Do Bark Beetle Outbreaks Increase Wildfire Risks in the Central U.S. Rocky Mountains? Implications from Recent Research

Authors: Black, Scott H., Kulakowski, Dominik, Noon, Barry R., and DellaSala, Dominick A.

Source: Natural Areas Journal, 33(1) : 59-65

Published By: Natural Areas Association

URL: https://doi.org/10.3375/043.033.0107
ABSTRACT: Appropriate response to recent, widespread bark beetle (Dendroctonus spp.) outbreaks in the western United States has been the subject of much debate in scientific and policy circles. Among the proposed responses have been landscape-level mechanical treatments to prevent the further spread of outbreaks and to reduce the fire risk that is believed to be associated with insect-killed trees. We review the literature on the efficacy of silvicultural practices to control outbreaks and on fire risk following bark beetle outbreaks in several forest types. While research is ongoing and important questions remain unresolved, to date most available evidence indicates that bark beetle outbreaks do not substantially increase the risk of active crown fire in lodgepole pine (Pinus contorta) and spruce (Picea engelmannii)-fir (Abies spp.) forests under most conditions. Instead, active crown fires in these forest types are primarily contingent on dry conditions rather than variations in stand structure, such as those brought about by outbreaks. Preemptive thinning may reduce susceptibility to small outbreaks but is unlikely to reduce susceptibility to large, landscape-scale epidemics. Once beetle populations reach widespread epidemic levels, silvicultural strategies aimed at stopping them are not likely to reduce forest susceptibility to outbreaks. Furthermore, such silvicultural treatments could have substantial, unintended short- and long-term ecological costs associated with road access and an overall degradation of natural areas.

Index terms: bark beetles, Dendroctonus, forest health, forest management, wildfire

INTRODUCTION

Forests in the western United States are being affected by the largest outbreaks of bark beetles in at least a century, which has caused concern about forest health and wildfire risk and led to proposals for tree removal in natural areas such as roadless forests. Such proposals stem in part from the rationale that bark beetle outbreaks increase wildfire risks due to increased dead fuels and that widespread treatment in beetle-affected forests is needed to lower such risks. Here, we review available peer-reviewed literature to determine if: (1) bark beetle outbreaks are associated with a higher incidence of wildfires in forest types in the central Rockies; and (2) if silvicultural treatments are effective at lowering beetle-associated tree mortality before, during, and after outbreaks. We briefly review the impacts that additional logging roads associated with broad-scale tree removal may have on the ecology of roadless natural areas. Our results may have broader policy implications in western forests as concerns over insect outbreaks have led to proposals to reduce environmental protections in favor of widespread thinning and post-disturbance tree removal.

INTERACTIONS AMONG FOREST INSECTS AND FIRES

We examined the long-standing belief that insect outbreaks lead to increased risk of fire (USDA Forest Service 2011). A large body of literature indicates that the occurrence of large, severe fires in subalpine, lodgepole pine (Pinus contorta), and spruce (Picea engelmannii)-fir (Abies spp.) forests is strongly contingent on climatic conditions, especially drought (e.g., Kipfmuller and Baker 2000; Romme et al. 2006; Sibold and Veblen 2006; Schoennagel et al. 2007; Jenkins et al. 2008; Simard et al. 2008, 2011).

The debate on how outbreaks affect fire risk and hazard is ongoing, but recent work emphasizes that the effect of outbreaks on subsequent fire risk is complex and is contingent on time since last outbreak and on biophysical setting. To date, the majority of studies have found no increase in fire occurrence, extent, or severity following outbreaks of spruce beetle (Dendroctonus rufipennis) and mountain pine beetle (Dendroctonus ponderosae) in Colorado, Wyoming, and other areas (Bebi et al. 2003; Kulakowski et al. 2003; Bigler et al. 2005; Kulakowski and Veblen 2007; Jenkins et al. 2008; Simard et al. 2008, 2011).

Theoretically, the effect of outbreaks on subsequent fires may vary with the time since the outbreak occurred (Romme et al. 2006). For example, it is reasonable to expect that foliar moisture in trees killed by beetles will decrease and canopy density will be reduced during and immediately after an outbreak. In subsequent years, canopy density may be further reduced as dead needles and small branches fall from killed trees reducing canopy bulk
density, but increasing surface fire hazard (i.e., the type, volume, and arrangement of fuels that determines the ease of ignition and resistance to control regardless of the fuel type's weather-influenced moisture content). Although such a relationship may theoretically increase the risk of surface fires, studies on the influence of outbreaks on subsequent stand-replacing fires, over a range of years since outbreak, have found little or no increase in surface or canopy fire occurrence, extent, or severity (Bebi et al. 2003; Kulakowski et al. 2003; Bigler et al. 2005; Kulakowski and Veblen 2007; Jenkins et al. 2008; Simard et al. 2008, 2011) (Table 1).

Fire and Mountain Pine Beetle Outbreaks in Lodgepole Pine Forests

Although outbreaks of mountain pine beetle do alter fuel structure (Page and Jenkins 2007; Klutsch et al. 2009; Simard et al. 2011), the actual effects of these changes in fuels on subsequent fire risk (i.e., the chance that a fire might start based on all causative agents such as fuel hazard, ignition source, and weather) are complex, contradictory, and appear counterintuitive. For instance, lodgepole stands in which > 50% of susceptible trees were killed by beetles in the 5 to 15 years preceding the 1988 Yellowstone fires had a higher incidence of crown fire than stands in which mortality was not as high (Turner et al. 1999). In contrast, stands with low to moderate beetle mortality (< 50% tree kill) had a lower incidence of high-severity crown fires. However, it is unclear whether these differences in fire behavior were primarily the result of the outbreak or of pre-outbreak stand structure (Simard et al. 2008), because beetle mortality occurred preferentially in older stands that were, in turn, inherently more likely to burn at high severity than younger stands because of differences in fuel structures even in the absence of beetle activity (Renkin and Despain 1992).

Other studies have found that beetle-kill may have decreased the hazard of high-severity crown fire by reducing the continuity of the canopy. For example, beetle-killed lodgepole pine stands, characterized by lower stand density, were affected by

<table>
<thead>
<tr>
<th>Forest Type</th>
<th>Location</th>
<th>Insect-fire Link</th>
<th>Citations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lodgepole</td>
<td>Yellowstone</td>
<td>Beetles killed stands had significantly lower fire severity.</td>
<td>Omi 1997</td>
</tr>
<tr>
<td>Lodgepole</td>
<td>Yellowstone</td>
<td>Stands with higher mortality from bark beetles had higher incidence of crown fires.</td>
<td>Turner et al. 1999</td>
</tr>
<tr>
<td>Lodgepole</td>
<td>Yellowstone</td>
<td>Stands with low to moderate beetle mortality had a lower incidence of crown fires.</td>
<td>Lynch et al. 2006</td>
</tr>
<tr>
<td>Lodgepole</td>
<td>Yellowstone</td>
<td>Stands affected by outbreak in 1972-1973 were associated with a slightly higher probability of fire.</td>
<td>Turner et al. 1999</td>
</tr>
<tr>
<td>Lodgepole</td>
<td>Yellowstone</td>
<td>Bark beetle outbreak did not affect the extent or severity of fire.</td>
<td>Kulakowski and Veblen 2007</td>
</tr>
<tr>
<td>Lodgepole</td>
<td>Lodgepole and spruce</td>
<td>The probability of active crown fire in stands affected by outbreak in 1980-1983 was not significantly lower than in stands not affected by beetles.</td>
<td>Simard et al. 2011</td>
</tr>
<tr>
<td>Lodgepole</td>
<td>Lodgepole and spruce</td>
<td>Modeling study predicted a reduced risk of active crown fire 5 to 60 years after outbreaks.</td>
<td>Simard et al. 2011</td>
</tr>
<tr>
<td>Lodgepole</td>
<td>Lodgepole and spruce</td>
<td>Beetle-affected stands were not more susceptible to a low-severity fire.</td>
<td>Simard et al. 2011</td>
</tr>
<tr>
<td>Lodgepole</td>
<td>Lodgepole and spruce</td>
<td>Previous bark beetle outbreaks had only a minor influence on fire severity.</td>
<td>Bigler et al. 2005</td>
</tr>
<tr>
<td>Lodgepole</td>
<td>Spruce</td>
<td>Beetles caused no increase in the numbers of fires.</td>
<td>Simard et al. 2011</td>
</tr>
<tr>
<td>Lodgepole</td>
<td>Spruce</td>
<td>Modeling studies predicted reductions in the probability of active crown fire after bark beetle outbreaks.</td>
<td>DeRose and Long 2009</td>
</tr>
<tr>
<td>Lodgepole</td>
<td>Central Rocky Mountains</td>
<td>Beetle-affected stands were not more susceptible to a low-severity fire.</td>
<td>Simard et al. 2011</td>
</tr>
<tr>
<td>Lodgepole</td>
<td>Central Rocky Mountains</td>
<td>Previous bark beetle outbreaks had only a minor influence on fire severity.</td>
<td>Bigler et al. 2005</td>
</tr>
<tr>
<td>Lodgepole</td>
<td>Central Rocky Mountains</td>
<td>Modeling studies predicted reductions in the probability of active crown fire after bark beetle outbreaks.</td>
<td>DeRose and Long 2009</td>
</tr>
</tbody>
</table>

Table 1. Forest types and relations between fire and insects in the Rocky Mountains.
significantly lower fire severity compared to adjacent burned areas that had not been affected by beetles in the 3400-hectare Robinson Fire that burned in Yellowstone National Park in 1994 (Omi 1997). Lynch et al. (2006) also examined the influence of previous beetle activity on the 1988 Yellowstone fires by testing whether beetle-affected stands were more likely to have burned than those stands not affected by beetles. Stands affected by outbreak from 1972 to 1975 had a higher probability of burning, but the increase was relatively minor (about 11% greater compared to areas unaffected by beetles). In contrast, stands that were affected by outbreak from 1980 to 1983 were not more likely to burn in comparison to unaffected stands (Lynch et al. 2006).

It has been hypothesized that the risk of fire may increase only during and immediately after outbreaks of bark beetles when the dry red needles are still on the trees (Romme et al. 2006). However, Kulakowski and Veblen (2007) found that ongoing outbreaks of mountain pine beetle (and spruce beetle) did not affect the extent or severity of fire and suggested that changes in fuels brought about by outbreaks may be overridden by climatic conditions. Simard et al. (2011) examined fuel conditions for 35 years following outbreaks of mountain pine beetle in Yellowstone National Park. They documented reduced canopy moisture content after an outbreak, which was coupled with reduced canopy bulk density. In simulation models of fire behavior, under intermediate wind conditions (40 to 60 kilometers per hour), the probability of active crown fire in stands recently affected by beetles was significantly lower than in stands not affected by beetles (Simard et al. 2011). In addition, if winds were below 40 kph or above 60 kph, stand structure had little effect on fire behavior. Thus, although the canopy was drier immediately after an outbreak, no increase in fire risk was observed, likely because of the more important effect of reductions in canopy bulk density. Other modeling studies also have predicted a reduced risk of active crown fire 5 to 60 years after outbreaks, due to decreased canopy bulk density (Jenkins et al. 2008). In sum, outbreaks of bark beetles in lodgepole pine may have little or no effect on subsequent fires and may in some cases actually reduce the risk of fire.

**Fire and Spruce Beetle in Subalpine Spruce-Fir Forests**

There is increasing evidence that spruce beetle outbreaks have little or no affect on the occurrence or severity of fires in spruce-fir forests (Simard et al. 2008). It is well established that in this forest type, extensive fires are highly dependent on infrequent, severe droughts (e.g., Schoennagel et al. 2007). Under such extreme drought conditions, increased dead fuels from bark beetle outbreaks appear to play only a minor role, if any, in increasing fire risk. For instance, after a 1940s spruce beetle outbreak that resulted in dead-standing trees over thousands of hectares of subalpine forests in the White River National Forest of western Colorado, there was no increase in the numbers of fires compared to unaffected subalpine forests (Bebi et al. 2003). Beetle-affected stands were not more susceptible to a low-severity fire that spread through adjacent forests several years after the outbreak subsided (Kulakowski et al. 2003). During the extreme drought of 2002, large fires affected extensive areas of Colorado, including some spruce-fir stands that were previously affected by the 1940s outbreak of spruce beetle. Despite the expectation that these outbreaks would have led to an increased risk of severe fires, they had only a minor influence on fire severity (Bigler et al. 2005). Likewise, ongoing outbreaks of spruce beetle (and mountain pine beetle) had no detectable effect on the extent or severity of fires in 2002 (Kulakowski and Veblen 2007). These empirical findings are consistent with modeling studies that predict reductions in the probability of active crown fire for one to two decades after high-severity bark beetle outbreaks in pure stands of Engelmann spruce (*Picea engelmannii*) (DeRose and Long 2009). Other modeling studies have likewise predicted a reduced risk of active crown fire 5 to 60 years after outbreaks, due to decreased canopy bulk density (Jenkins et al. 2008).

The emerging view is that for lodgepole pine and spruce-fir forests: (1) the effect of bark beetle outbreaks on fuels is complex; and (2) weather and climate are more important in influencing fire risk and behavior the effects of insect outbreaks. When evaluating the influence of bark beetle outbreaks, it is important to recognize that outbreaks not only reduce foliar moisture content and increase the volume of dead wood, which can increase fire hazard, but that outbreaks also reduce canopy density, which can decrease fire risk (Simard et al. 2011). Therefore, when assessing the risk of wildfires following outbreaks, it is essential to recognize the relative importance of weather and climate to overall fire risk.

**Efficacy of Bark Beetle Containment Measures**

**Prior to Outbreaks**

The effectiveness of thinning to reduce forest susceptibility to bark beetles is believed to be related to tree vigor (Fettig et al. 2007); which may increase as moisture stress is decreased, and which in turn may make trees less susceptible to insect infestation. The premise is that if the trees are healthy and vigorous, they may be able to “pitch out” the attacking beetles, essentially flooding the entrance site with resin that can push out or drown the beetle (Figure 1).

Some studies have suggested that competition for light and water may reduce the vigor of surviving trees and increase susceptibility to bark beetle attacks (Fettig et al. 2007) and that thinning may, therefore, improve outbreak resistance. For instance, low-vigor ponderosa pine (*Pinus ponderosa*) in central Oregon was more often attacked by beetles than high-vigor trees during early stages of outbreaks (Larsson et al. 1983). Similarly, beetle activity has been associated with high tree densities in ponderosa pine and Douglas-fir (*Pseudotsuga sp.*) stands (Negrón et al. 2001; Negrón and Popp 2004). Ponderosa pine study plots in Colorado’s Front Range infested by mountain pine beetle had significantly higher tree basal area and density (Negrón and Popp 2004). Douglas-fir beetle (*D. pseudotsugae*) more often attacked stands...
containing a high percentage of basal area represented by high densities of Douglas-fir and slow growth during the five years prior to attack in Colorado’s Front Range (Negrón et al. 2001).

Studies that have looked directly at thinning and its effects on tree vigor in Western forests have shown mixed results. While some studies have found that thinning reduces stand susceptibility in some circumstances (Fettig et al. 2007), other research has found bark beetles do not preferentially infest trees with declining growth. For example, Sánchez-Martínez and Wagner (2002) found that ponderosa pine forests of northern Arizona growing in dense stands were not more likely to be colonized by bark beetles. Under some circumstances, thinning may alleviate tree stress at the stand level but is unlikely to be effective at mitigating susceptibility against extensive or severe outbreaks (Safranyik and Carroll 2006). Preisler and Mitchell (1993) found that thinned plots of lodgepole pine in Oregon were initially unattractive to mountain pine beetles; but when large numbers of attacks occurred, colonization rates were similar to those in unthinned plots. Similarly, Amman et al. (1988) studied the effects of spacing and diameter of trees and concluded that tree mortality was reduced as basal area was lowered. However, if the stand was in the path of an ongoing mountain pine beetle epidemic, spacing and density of trees had little effect (Amman et al. 1988).

While thinning has the potential to reduce tree stress, which can reduce susceptibility to insect attack, it also has the potential to bring about other conditions that can increase susceptibility. For example, thinning may injure surviving trees and their roots, which can provide entry points for pathogens and ultimately reduce tree resistance to other organisms (Hagle and Schmitz 1993; Paine and Baker 1993; Goyer et al. 1998). Although thinning can be effective in maintaining adequate growing space and resources, there is accumulating evidence to suggest that tree injury, soil compaction, and temporary stress due to changed environmental conditions caused by thinning may increase susceptibility of trees to bark beetles and pathogens (Hagle and Schmitz 1993).

From an adaptive management standpoint, it is most prudent to implement thinning in appropriate settings (e.g., already degraded areas in need of restoration) with sufficient controls that would lead to an improved understanding of the efficacy of these approaches, particularly under a range of climatic conditions. It is also important to consider how such strategies may alter normal stand structure. For example, thinning in Engelmann spruce forests is likely to create novel conditions that would be atypical for these ecosystems due to their naturally high tree densities (Daubenmire 1943). Further, thinning forest stands before epidemics is not likely to prevent major outbreaks, due to the inherent difficulties of manipulating stand structure over large enough areas and the overriding influence of climatic stress in driving outbreaks.

During Outbreaks

There is general agreement that silvicultural treatments cannot effectively stop outbreaks once a large-scale insect infestation has started. Citing multiple sources, Hughes and Drever (2001) found that most control efforts have had little effect on the final size of outbreaks. In another review, Romme et al. (2006) point out that once an extensive outbreak has started, timber management is unlikely to stop it. Control of such outbreaks is theoretically possible, but it would require treatment of almost all of the infected trees (Hughes and Drever 2001). Amman and Logan (1998) point to failed attempts to use direct control
measures, such as pesticides and logging, after an infestation starts. They suggest that by the early 1970s, it was apparent that attempts to control the extensive mountain pine beetle outbreaks that were occurring in the northern Rockies, by directly killing the beetles, were not working.

If a bark beetle infestation is relatively restricted and concentrated in a limited area, it may be feasible to reduce the impact of that outbreak by removing infested trees from a forest stand, or by thinning a stand to reduce stress of trees competing for limited nutrients, sunlight, and moisture. However, specific climatic conditions are believed to be required for beetle populations to reach epidemic levels. As such, a small population of beetles is not sufficient for an outbreak to occur and would not necessarily lead to an outbreak. Conversely, under climatic conditions favorable for an outbreak, bark beetle outbreaks can erupt simultaneously in numerous, dispersed stands across the landscape. Thus, even if a growing population of beetles is successfully removed from one stand or the stand is thinned to increase vigor, under climatic conditions suitable for outbreaks, beetles from other stands are likely to spread over a landscape. Given that climate typically favors beetle populations and stresses trees over very large areas, successfully identifying and treating stands over a large enough region to have a significant impact on the overall infestation is impractical and costly.

Following Outbreaks

Post-disturbance harvest is common practice on forest lands and is designed to remove trees or other biomass in order to produce timber or other resources. This type of resource extraction has the potential to inadvertently lead to heightened insect activity (Nebeker 1989; Hughes and Drever 2001; Romme et al. 2006). In particular, snags and fallen logs contribute to the protection of soils and water quality and provide habitat for numerous cavity- and snag-dependent species (Romme et al. 2006), many of which prey on bark beetles and other economically destructive insects. Therefore, outbreaks could be prolonged because of a reduction in the beetle’s natural enemies (Nebeker 1989), including both insects and bird species that feed on mountain pine beetles (Koplin and Baldwin 1970; Shook and Baldwin 1970; Otvos 1979). Furthermore, post-disturbance harvest can damage soil and roots by compacting them (Lindennayer et al. 2008) leading to greater water stress in trees, which may reduce conifer regeneration by increasing sapling mortality (Donato et al. 2006) and, in general, may cause more damage to forests than that caused by natural disturbance events (DellaSala et al. 2006).

ROAD BUILDING FOR BARK BEETLE CONTROL

A broad scale program to treat forests that have been affected by bark beetle will require an extensive road system, which will likely have significant impacts to forest and aquatic ecosystems.

In general, the major physical results of roads on the terrestrial environment are increases in forest fragmentation and disruption of the movement of organisms and flow of ecological processes across the landscape (Lindennayer and Fisher 2006). Aquatic systems have been impacted through the disruption of natural infiltration of water into the soil and increased runoff to streams (Forman and Alexander 1998). These effects have been particularly pronounced in mountainous regions, especially on high gradient streams and headwaters (Ziegler et al. 2001). Increased sediment input to streams can result in changes to channel morphology and channel substrate, as well as the creation of shallow pools (Beschta 1978). These changes to stream structure, an indirect effect of road construction, often adversely affect native fish habitat. Thus, any road network constructed to thin or harvest insect-infested stands will have to be carefully engineered to prevent increased sedimentation rates or alteration of hill slope processes (Beschta 1978). While proper engineering can help mitigate some negative effects, it does not mitigate the overall impact of roads on hydrologic processes, water flow, and fragmentation of wildlife habitat.

CONCLUSIONS AND RECOMMENDATIONS

Climate change and other factors are leading to unprecedented changes in western forest ecosystems (Logan et al. 2003; Carroll et al. 2004; Breshears et al. 2005; Bentz et al. 2009). One consequence of recent and predicted climate change is increased bark beetle activity leading to tree mortality over large areas (Logan and Powell 2001; Williams and Liebhold 2002; Carroll et al. 2004). Such ongoing outbreaks have led to widespread public concern about increased fire risk; however, outbreaks of mountain pine beetle and spruce beetle do not appear to substantially increase the risk of subsequent fire under most conditions. Instead, fire risk in spruce-fir and lodgepole pine is strongly tied to warm and dry conditions, such as those of recent decades. Insect containment measures have yielded mixed results and may pose significant risks to forested ecosystems. We recommend that priority be given to removing hazardous trees, which were killed by fire or insects and that might fall across roads or in campgrounds in areas of high human use to limit damages and potential loss of life. Moreover, in order to reduce existing and future risks of fire, it would be prudent to concentrate fuel reduction measures in the wildland-urban interface by creating defensible space, as the 40-meter zone around homes and structures has been shown to be critical to a home’s ignitability (Cohen 1999). Thus, to be effective at reducing fire hazard to communities, tree-cutting can be directed at removing all flammable material (not just economically valuable timber) in the immediate vicinity of homes and settlements.

ACKNOWLEDGMENTS

For helpful comments on earlier drafts of this report we thank J. Hicke, D. Jarvis, A. Minnerath, W.H. Romme, T. Schoennagel, M. Simard, R. Spivak, T. Veblen and C.D. Williams. This material was supported by the National Science Foundation, the New Land Foundation, the Maki Foundation, and the Bullitt Foundation. The authors of this report take sole responsibility for its content.
Scott H. Black is the Executive Director with the Xerces Society for Invertebrate Conservation. He also serves as the Chair of the International Union for Conservation of Nature (IUCN) Butterfly Specialist Group and as a member of the IUCN Invertebrate Conservation Subcommittee. He has a Master of Science Degree from the Graduate Degree Program in Ecology, through the College of Agricultural Sciences at Colorado State University. Scott has authored over 100 scientific and popular publications, co-authored two books and dozens of reports on land management issues. Scott recently received the 2011 Colorado State University College of Agricultural Sciences Honor Alumnus Award.

Dominik Kulakowski is an assistant professor of geography and biology at Clark University in Worcester, MA. He earned a Master of Science in Ecology from Pennsylvania State University in 1997 and a Ph.D. in Geography from the University of Colorado in 2002. Prior to coming to Clark University, he was a research associate and lecturer with the University of Colorado, Department of Geography, from 2002–2007, and a research associate with the Swiss Federal Institute for Snow and Avalanche Research in Davos, Switzerland, a division of the Alpine Environment, from 2004–2005.

Barry R. Noon is a Professor in the Department of Fish, Wildlife, and Conservation Biology at Colorado State University in Fort Collins, CO. He has conducted research on the effects of land management practices on wildlife populations for the past 36 years. During this period, he has published about 100 scientific papers and co-authored four book-length reports to the federal government on the sustainable management of public lands. For 11 years, he directed a Forest Service Research Lab in the Pacific Northwest (USA) and served for a year as Chief Scientist of the National Biological Service, Department of the Interior during the administration of President Clinton.

Dominick A. DellaSala is the Chief Scientist and President of the Geos Institute and President of the Society for Conservation Biology, North America Section, and he lives in Ashland, OR. He is an international author of over 150 technical publications, including Temperate and Boreal Rainforests of the World: Ecology and Conservation (www.islandpress.org/dellaisalas). Dominick has received conservation leadership awards from World Wildlife Fund (2000, 2004) and Wilburforce Foundation (2006); his rainforest book was acknowledged for “outstanding academic excellence” from Choice magazine (2012).

LITERATURE CITED


Kulakowski, D., T.T. Veblen, and P. Bebi. 2003. A
Volume 33 (1), 2013 Natural Areas Journal 65
Koplin, J.R., and P.H. Baldwin. 1970. Wood-
pecker predation on an endemic population of Engelmann spruce beetles, The American
Midland Naturalist 83:510-515.
legacies on the disturbance regime of a subalpine forest in Colorado. Journal of
Biogeography 30:1445-1456.
Kulakowski, D., and T.T. Veblen. 2007. Effects of
prior disturbances on the extent and severity of wildfire in Colorado subalpine