A. Logan, J. Powell, and D. S. Ojima. 2006. Changing temperatures influence suitability for modeled mountain pine beetle (*Dendroctonus ponderosae*) outbreaks in the western United States. *Journal of Geophysical Research-Biogeosciences* **111**:G02019.
- Johnson, E. A. 1992. *Fire and vegetation dynamics: studies from the North American boreal forest*. Cambridge University Press, Cambridge, UK.
- Johnson, E. A., and D. R. Wowchuk. 1993. Wildfires in the southern Canadian Rocky Mountains and their relationship to mid-tropospheric anomalies. *Canadian Journal of Forest Research* **23**:1213-1222.
- Kurz, W. A., and M. J. Apps. 1999. A 70-year retrospective analysis of carbon fluxes in the Canadian forest sector. *Ecological Applications* **9**:526-547.
- Logan, J. A., J. Régnière, and J. A. Powell. 2003. Assessing the impacts of global warming on forest pest dynamics. *Frontiers in Ecology and the Environment* **1**:130-137.
- Raffa, K. F., B. H. Aukema, B. J. Bentz, A. L. Carroll, J. A. Hicke, M. G. Turner, and W. H. Romme. in press. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: dynamics of biome-wide bark beetle eruptions. *BioScience*.
- Schoennagel, T., M. G. Turner, D. M. Kashian, and A. Fall. 2006. Influence of fire regimes on lodgepole pine stand age and density across the Yellowstone National Park (USA) landscape. *Landscape Ecology* **21**:1281-1296.
- Schoennagel, T., T. T. Veblen, and W. H. Romme. 2004. The interaction of fire, fuels, and climate across rocky mountain forests. *BioScience* **54**:661-676.
- Stephens, S. L., and L. W. Ruth. 2005. Federal forest-fire policy in the United States. *Ecological Applications* **15**:532-542.

- Turner, M. G., and W. H. Romme. 1994. Landscape dynamics in crown fire ecosystems. *Landscape Ecology* **9**:59-77.
- Tymstra, C., M. D. Flannigan, O. B. Armitage, and K. Logan. 2007. Impact of climate change on area burned in Alberta's boreal forest. *International Journal of Wildland Fire* **16**:153-160.
- Westerling, A. L., H. G. Hidalgo, D. R. Cayan, and T. W. Swetnam. 2006. Warming and earlier spring increase western U.S. forest wildfire activity. *Science* **313**:940-943.
- Whitlock, C., S. L. Shafer, and J. Marlon. 2003. The role of climate and vegetation change in shaping past and future fire regimes in the northwestern US and the implications for ecosystem management. *Forest Ecology and Management* **178**:5-21.

Bibliography for part II. Beetle effects on fire activity

- 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.
- 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.
- Brown, J. K. 1975. Fire cycles and community dynamics in lodgepole pine forests. Pages 430-456 *in* D. M. Baumgartner, editor. *Symposium proceedings: Management of lodgepole pine ecosystems*. Washington State University Cooperative Extension Service, Pullman, WA.
- Gara, R. I., W. R. Littke, J. K. Agee, D. R. Geiszler, J. D. Stuart, and C. H. Driver. 1985. Influences of fires, fungi, and mountain pine beetles on development of a lodgepole pine forest in south-central Oregon. Pages 153-162 *in* D. M. Baumgartner, editor. *Lodgepole pine: the species and its management*. Symposium proceedings. Washington State University Conferences and Institutes, Pullman, WA.
- 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.
- Hopkins, A. D. 1909. Practical information on the Scolytid beetles of North American forests. I. Bark beetles of the genus *Dendroctonus*. USDA Bureau of Entomology Bulletin 83, U.S. Government Printing Office, Washington, D.C., USA.
- Jenkins, M. J., E. Hebertson, W. G. 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.
- Kulakowski, D., and T. T. Veblen. 2007. Effects of prior disturbances on the extent and severity of wildfire in Colorado subalpine forests. *Ecology* **88**:759-769.
- 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.

- Lynch, H. J. 2006. Spatiotemporal dynamics of insect-fire interactions. Ph.D. dissertation. Harvard University, Cambridge, MA.
- 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.
- McCullough, D. G., R. A. Werner, and D. Neumann. 1998. Fire and insects in northern and boreal ecosystems of North America. *Annual Review of Entomology* **43**:107-127.
- 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. G., 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, Yellowstone National Park. USDA For. Serv., Southwestern Region.
- 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.
- 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.
- Romme, W. H., J. Clement, J. A. Hicke, D. Kulakowski, L. H. MacDonald, T. Schoennagel, and T. T. Veblen. 2006. Recent forest insect outbreaks and fire risk in Colorado forests: a brief synthesis of relevant research. Colorado Forest Restoration Institute, Colorado State University, Fort Collins, CO. URL: http://www.cfri.colostate.edu/docs/cfri_insect.pdf
- Schmid, J. M., and G. D. Amman. 1992. *Dendroctonus* beetles and old-growth forests in the Rockies. in M. R. Kaufmann, W. H. Moir, and R. L. Bassett, editors. Old-growth forests in the Southwest and Rocky Mountain regions. Proceedings of a workshop. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, General Technical Report RM-213, Fort Collins, CO.
- 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.

Bibliography for part III. Fire effects on beetle activity

- Amman, G. D., and K. C. Ryan. 1991. Insect infestation of fire-injured trees in the Greater Yellowstone Area. Res. Note INT-398, USDA For. Serv., Interm. Res. Stn, Ogden, UT.
- Barclay, H. J., C. Li, L. Benson, S. Taylor, and T. Shore. 2005. Effects of fire return rates on traversability of lodgepole pine forests for mountain pine beetle (Coleoptera : Scolytidae) and the use of patch metrics to estimate traversability. *Canadian Entomologist* **137**:566-583.

- 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.
- 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.
- Cunningham, C. A., M. J. Jenkins, and D. W. Roberts. 2005. Attack and brood production by the Douglas-fir beetle (Coleoptera : Scolytidae) in Douglas-fir, *Pseudotsuga menziesii* var. *glauca* (Pinaceae), following a wildfire. *Western North American Naturalist* **65**:70-79.
- 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.
- Evans, W. G. 1964. Infra-Red Receptors in *Melanophila acuminata* De Geer. *Nature* **202**:211.
- Evans, W. G. 1966. Perception of infrared radiation from forest fires by *Melanophila acuminata* de Geer (Buprestidae, Coleoptera). *Ecology* **47**:1061-1065.
- Furniss, M. M. 1965. Susceptibility of fire-injured Douglas-fir to bark beetle attack in Southern Idaho. *Journal of Forestry* **63**:8-11.
- Gara, R. I., R. A. Werner, M. C. Whitmore, and E. H. Holsten. 1995. Arthropod associates of the spruce beetle *Dendroctonus rufipennis* (Kirby) (Col, Scolytidae) in spruce stands of south-central and interior Alaska. *Journal of Applied Entomology-Zeitschrift Fur Angewandte Entomologie* **119**:585-590.
- 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.
- Geiszler, D. R., R. I. Gara, and W. R. Littke. 1984. Bark beetle infestations of lodgepole pine following a fire in South Central Oregon. *Zeitschrift Fur Angewandte Entomologie-Journal of Applied Entomology* **98**:389-394.
- Hood, S., and B. Bentz. 2007. Predicting postfire Douglas-fir beetle attacks and tree mortality in the northern Rocky Mountains. *Canadian Journal of Forest Research* **37**:1058-1069.
- Klepzig, K. D., K. F. Raffa, and E. B. Smalley. 1991. Association of an insect-fungal complex with red pine decline in Wisconsin. *Forest Science* **37**:1119-1139.
- 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.
- 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.
- Lynch, H. J. 2006. Spatiotemporal dynamics of insect-fire interactions. Ph.D. dissertation. Harvard University, Cambridge, MA.
- McCullough, D. G., R. A. Werner, and D. Neumann. 1998. Fire and insects in northern and boreal 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.
- Negron, J. F. 1998. Probability of infestation and extent of mortality associated with the Douglas-fir beetle in the Colorado Front Range. *Forest Ecology and Management* **107**:71-85.
- Negron, J. F., and J. B. Popp. 2004. Probability of ponderosa pine infestation by mountain pine beetle in the Colorado Front Range. *Forest Ecology and Management* **191**:17-27.
- 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.
- Perkins, D. L., and D. W. Roberts. 2003. Predictive models of whitebark pine mortality from mountain pine beetle. *Forest Ecology and Management* **174**:495-510.
- 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. Res. Pap. INT-RP-487, USDA For. Serv., Interm. Res. Stn, Ogden, UT.
- Reynolds, K. M., and E. H. Holsten. 1994. Relative importance of risk factors for spruce beetle outbreaks. *Canadian Journal of Forest Research* **24**:2089-2095.
- Ross, D. A. 1960. Damage by long-horned wood borers in fire-killed spruce, central British Columbia. *Forestry Chronicle* **36**:355-360.
- 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.
- Shore, T. L., L. Safranyik, and J. P. Lemieux. 2000. Susceptibility of lodgepole pine stands to the mountain pine beetle: testing of a rating system. *Canadian Journal of Forest Research* **30**:44-49.
- Sullivan, B. T., C. J. Fettig, W. J. Orosina, 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.
- 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.
- White WB, GA DeNitto, JB Hanson, MD Bellinger, TH Russell Jr. 1992. Conference Proceedings: Pest risk assessment on the importation of *Pinus radiata* and Douglas-fir logs from New Zealand. pp. 1-61.

Wickman, B. E. 1964. Freshly scorched pines attract large numbers of *Arhopalus asperatus* adults (Coleoptera: Cerambycidae). *The Pan-Pacific Entomologist* **40**:59-60.