The susceptibility of ponderosa pine to mountain pine beetle in the Colorado Front Range

Meredith H. Gartner and Thomas T. Veblen
Department of Geography, University of Colorado, Boulder, Colorado

Introduction

Mountain pine beetle (MPB) populations naturally occur in the western U.S. and Canada and have an important role in the functioning of ecosystems dominated by pine species such as whitebark pine (*Pinus albicaulis)*, limber pine (*Pinus flexilis*), lodgepole pine (*Pinus contorta*), ponderosa pine and others (Jenkins et al. 2008). At endemic levels, tree mortality due to MPB is limited to a relatively small proportion of trees within a stand that had been weakened by drought, disease, or other predisposing factors. However, under epidemic conditions beetle populations mount mass attacks that overwhelm the defenses of healthy trees and result in high mortality rates of the host species population over thousands of hectares (Samman and Logan 2000, Raffa 2001, Safranyik 2004, Campbell et al. 2007). Recent (i.e. post 1995) mountain pine beetle outbreaks have killed millions of acres of host trees, especially lodgepole pine and ponderosa pine, in the western U.S. and Canada (Bentz et al. 2009). The extent of recent MPB outbreaks has been linked to warmer and drier conditions across western North America (Logan and Powell 2001, Carroll et al. 2004) and in some places to the existence of large populations of old beetle-susceptible trees due to fire suppression or other land-use practices (Taylor and Carroll 2004). However, the role of fire suppression in creating stand attributes that have promoted the current MPB outbreak in northern Colorado is uncertain and controversial (Kauffman et al. 2006, Romme et al. 2006) partially because of the uncertainty about differences between pre-20th century fire regimes and fire regimes during the 20th-century fire suppression period (Sherriff and Veblen 2006, 2007).

Periods of warm temperatures and drought promote epidemic bark beetle populations and stress potential host trees resulting in widespread tree mortality (Bentz et al. 1991, Carroll et al. 2004, Raffa et al. 2008). Susceptibility of host trees to bark beetle may be influenced by complex interactions among multi-scale factors, which are dynamic in time. Recent research has focused on the widespread outbreak in lodgepole pine forests and identified stand structure and climate as important components to determine susceptibility to infestation (Shore and Safranyik 1992, Hicke and Jenkins 2008). Since the current MPB outbreak in ponderosa pine forests has received far less attention and is increasing in extent and severity, there is an opportunity to investigate the tree- and stand-level factors that determine ponderosa pine susceptibility to MPB infestation.

Previous work has shown that larger, more dominant ponderosa are the most susceptible to successful MPB infestation. Specifically, DBH (Chojnacky et al. 2000, Negron and Popp 2004) has been identified as an important tree-level determinant of infestation (Negron and Popp 2004). Also, the presence of dwarf mistletoe (*Arceuthobium vaginatum*) in a crown increased susceptibility of host trees and its neighbors due to decreased tree defenses (McCambridge et al. 1982). Since MPB-infested ponderosa pine trees often have a patchy distribution, the current study aims to clarify the factors that determine individual tree infestation. At the stand scale, high tree density has been shown to increase susceptibility of ponderosa pine to MPB infestation (McCambridge et al. 1982, Bartos and Amman 1989, Amman and Logan 1998, Chojnacky et al. 2000, Negron and Popp 2004, Negron et al. 2008). In the Black Hills of South Dakota, MPB-infested stands had higher basal area and stand density index than non-

infested stands (Negron et al. 2008); competition among trees in high density stands may result in decreased tree defenses and consequently increased risk of infestation. Similarly, in the Colorado Front Range, MPB-infested stands had significantly higher basal area and stand density for all species present and only ponderosa pine (Negron and Popp 2004). Some forest managers utilize current knowledge on the apparent association between stand density and stand susceptibility to MPB attack to manage forest structure in an attempt to mitigate risk of MPB outbreak. However, decreased tree vigor as a mechanism of high intra-specific competition has not been investigated in the current outbreak.

Disturbances such as fire create forest mosaics of varying density and composition in a landscape, therefore, the extent and severity of subsequent ecological processes or disturbances are likely affected. Since previous studies have identified tree density and size as determinants of ponderosa pine susceptibility to MPB infestation, effects of past fires on current susceptibility of ponderosa pine to MPB attack must be examined because time since the last severe fire strongly influences tree size and stand density in these forests (Veblen and Lorenz 1986, Sherriff 2004, Sherriff and Veblen 2006). Previous studies have identified the time since the previous stand-replacing fire as an important factor in other bark beetle outbreaks in other forest types (Veblen et al. 1994, Bebi et al. 2003, Bigler et al. 2005, Axelson et al. 2009). The spatial extent of recent spruce beetle outbreaks in Colorado were influenced by previous fire (Bebi et al. 2003). Studies in ponderosa pine forests previously have been inconclusive as to the effects of surface fires, which can cause structural damage to trees, on ponderosa pine susceptibility to MPB. While several studies have identified increased bark beetle infestation in fire damaged trees (Thomas and Agee 1986, McCullough et al. 1998, Santoro et al. 2001, Wallin et al. 2003, Hood and Bentz 2007), others have found no elevated infestation (Amman and Ryan 1991, Rasmussen et al. 1996, McHugh et al 2003).

In addition to potential influences of past fires on tree susceptibility to MPB infestation, proximity of alternative hosts of MPB may affect its spread at short time scales of a few years. Although it is widely considered unusual for MPB to switch host tree species during an active outbreak, there have been no studies that investigate the dynamics between concurrent MPB outbreaks in different host species. Since both ponderosa and lodgepole pine are host species for MPB and can co-dominate at high elevations within the montane zone, the presence of MPB-infested lodgepole may be an important determinant of the presence of MPB in ponderosa pines in the same stand over time scales of a few years. This type of neighborhood effect has previously been documented for Douglas-fir bark beetle (*Dendroctonus pseudotsugae*) based on proximity of target trees to surrounding areas of host species (Powers et al. 1999) but has not yet been thoroughly examined for alternative host species for MPB.

Two key questions are central to the current research:

1) How have biotic (tree and vegetation attributes) and abiotic (terrain) factors affected the spread of recent MPB activity in ponderosa pine in the montane zone of the eastern slope of the Colorado Front Range at the tree, stand, and landscape scales?

2) In a heterogeneous landscape of different community types and vegetation structures affected by a complex disturbance history, how do previous fires affect the probability of occurrence and severity of MPB activity in ponderosa pine stands? Thus, how do disturbances interact at multi-decadal and multi-century time scales to create a landscape template of differential susceptibility to MPB activity?

Methods

Data were collected in the montane zone (1800 to 2743 m) of the central and northern Colorado Front Range (Figure 1). Climate varies greatly with elevation but data from the Evergreen climate station (1970-2000) at 2325 m are broadly representative of the mid-elevations of the montane zone. At Evergreen mean annual precipitation averages 490 mm, average winter temperature is -2.4°C, and average summer temperature is 16.5°C (Western Regional Climate Center 2009). Vegetation patterns are determined by elevation and aspect in the northern Front Range (Peet 1981, Veblen and Donnegan 2005, Kauffman et al. 2006). The vegetation of the montane zone is primarily composed of forests with the presence of some grasslands and shrublands (Marr 1961). Ponderosa pine occurs throughout the elevation zone and is commonly co-dominant with Douglas fir (*Pseudotsuga menziesii*) on north-facing slopes. In the lower montane zone (1800 to 2438 m) and on xeric slopes at higher elevations, ponderosa pine increases its proportion of dominance. In the upper montane zone (2438 to 2743 m) or on mesic hillslopes, Douglas fir often dominates and lodgepole pine, aspen (*Populus tremuloides*), and limber pine can be present (Peet 1981, Kauffman et al. 2006).

Between 1988 and 2008, the fire histories of 118 homogenous stands in the ponderosa pine elevation zone of the study area were determined by sampling fire scars (fire frequency) and stand ages and other dendroecological evidence of fire severity by various participants in the Veblen Lab (Veblen et al. 2000, Sherriff and Veblen, 2006, 2007). The spatially explicit dataset of fire dates and ecological effects (tree establishment dates and fire-caused tree mortality) across the study area provided opportunity to locate sample sites within areas of known fire history. During the summer of 2010, 20 paired plots (two within Boulder County Open Space and one within City of Boulder Open Space) were sampled within the boundaries of the previously sampled fire history polygons to address the susceptibility of ponderosa pine to MPB at the tree and stand scales (Figure 1). Within a previously sampled fire history polygon, MPB-caused mortality in ponderosa pine (infested plot) and an area of similar abiotic and vegetative conditions without MPB-caused mortality in ponderosa (non-infested plot) were located. At each location, a variable sized plot encompassing 80 trees (>4 cm DBH) was established. GPS coordinates were recorded and the following information was documented: species, DBH, tree status (live, dead, infested, MPB-killed), crown position (dominant, co-dominant, intermediate, suppressed, open growth), tree damage (e.g. fire or animal scarring), dwarf mistletoe rating (Hawksworth 1977), and evidence of other insects or pathogens. Twenty-five of the trees were cored using increment borers. The decay classes of the dead trees defined using protocol from Mast and Veblen (1994): A = needles, twigs and branches remaining, B = twigs and branches remaining, C = branches remaining, and D = only main trunk remaining.
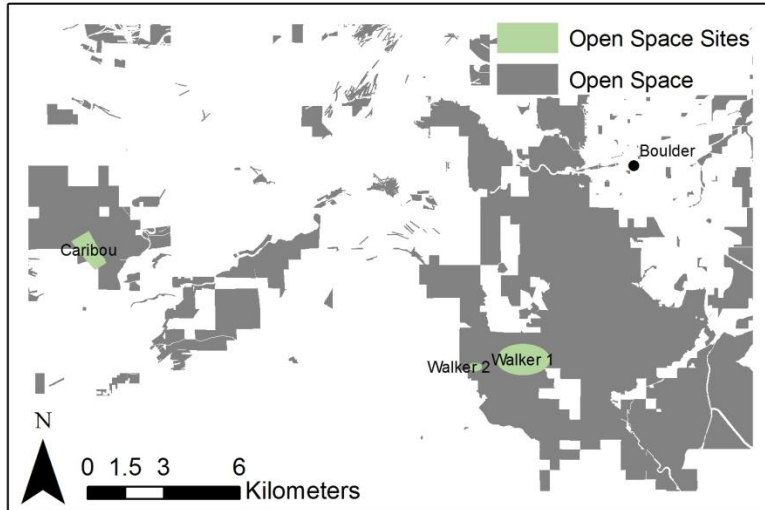
Figure 1. Site areas in Boulder County and City Open Space in Walker Ranch and Caribou Ranch.

Tree cores have been processed following standard techniques and cores from dead trees were crossdated using COFECHA (Stokes and Smiley 1968, Holmes 1983). In this report, data from the three Open Space sites are presented and patterns are explored. Data from the remaining 17 sites sampled on Arapaho-Roosevelt National Forest are not included as tree cores are currently being processed. Due to the small number of processed sites, statistics examining the differences between infested and non-infested site characteristics are not yet be performed. Once all data have been processed, statistics will be used to compare tree-level factors within infested sites and stand-level factors between infested and non-infested sites.

Results and Interpretations

In the infested plots, MPB preferentially attacked larger diameter trees, with the 30-35 cm diameter trees showing greatest proportion of infestation (Figure 2). This result is consistent with previous studies (e.g. Negron and Popp 2004) and may be explained by the benefit of thick bark and abundant cambium for larval winter survival.
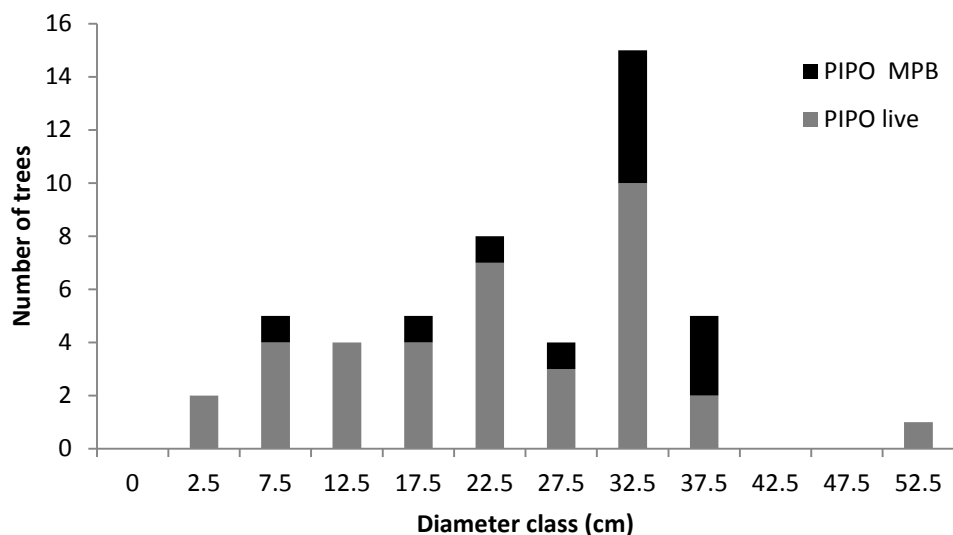
Figure 2. The number of ponderosa pine (PIPO) trees in each diameter class (indicated by the mid-point) alive or attacked or infested by MPB in the infested plots.

Stands with higher tree densities do not show greater susceptibility to MPB; the Walker Ranch I and Caribou Ranch sites have higher stand densities of all trees and ponderosa pines in the non-infested plots than infested plots (Table 1). In the Caribou Ranch plots, MPB-infested lodgepole pine is only present in the infested plot. This observation is consistent with general field observations in the upper montane zone where areas with previously infested lodgepole pines also contain infested ponderosa pine trees. The results highlight the importance of the MPB outbreak in lodgepole pine on ponderosa pine-MPB dynamics.

Table 1. Tree density (trees per hectare) for all trees, ponderosa (PIPO) and lodgepole (PICO) pines, and MPB-killed or infested ponderosa and lodgepole pines, and percentage of MPB-killed or infested ponderosa and lodgepole. All statistics were calculated using data from the 25 cored trees in the infested and non-infested plots

	All tree density	PIPO density	PICO density	MPB- PIPO density	MPB-PICO density	% MPB- PIPO	% MPB- PICO
Walker Ranch 1							
Infested	364	335	0.0	73	0.00	21.74	0.0
Non-infested	3378	3378	0.0	0.0	0.00	0.00	0.0
Walker Ranch 2							
Infested	500	380	0.0	80	0.00	21.05	0.0
Non-infested	425	323	0.0	0.0	0.00	0.00	0.0
Caribou Ranch							
Infested	590	236	330	94	283.02	40	86
Non-infested	702	365	309	0.0	0.00	0.0	0.0

The previously sampled fire history polygon data from Walker Ranch I and 2 indicated high-severity fires occurred in the mid-19th century. Tree rings dated from the paired plots confirm a stand structure indicative of a post-fire cohort (Figure 3a and b). Fire scar evidence does not indicate previous surface fires within these sites (Table 2). Caribou Ranch similarly experienced a high-severity fire in 1860, and a subsequent surface fire in 1912 (Table 2, Figure 3c).

Table 2. Site information for the fire history (FH) polygons encompassing each sampled paired plot. The number of sampled fire events (at least 2 trees record the same fire date), the earliest and latest recorded fire events, and the year of the last stand-replacing and surface fires are listed for each site. Fire history data is from Sherriff and Veblen (2007).

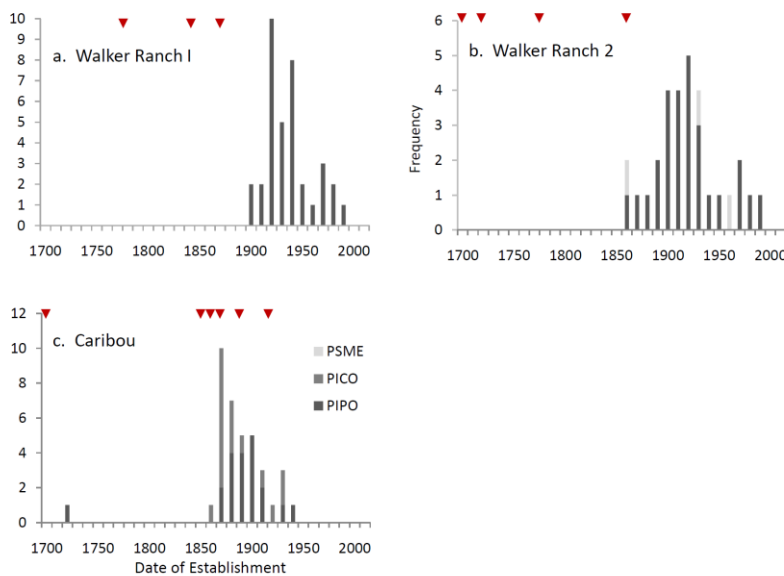| Paired Plot	FH polygon code	Mean elevation (m)	Mean slope (degrees)	Mean aspect (degrees)	# fire events	Earliest fire event	Latest fire event	Last stand-replacing fire	Last surface fire
Walker 1	TTV12	2096.92	17.9204	S	4	1684	1870	1870	-
Walker 2	TTV13	2170.56	16.6824	SE	6	1597	1860	1860	-
Caribou	RS10	2605.74	8.43	SE	6	1709	1912	1860	1912

Figure 3: Previous fire events (red triangles), age structure in 10 year bins, and species composition for sampled paired plots in Walker Ranch 1 (a.), Walker Ranch 2 (b.), and Caribou Ranch (c.).

Conclusions

The presented data are compiled from the three sites sampled on Open Space land, limiting our ability to perform statistics and identify trends. The inclusion of the remaining 17 paired plots will provide quantitative information on the susceptibility of ponderosa pine to MPB in the Front Range of Colorado at the tree, stand and landscape scales. At the tree scale, the presented data show larger diameter trees may have increased susceptibility to MPB. Increased stand density does not appear to be an important factor to MPB-susceptibility, but the presence of an established MPB infestation in lodgepole pine may increase the likelihood of spillover to nearby ponderosa pines. The inclusion of tree ring data from the remaining paired plots will allow for the quantification of the constraints on the MPB

infestation of ponderosa pine at different severities of activity. Also, the study will explore the influence of previous fire history on ponderosa susceptibility to MPB. Large, infrequent disturbances such as fire and bark beetle are important influences on forest composition and structure which in turn may affect susceptibility to subsequent disturbances (Veblen et al. 1994, Turner and Dale 1998, Bebi et al. 2003, Kulakowski and Veblen 2007). Evaluating the interactions between fire and bark beetles in montane forests will identify potential sources of feedback that could further promote future disturbance probability or severity.

References

Amman, G.D. and J.A. Logan. 1998. Silvicultural control of mountain pine beetle: prescriptions and the influence of microclimate. American Entomology 44: 166-177.

Amman, G.D. and K.C. Ryan. 1991. Insect infestation of fire-injured trees in the Greater Yellowstone area. USDA Forest Service, Intermountain Research Station, Gen. Tech. Rep, INT-398. 9 pp.

Axelson, J.N., R.I. Alfaro, and B.C. Hawkes. 2009. Influence of fire and mountain pine beetle on the dynamics of lodgepole pine stands in British Columbia, Canada. Forest Ecology and Management, 257: 1874-1882.

Bartos, D.L. and G.D. Amman. 1989. Microclimate: An alternative to tree vigor as a basis for mountain pine beetle infestations. Research Paper INT-400. USDA Forest Service, Intermountain Research Station, Ogden, UT, 10 pp.

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

Bentz, B.J., C.D. Allen, M. Ayres, E. Berg, A. Carroll, M. Hansen, J. Hicke, L. Joyce, J. Logan, W. MacFarlane, J. MacMahon, S. Munson, J. Negron, T. Paine, J. Powell, K. Raffa, J. Régnière, M. Reid, W. Romme, S. Seybold, D. Six, D. Tomback, J. Vandygriff, T. Veblen, M. White, J. Witcosky, and D. Wood. 2009. Bark Beetle Outbreaks in Western North America: Causes and Consequences. University of Utah Press.

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.Campbell, E.M., R.I. Alfaro, and B. Hawkes. 2007. Spatial distribution of mountain pine beetle outbreaks in relation to climate and stand characteristics: a dendroecological analysis. Journal of Integrative Plant Biology 49: 168-178.

Carroll, A., S. Taylor, J. Régnière, and L. Safranyik. 2004. Effects of climate change on range expansion by the mountain pine beetle in British Columbia. In: Shore T.L., J.E. Brooks, J.E. Stone, (editors). Mountain Pine Beetle Symposium: Challenges and Solutions. Canadian Forest Service, Victoria BC. Inf. Rep. BC-X-399. pp 223-232.

Chojnacky, D.C., B.J. Bentz, and J.A. Logan. 2000. Mountain pine beetle attack in ponderosa pine: comparing methods for rating susceptibility. Research paper RMRS-26. USDA Forest Service, Rocky Mountain Research Station, Forest Collins, CO, 10 pp.

Hawksworth, F.G.. 1977. The 6-class dwarf mistletoe rating system. General Technical Report RM-48. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO, 7 pp.

Hicke, J.A. and J.C. Jenkins. 2008. Mapping lodgepole pine stand structure susceptibility to mountain pine beetle attack across the western United States. Forest Ecology and Management 255: 1536-1547.

Holmes, R.. 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-ring Bulletin 43: 69-78.

Hood, S. and B.J. Bentz. 2007. Predicting post-fire Douglas-fire beetle attacks and tree mortality in the northern Rocky Mountains. Canadian Journal of Forest Research 37: 1058-1069.

Kaufmann, M.R., T.T. Veblen, and W.H. Romme. 2006. Historical fire regimes in ponderosa pine forests of the Colorado Front Range, and recommendations for ecological restoration and fuels management. Front Range Fuels Treatment Partnership Roundtable, findings of the Ecology Workgroup. www.frftp.org/roundtable/pipo.pdf.

Kulakowski, D. and T.T. Veblen. 2007. Effect of prior disturbances on the extent and severity of a 2002 wildfire in Colorado subalpine forests. Ecology 88:759-69.

Larsson, S., R. Oren, R.H. Waring, and J.W. Barrett. 1983. Attacks of mountain pine beetle as related to tree vigor of ponderosa pine. Forest Science 29: 395-402.

Marr, J.W.. 1961. Ecosystems of the east slope of the Front Range in Colorado. University of Colorado Press, Boulder, Colorado.

McCambridge, W.F., F.G. Hawskworth, C.B. Edminster, and J.G. Laut. 1982. Ponderosa pine mortality resulting from a mountain pine beetle outbreak. Research Paper RM-235. USDA Forest Service, Rocky Mountain Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO, 7 pp.

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.

Negron, J.F., K. Allen, B. Cook, and J.R. Winthrow Jr. 2008. Susceptibility of ponderosa pine, *Pinus ponderosa* (Dougl. Ex Laws.), to mountain pine beetle, *Dendroctonus ponderosae* Hopkins, attack in uneven-aged stands in the Black Hills of South Dakota and Wyoming USA. Forest Ecology and Management 254: 327-334.

Negron, J.F. and J.B. Popp. 2004. Probability of ponderosa pine infestation of mountain pine beetle in the Colorado Front Range. Forest Ecology and Management 191: 17-27.

Peet, R.K. 1981. Forest vegetation of the Colorado Front Range: composition and dynamics. Vegetatio 45: 3-75.

Powers, J. S., P. Sollins, M.E. Harmon, J. A. Jones. 1999. Plant-pest interactions in time and space: A Douglas-fire bark beetle outbreak as a case study. Landscape Ecology 14: 105-120.

Raffa, K.F.. 2001. Mixed messages across multiple trophic levels: the ecology of bark beetle chemical communication systems. Chemoecology 11: 49-65.

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

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, Intermountain Research Station, Gen. Tech. Rep. INT–487.

Romme W.H., J. Clement, J. Hicke, D. Kulakowski, L.H. MacDonald, T.L. 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.

Safranyik, L.. 2004. Mountain pine beetle epidemiology in lodgepole pine. Pages 33-40 in T.L. Shore, J.E. Brooks, and J.E. Stone (editors), Mountain Pine Beetle Symposium: Challenges and Solutions. October 30 31, 2003, Kelowna, British Columbia. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Information Report BC X 399, Victoria, BC. 298 pp.

Samman, S., and J. Logan. 2000. Assessment and response to bark beetle outbreaks in the Rocky Mountain area. USDA Forest Service, Rocky Mountain Research Station, Gen. Tech. Rep. INT-262, pp 9-12.

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.

Sherriff, R.L.. 2004. The historic range of variability of ponderosa pine in the northern Colorado Front Range: Past fire types and fire effects. Ph.D. Dissertation. University of Colorado, Boulder, Colorado. 220 pp.

Sherriff, R.L. and T.T. Veblen. 2006. Ecological effects of changes in fire regimes in *Pinus ponderosa* ecosystems in the Colorado Front Range. Journal of Vegetation Science 17: 705-718.

Sherriff, R.L. and T.T. Veblen. 2007. A Spatially-Explicit Reconstruction of Historical Fire Occurrence in the Ponderosa Pine Zone of the Colorado Front Range. Ecosystems 9: 1342-1347.

Shore, T.L. and L. Safranyik. 1992. Susceptibility and risk rating system for the mountain pine beetle in lodgepole pine stands. BC-X-336, Forestry Canada.

Stokes, M.A. and T.L. Smiley. 1968. An introduction to tree-ring dating. The University of Chicago Press, Chicago and London.

Taylor, S. and A. Carroll. 2004. Disturbance, forest age, and mountain pine beetle outbreak dynamics in BC: A historical perspective. Pages 41-51 in T.L. Shore, J.E. Brooks, and J.E. Stone (editors). Mountain Pine Beetle Symposium: Challenges and Solutions. October 30-31, 2003, Kelowna, British Columbia. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Information Report BC-X-399, Victoria, BC. 298 pp.

Thomas, T.L. and J.K. Agee. 1986. Prescribed fire effects on mixed conifer forest structure at Carter Lake, Oregon. Canadian Journal of Forest Research 16: 1082-1087.

Turner, M.G. and V.H. Dale. 1998. Comparing large infrequent disturbances: what have we learned? Ecosystems 1: 493-496.

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

Veblen, T.T. and J.A. Donnegan. 2005. Historical range of variability assessment for forest vegetation of the national forests of the Colorado Front Range. Colorado Forest Restoration Institute and USDA Forest Service, Rocky Mountain Region. http://www.fs.fed.us/r2/projects/scp/tea/HRVFrontRange.pdf.

Veblen, T.T. and D.C. Lorenz. 1986. Anthropogenic disturbance and recovery patterns in montane forests, Colorado Front Range. Physical Geography 7: 1-24.

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.

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.