Lodgepole Pine Regeneration following Mountain Pine Beetle Outbreak in Subalpine Forests of Northern Colorado

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Abstract

The recent mountain pine beetle (*Dendroctonus ponderosae* Hopkins; MPB) outbreak throughout North America has affected thousands of hectares of lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Englemann) in northern Colorado. This severe disturbance in subalpine forests has created conditions leading to the advance regeneration and new recruitment of the shade-tolerant species Englemann spruce (*Picea Englemannii*) and subalpine fir (*Abies lasiocarpa*). Contrarily, a variety of factors including canopy opening and litter depth limit lodgepole pine seedling regeneration in MPB-attacked lodgepole pine stands. Significantly higher densities of subalpine fir and Englemann spruce seedlings following MPB outbreak suggest that severe MPB outbreak accelerates the succession of lodgepole pine and mixed subalpine stands toward a canopy codominated by more shade-tolerant species.

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Northern Colorado

The recent mountain pine beetle (Dendroctonus ponderosae Hopkins; MPB) outbreak affecting subalpine forests throughout much of northern Colorado is the largest ever recorded (Axelson et al. 2009). The outbreak has affected over 13 million hectares of lodgepole pine (Pinus contorta Douglas var. latifolia Englemann) in British Columbia and almost 900,000 hectares throughout the United States (Axelson et al. 2010, Wulder et al. 2006). MPB outbreak is a natural disturbance in stands of lodgepole pine. "A disturbance is any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment" (Pickett and White 1985). MPB outbreaks, infrequent fires, and blowdowns are important disturbances that influence forest dynamics and structure (Veblen et al. 1989, Klutsch et al. 2009). MPB outbreaks, the focus of the current study, are discrete events in time when infestation severity reaches epidemic levels and tree mortality becomes widespread. The severe tree mortality caused by a MPB outbreak or by similar disturbances such as wind damage is important in terms of altering understory environments and changing the availability of resources to other plants (Veblen et al. 1989, Axelson et al. 2010). How tree regeneration may or may not result from the release of these resources is the essence of Pickett and White's (1985) definition of disturbance. In the current study, I examine tree regeneration responses to recent MPB outbreak in subalpine forests of the Routt and White River National Forests in northern Colorado.

Following a severe canopy disturbance that kills many mature trees but leaves the understory intact, there are two general patterns of vegetation response (Marks 1974, Canham and Marks 1985, Veblen 1992). The first is termed *the reorganization response* and involves

accelerated growth of plants already established at the time of the canopy disturbance. Examples include increases in biomass of understory herbs and shrubs, suckering and other forms of vegetative reproduction of small trees, and also accelerated growth of tree seedlings that are already present in the understory. Foresters commonly use the term "advance regeneration" to refer to juvenile trees (seedling and sapling size classes) that are present in the understory but only growing very slowly until a canopy disturbance increases resource availability (i.e. increased solar radiation) resulting in a sustained growth increase or so-called "growth release" (Veblen 1992). The second pattern is termed the new establishment response and includes both establishment of seedlings from dormant seeds already present at the time of the disturbance (i.e. viable seed buried in the soil or held on plants), as well as establishment resulting from dispersal of seed to the disturbed site. In the case of a lodgepole pine stand severely disturbed by a MPB outbreak, it is logical to expect that the post-MPB regeneration of lodgepole pine and other tree species will include some mixture of reorganization responses (i.e. growth releases of advance regeneration and vegetative reproduction such as root suckering) as well as new establishment from either resident populations of seeds or from seeds newly dispersed to the site. The overall goal of the current study is to evaluate the relative abundance of juveniles (newly established seedlings as well as released advance regeneration) of different tree species soon after severe canopy disturbance of lodgepole pine forests by MPB.

Lodgepole Pine Ecology and Associated Subalpine Zone Species

Lodgepole pine occupies 15% of Rocky Mountain forests in the U.S and 22% of the forests of western Canada. The subspecies *latifolia*, the most extensive and economically viable of the species, inhabits the subalpine forests of Colorado (Despain 2001). Lodgepole pine is a shade-intolerant pioneer species that typically establishes on sites with bare mineral soil. This

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makes post-fire sites opportune places for lodgepole pine to establish due to the lack of canopy cover and forest litter. In high elevation lodgepole pine forests (subalpine forests) fires occur infrequently. However, the high intensities of these fires often replace entire tree stands (Romme et al. 2006). Following fires, lodgepole pine show high rates of recruitment in the first decade following wildfire (Johnson and Fryer 1989). As a post-fire pioneer species, lodgepole pine has developed a pine cone adaptation to fire called serotiny. Serotinous pine cones remain sealed closed at maturity by resin until high temperatures during a fire melt the resin to allow seed dispersal (Romme et al. 2006). Serotiny varies both in the range and age of lodgepole pine; serotiny is more common at lower elevations than at higher elevations and in older stands than younger stands (Despain 2001, Schoennagel et al. 2003). Serotiny also varies within a single stand, but trees in the same stand are typically serotinous or not serotinous (Koch 1996). The effects of serotiny on post-fire lodgepole pine regeneration has been extensively researched, but the effects of serotiny on post-MPB lodgepole pine regeneration remains a question of critical concern to forest managers and researchers. Will serotinous cones unopened by fire temperatures limit seed availability of lodgepole pine following an MPB outbreak?

In addition to serotiny, several other limiting factors may affect lodgepole pine establishment following a mountain pine beetle outbreak. Lodgepole pine's affinity to establish on bare mineral soil is limited after an MPB outbreak because litter depth increases from fallen pine needles. Canopy densities in MPB-attacked stands can vary based on the percent of canopy trees killed and the time at which the outbreak occurred in the area. Lodgepole pine is a shadeintolerant species; therefore, shade from the canopy may limit seedling regeneration in the initial years of tree mortality; gaps due to mortality or the removal of a single tree do not provide

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enough sunlight for the establishment of lodgepole pine (Despain 2001). Finally, although lodgepole pine is highly drought-tolerant, water availability can limit any species' recruitment.

Englemann spruce (*Picea Englemannii*), subalpine fir (*Abies lasiocarpa*), and quaking aspen (*Populus tremuloides*) are also species commonly associated with the subalpine forests of northern Colorado. Englemann spruce and subalpine fir succeed shade-intolerant species like lodgepole pine and quaking aspen (Veblen and Donnegan 2005). Spruce and fir can regenerate directly following fires, especially spruce which is found in greater abundance, but their main role in the mixed subalpine forests of northern Colorado is to succeed post-fire pioneer species. Suppressed spruce and fir seedlings exist in stands dominated by lodgepole pine as advance regeneration "waiting" for a growth release. Fir is typically more abundant in the seedling size class, but spruce has a substantially longer lifespan and has lower adult mortality rates (Veblen 1992). As a result, these two species coexist with one another in subalpine forests. Quaking aspen is a shade-intolerant pioneer species that establishes quickly after a fire. Aspen exists in a broad range of habitats varying in elevation and moisture availability. Aspen is unique compared to the associated coniferous species of the subalpine zone; it primarily reproduces asexually through vegetative shoots, or suckers. This adaptation allows aspen to resprout rapidly following fire. Aspen may co-dominate with conifers or be part of self-replacing stands, but aspen's shorter lifespan and open canopy may allow coniferous species to grow up through its canopy (Veblen and Donnegan 2005).

Mountain Pine Beetle Ecology

The mountain pine beetle is native to Colorado and has coexisted with its host species for thousands of years. MPB can infest lodgepole pine, ponderosa pine (*Pinus ponderosa*), and limber pine (*Pinus flexilis*), but lodgepole pine is considered its primary host (Romme et al.

2006, Wulder et al. 2006). Several tree-killing beetles such as the MPB exist in the forest at all times, but at low levels; these populations are considered endemic (small). When beetles increase their birthing rates under certain circumstances, epidemic (large) populations affect large numbers of trees (Christiansen et al. 1987). Epidemic MPB populations are forest disturbances because they disrupt the ecosystem and population structure and can change resources, substrate availability, and the physical environment.

Like all bark beetles, MPB deposit their eggs in the phloem, cambium, and outer sapwoods of trees in galleries which adult beetles excavate upon boring into a tree (Christiansen et al. 1987). Epidemic MPB populations affect stands of lodgepole pine with large diameters at breast height (DBH), older ages, and higher densities of trees; the most susceptible trees are between the ages of 80 to 100 years and with DBHs greater than 25 cm (Romme et al. 2006, Dordel et al. 2008). Emitting pheromones to attract other members of their species, mountain pine beetles typically gather on more susceptible trees (Christiansen et al. 1987). The recent outbreak has shown that MPB will attack even the healthiest trees when all most-susceptible trees have already been killed (Romme et al. 2006). Mountain pine beetles use two mechanisms to attack their host species: (1) feeding on the phloem of trees and (2) the beetles' mutualistic relationship with blue stain fungi (Grosmannia clavigera). Beetles carry the fungi to their new tree host and the fungi provides beetles with nutrition and help in slowing the defenses of trees (Rice and Langor 2009); the blue stain fungus blocks the transpiration stream of lodgepole pine (Christiansen et al. 1987). Lodgepole pine have developed a defense to MPB infestation, but when defending against epidemic populations of beetles, the threshold of this defense can be overcome; lodgepole pine posses a system of resin ducts in their phloem and xylem from which trees can "pitch out" beetles who have bored into the phloem (Christiansen et al. 1987; Figure 1).

Effects of Mountain Pine Beetle Outbreak in Subalpine Forests

Drawn-out MPB outbreaks are often associated with droughts (Christiansen et al. 1987), but could also be due to warm summers, warm winters, and abundant host trees for beetles (Romme et al. 2006). The large extent and duration of the recent outbreak can be attributed to two phenomena related to the climate: (1) Temperatures below -25° C in the fall or -40° C in the winter have not occurred for prolonged periods of time in recent years; these temperatures for prolonged periods of time will kill the beetle (Dordel et al. 2008). (2) Warming temperatures in the last decade have allowed the MPB to infest areas of forest that may or may not have previous history of outbreak. MPB outbreak has now been reported at "unusually high elevations" (Romme et al. 2006).

In southern British Columbia, Axelson et al. (2009) and Heath and Alfaro (1990) found that Douglas-fir (*Pseudotsuga menziesii*) succeeded lodgepole pine in MPB-attacked stands. However, in subalpine forests where Douglas-fir is absent (i.e. the forests of the current study), MPB outbreak appears to support the growth release of two other shade-tolerant, non-susceptible species—subalpine fir and Englemann spruce (e.g. Axelson et al. 2010, Romme et al. 2006, Sibold et al. 2007). New establishment from an available seedbed may also occur in canopy gaps (Klutsch et al. 2009). The existence of large densities of subalpine fir seedlings following an MPB outbreak does not necessarily mean that subalpine fir will dominate the future forest canopy. For example, spruce may codominate with fir because of the greater longevity of the former and higher mortality rate of the latter (Veblen 1986b, Veblen et al. 1991b). Following a stand-replacing disturbance such as a severe fire, the typical succession involves initial dominance by lodgepole pine and sometimes Engelmann spruce and aspen. However, over time, successional development results in the replacement of aspen and lodgepole pine by spruce and

fir (Veblen 1986a). In the context of this successional sequence, a severe canopy disturbance will accelerate successional replacement of the shade-intolerant species by the more shade-tolerant subalpine fir and Englemann spruce (Veblen et al. 1989, Sibold et al. 2007).

Objectives

- To evaluate the likely impacts of MPB outbreak on the future forest composition of Routt and White River National Forests.
- To quantify the relative abundances of tree seedlings (both new establishment and released advance regeneration) of different species in stands recently attacked by MPB.
- 3. To evaluate potential limiting factors of lodgepole pine regeneration following a large-scale MPB outbreak.

Method

Study Area

The study area of the current study encompasses Routt and White River National Forests of northern Colorado (Figure 2). Routt National Forest extends to Wyoming's southern border and is often included in with the Medicine Bow National Forest of the southern Rocky Mountains. The portions of Routt and White River National Forests that were studied include the Sarvis Creek Wilderness, located near Rabbit Ears Pass, and the Mount Zirkel Wilderness. Although much diversity in canopy composition occurs throughout these forests, the stands of the areas are primarily subalpine, mixed conifer forests which are home to the four main species accounted for in this study: lodgepole pine, subalpine fir, Englemann spruce, and quaking aspen. The region has a continental climate that provides about 21 inches (~53 cm) of precipitation annually, peaking in the late winter and early spring (data *available online*).¹ The 22 sites studied exist between 2500 and 3000 meters of elevation and are characteristic of subalpine forest stands. Pre-evaluation of suitable stands was accomplished using a Geographic Information System (GIS). This evaluation required that study sites meet three criteria: (1) lodgepole pine was listed as a dominant life form in the forests' vegetation database, (2) the lodgepole forests of the area were recorded as MPB-infected, and (3) the stands were located near the edge of a 2002 wildfire boundary in order to pair burned and unburned sites as part of a larger study conducted by Teresa Chapman and Dr. Thomas T. Veblen comparing lodgepole pine regeneration following two different disturbances. Thus, sites were named based on the nearest 2002 wildfire. The fires studied include the Big Fish (BF), Burn Ridge (BR), Green Creek (GC), and Hinman (H) fires of 2002.

When in the field, site selection further depended on in-the-field factors unaccounted for in the GIS. Signs of logging, surface fire, and blowdown limited site selection due to the frequency of these events throughout the forest. These areas were avoided due to the fact that secondary disturbances could adversely affect our ability to study the influence MPB outbreak on the regeneration of lodgepole pine.

Field Sampling

One site consisted of two transects; rectangular transects were built by measuring 50 meters from the beginning of each transect with a measuring tape. Perpendicular from the tape, each transect extended one meter on each side to create a total transect area of $100m^2$ (50m × 2m). Two transects are considered one site because the data collected in both transects were

¹ < http://www.wrcc.dri.edu/>

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considered part of the same tree stand. Sites were spaced at least 400 meters apart to avoid spatial autocorrelation between stands. Transects were then further divided into ten microplots. Every five meters along the measuring tape represented the end of one microplot and the beginning of another until reaching the end of each transect at 50 meters (Figure 3).

Field sampling at each transect involved four major tasks: site description, microplot description, seedling census, and tree census. For each site description, habitat description was briefly described by identifying nearby understory vegetation and apparent moisture availability (i.e. one site appeared to be boggy). The elevation and geographic coordinates of the beginning of each transect were recorded using a handheld GPS unit. Aspect and transect direction were recorded using a compass and slope was recorded in degrees using a clinometer.

A team of two researchers measured and recorded microplot descriptions. For each $10m^2$ microplot, ground cover types were recorded using a "bird's eye view" from the center of each transect; bare mineral soil, rock, fine litter, coarse litter, coarse woody debris, woody plants, graminoids, and forbs were recorded using this method. Cover types were given a value of zero to five: 0 = <1% cover, 1 = 1.5% cover, 2 = 5.25% cover, 3 = 25.50% cover, 4 = 50.75% cover, and 5 = >75% cover. Microplot descriptions also included litter depth measurement, canopy density measurement, and distance to seed sources for each seedling species recorded in each microplot. Litter depth was recorded using a trowel and a measuring stick. Four canopy densities were recorded in each microplot using a densiometer; researchers turned 90 degrees for each of the four measurements, and densiometer readings were converted to percents to represent the openness of the canopy. Lodgepole pine seed sources included live lodgepole pine trees and dead lodgepole pine trees with open cones. Only live trees were recorded as seed sources for

subalpine fir and Englemann spruce, but dead and live trees were counted as seed sources for quaking aspen because aspen is known to reproduce through root suckering.

Seedling censuses were conducted in each transect. Seedling density was accounted for by recording the transect and microplot number that each seedling existed in. The species, seedling height (cm), and substrate were recorded to account for these characteristics. Substrates, or the surfaces on which organisms grow, included bare mineral soil, litter, coarse woody debris, moss, mounds, and pits. For lodgepole pine seedlings, we recorded the number of whorls (rows of branches) to determine an estimate of age for each seedling; lodgepole pine grow a new whorl every growing season and this information can be used to estimate the date of establishment of a particular seedling.

Finally, after completing the seedling census, researchers conducted a tree census. For the purpose of more accurately recording tree density, tree census transects were extended two meters on either side of the measuring tape; transects now measured 200m² (50m x 4m). Similar to the seedling census, tree species and heights were recorded. Using a DBH (diameter at breast height) tape measure, researchers measured the DBH of each tree and also recorded whether the tree was dead or alive. Trees angled lower than 45 degrees were not considered in the tree census as they were accounted for as coarse woody debris. For every lodgepole pine tree, further measurements were obtained: the percent of serotiny was measured by eye (0-100%) and visible signs of MPB attack were used to determine if the tree was attacked by MPB (visibility of MPB galleries or resin pitch are visible signs of attack).

Statistical Analysis

Data collected in the field was tabulated in an Excel spreadsheet and converted to tables to be read in R. All variables except for seedling and tree densities represent averaged values compiled by each site. All seedling densities were converted from density/200m² to density/ha and tree densities were converted from density/400 or $500m^2$ to density/ha; density values for each transect were then averaged together to create a value for each site. Aspect was one variable that required transformation; aspect is measured in 360 degrees. We took the cosine of each site's aspect value to determine northness versus southness. Variables closer to one represent aspects with greater northness and variables closer to negative one represent aspects with greater southness (1 = 0° and 360° N, -1 = 180° S).

All values were compiled by site name in order to create a final data table from which relationships could be tested using linear and logistic regression. Collinearity between variables was avoided by testing the collinearity of all variables before using them in regressions; this method was used on all variables accounted for when observing relationships with seedling densities. Variables were considered collinear if the variance inflation factor (VIF) was greater than five; in the case of collinearity, one of the two collinear variables was excluded from my analysis based on its understood importance to the study.

Results

Data was collected from 44 transects at 22 sites; of these 22 sites, seven sites were at the perimeter of the Green Creek Fire in the Sarvis Creek Wilderness and five sites were at each of the remaining fire perimeters: the Big Fish Fire, the Burn Ridge Fire, and the Hinman Fire. Sites varied in elevation, slope, and aspect (Table 1). Elevations ranged from 2548 meters to 2955 meters—the middle range of the subalpine forest in Routt and White River National Forests. Sites were chosen based on the canopy composition; lodgepole pine always existed and was primarily the dominant species in the canopy. The absence of secondary disturbances was also required: blowdown, logging, surface fire, etc.

Pre-Outbreak Canopy Composition

The canopy composition prior to the recent mountain pine beetle outbreak was characteristic of a mixed subalpine forest due to its canopy composition (Table 2). Lodgepole pine and subalpine fir were present in all stands; these two species codominated at most sites and lodgepole pine was always the first or second dominant life form in each stand. Englemann spruce existed in the canopy of 13 of the 22 sites and quaking aspen only existed in 8 sites; aspen was only over 20% of the canopy composition at two sites: GC1 and H4. Total tree densities ranged from 1125 trees/ha to 3475 trees/ha with a mean density of 2115 trees/ha.

Effects of Mountain Pine Beetle on Canopy Composition

On average, the MPB outbreak killed 721.8 lodgepole pine trees/ha in the canopies of Routt and White River National Forests. The appearance of MPB galleries and bore holes on the trunks of most lodgepole pine trees indicated a high attack rate of MPB. This was later confirmed after analyzing the data; two-thirds of our sites had between 56.85% and 88.35% of their lodgepole pine trees attacked by the MPB. The mean lodgepole pine mortality was 70.71% at the 22 sites. The relationship between elevation and lodgepole pine mortality was nearly significant (t(20)=-2, p=.059); as elevation increases, lodgepole pine mortality appears to decrease. The percent mortality for lodgepole pine ranged from 34% to 96%, but two-thirds of this data fall between 53% and 88% lodgepole pine mortality. This suggests that there is a high severity of lodgepole pine mortality in MPB-attacked stands in northern Colorado.

I observed that a significant relationship with average lodgepole pine DBH may affect MPB severity. The average DBH of lodgepole pine attacked by MPB was significantly higher than the average DBH of lodgepole pine still alive (t(42)=4.33, p<.0001); the average DBH of alive MPB trees was 17.11 cm and the average DBH of MPB-attacked lodgepole pine was 26.39

cm. This confirms that MPB target hosts with larger girths. Across our 22 sites, as average lodgepole pine DBH increases by 10 cm, the percent of lodgepole pine attacked by MPB significantly increased by 17.15% (t(20)=3.83, p=.001; Figure 4). We also observed that the average DBH for lodgepole pine attacked by MPB was significantly lower on north-facing slopes than on south-facing slopes (t(20)=-2.09, p=.0499). Thus, I expect MPB severity to be higher on south-facing slopes than north facing slopes.

Lodgepole pine tree density undoubtedly affects the number of lodgepole pine attacked by MPB in a given stand; stands with greater lodgepole pine tree densities will inherently have greater densities of MPB-attacked lodgepole pine simply because the number of MPB host species is greater. However, I observed no relationship between lodgepole pine tree densities and the percent of lodgepole pine attacked. In other words, I found no pattern that suggests that stands with a greater composition of lodgepole pine (% lodgepole pine) are more likely to experience greater MPB severity than stands with less lodgepole pine composition.

Effects of Mountain Pine Beetle on Litter Depth and Coarse Wood Debris

On average, our 22 sites had 2.68 cm of litter depth. No site averaged below 1.3 cm of litter depth. These litter depth measurements contrast greatly to nearby burn sites where litter depth was non-existent to very little (<2.5 cm). The top layers of litter were comprised mostly of fallen lodgepole pine needles. As lodgepole pine trees die from MPB infestation, their needles fall to the forest floor within the first three years of death (Wulder et al. 2006).

The near absence of fallen trees in at our sites suggests that the MPB outbreak occurred so recently that killed lodgepole pine trees have yet to fall. Coarse woody debris, which we would consider fallen trees, was never more than 20% of the cover type at any site; coarse

woody debris averaged only 6.68% of the cover type across our 22 sites and rarely exceeded 10%. Thus, I would expect high rates of lodgepole pine treefall in the next one to two decades.

Post-Outbreak Seedling Composition

Seedling composition following the MPB outbreak suggests a dominance of shadetolerant seedling regeneration. In particular, subalpine fir dominated seedling regeneration at all 22 sites (Table 3; Figure 5). Nevertheless, subalpine fir regeneration appears to be most limited by the amount of graminoids present in the understory. As the ground cover of graminoids increases by 10%, fir seedling density significantly decreases by 3169.0 seedlings per hectare (t(20)=-2.59, p=.018). The presence of graminoids in the understory may act as competition to fir seedlings. Fir regeneration may also be limited by canopy openness; this relationship was nearly significant (t(20)=-2.02, p=.057). As canopy gaps increase and more sunlight reaches the forest floor, the density of subalpine fir seedlings decreases. The average canopy openness of our 22 sites was only 29.19% opening which benefits shade-tolerant species over species like lodgepole pine. The shade-tolerance of subalpine fir may affect the recruitment rate of the species. As the mountain pine beetle outbreak creates gaps in the canopy due to lodgepole pine mortality, subalpine fir recruitment may actually reduce; subalpine fir establishment is most successful in the early years of an MPB epidemic because the canopy will continue to thin years after the outbreak. Englemann spruce and quaking aspen regeneration established at lower rates than subalpine fir-spruce averaged 297.7 seedlings/ha and aspen averaged 322.7 seedlings/ha compared to subalpine fir which averaged 7898.0 seedlings/ha over the 22 sites. Nonetheless, all three of these species' average seedling densities are higher than the average lodgepole pine seedling density of 220.5 seedlings/ha.

Lodgepole pine seedling regeneration may be limited by a number of factors. Due to the nature of our data on lodgepole pine seedling densities, a logistic regression was used: the large number of sites with zero lodgepole pine seedlings (ten sites) allowed us to create a variable of presence versus absence of lodgepole pine seedlings in each site—1 or 0, respectively. In sites where lodgepole pine seedlings were present, canopy opening appeared to be the most important factor in lodgepole pine regeneration. Stands with lodgepole pine regeneration had significantly more open canopies (z(21)=2.46, p=.014; Figure 6). This supports the suggestions that lodgepole pine is shade-intolerant and recruitment for the species is greater in stands with lower canopy densities.

Litter depth also significantly affected lodgepole pine seedling regeneration. Sites with lodgepole pine seedling presence had significantly lower litter depths than sites where lodgepole seedlings were absent (z(21)=-2.18, p=.029; Figure 6). Lodgepole pine seedling establishment occurs more often in areas with bare mineral soil or thin litter depths (<2.5 cm). However, bare mineral soil rarely occurs in MPB-attacked sites; only 4 of our 22 sites had over 5% bare mineral soil. The lack of bare mineral soil and the abundance of litter in the understory of MPB-attacked lodgepole pine limit the establishment of lodgepole pine. No other cover type variables (i.e. herbaceous cover, coarse woody debris, fine litter, coarse litter, etc.) significantly affected lodgepole pine seedling densities.

Effects of Serotiny on Lodgepole Pine Regeneration

Average percent serotiny varied between our 22 sites from 0% to 95%, suggesting that serotiny is highly variable across individual stands. Where lodgepole pine cone serotiny is high, we might expect to find lower rates of lodgepole pine regeneration, but this was not conclusive from the data collected in Routt and White River National Forests. Neither the percent of serotinous trees in the canopy nor the density of serotinous trees at each site significantly affected lodgepole pine seedling regeneration. Interestingly, site BR5 had the highest density of serotiny (1025 serotinous trees/ha) but also had the highest rate of lodgepole pine seedling regeneration (1050 seedlings/ha). Serotiny may not be as much of a limiting factor to lodgepole pine seedling regeneration after MPB outbreak as expected.

Post-Outbreak Timing of Lodgepole Pine Seedling Establishment

We measured the number of whorls on 1640 lodgepole pine seedlings across our 22 sites. The mean number of whorls for lodgepole pine across 22 sites was 5.2 whorls. Much error should be accounted for when counting whorls as an estimate of seedling age. Lodgepole pine seedlings may put on more than one whorl in a year and whorls can also be difficult to identify. Nonetheless, most lodgepole pine seedlings in our 22 sites appear to have established post-MPB outbreak (within eight years prior to 2010). These averages are also skewed upwards due to suppressed lodgepole pine trees present in the forest before the MPB outbreak—seedlings present before the outbreak as described as part of *the reorganization response* (Figure 7); at least five lodgepole pine trees with over 60 whorls were counted as seedlings because they were less than 1.5 meters in height. The majority of lodgepole pine seedlings established after the MPB outbreak, but lodgepole pine seedling densities hardly compare to the far greater densities of subalpine fir seedlings found in Routt and White River National Forests.

Discussion

The recent mountain pine beetle outbreak caused significant changes in the subalpine forest structures or northern Colorado. Lodgepole pine mortality in the mixed stands of the current study suggests that canopy composition will shift toward a canopy codominated by shade-tolerant species like subalpine fir and Englemann spruce. Unlike a stand-replacing, high

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intensity fire which is characteristic of subalpine forests, MPB outbreak does not cause mortality of all canopy species in mixed stands. The remaining non-host species—subalpine fir and Englemann spruce—remain in the canopy structure and shade-tolerant seedlings may germinate at higher rates than shade-intolerant species such as lodgepole pine and quaking aspen.

The seedling densities calculated from the data of the current study suggest that seedling regeneration after a severe MPB outbreak is dominated by fir and spruce. A number of limiting factors affect the regeneration of lodgepole pine seedlings underneath MPB-attacked lodgepole pine trees. Canopy openness and litter depth are most limiting to lodgepole pine regeneration; low seedling densities are expected where litter depths are high (>2.5 cm) and where canopy openness is limited by non-host trees. Lodgepole pine's affinity to germinate on bare mineral soil and in open canopies makes it an ideal pioneer species following wildfires in the subalpine zone. However, the nature of a MPB outbreak disturbance is entirely different from fire. Lodgepole pine needles may stay on dead lodgepole pine trees for years after MPB attack which limits canopy opening. Furthermore, once needles fall from lodgepole pine trees, the litter depths of stands with lodgepole increase significantly.

Serotiny and Lodgepole Pine Seedling Regeneration

Predation and weathering can complicate the study of serotiny. Predators break open and store serotinous cones in seed caches and weathering slowly wears away the resin of serotinous cones making serotiny harder to identify in the field. There is also an apparent difference in the serotinous cones of the western slope versus the eastern slope; increased precipitation on the western slope appears to have weathered serotinous cones more than on the drier eastern slope. Eastern slope serotinous cones retain their pointed shape longer. Correct identification of serotinous versus open cones was a difficult and potentially fallible aspect of the current study. Although the current study found no relationship between serotiny values and lodgepole pine seedling densities, further research on this relationship should be conducted.

Future Forest Composition

Average seedling densities at each site illustrate the large difference in seedling regeneration between lodgepole pine and shade-tolerant species: the average lodgepole pine seedling density for all 22 sites was 220.5 seedlings/ha, whereas the average subalpine fir seedling density was 7898.0 seedlings/ha. Thus, the future forest composition for stands attack by a severe MPB outbreak will be codominated by subalpine fir and Englemann spruce—species characteristic of old growth subalpine forests. MPB outbreak has accelerated succession of lodgepole pine-mixed stands toward more shade-tolerant species.

Although the average subalpine fir seedling density is significantly higher than both average densities of lodgepole pine and Englemann spruce seedlings, this does not necessarily indicate a fir-dominated forest in the future. Although fir has a superior ability to establish in greater litter depth than lodgepole pine and Englemann spruce, fir has a higher mortality rate due to higher susceptibility to pathogens. Fir is also shorter-lived as suggested by the greater number of downed fir after windthrow (Veblen et al. 1991a). Therefore, the large densities of subalpine fir following MPB outbreak recorded in the current study might be expected in the early years of vegetation response to the outbreak. However, in future years we might expect high subalpine fir mortality leading to a codominance of fir and spruce.

Lodgepole pine should also be considered when discussing the future forest composition because of its presence in some stands as both seedlings present before the outbreak and new seedlings which established after the outbreak. Most of *the new establishment response* was dominated by fir and spruce seedling regeneration, but the existence of several suppressed lodgepole pine from before MPB outbreak may cause limited growth acceleration of these lodgepole pine as part of *the reorganization response*. As determined by the logistic regressions on lodgepole pine seedling densities illustrated in the current study, quantifying seedling densities across the Routt and White River National Forests is not ideal for lodgepole pine like it is for subalpine fir. Rather, future subalpine forests stands will either include lodgepole pine or the species will be absent altogether.

Conclusion

Vegetation response to severe mountain pine beetle outbreak is of critical importance to forest managers because the response is an indicator of future forest composition. The ways in which spruce-fir forests respond to secondary disturbances such as fire and blowdown may differ from the way stands with lodgepole pine respond to similar disturbances. Although the recent MPB outbreak has concerned forest managers about the health of Colorado's subalpine forests, it is important to remember that such outbreaks are natural disturbances that have occurred many times in the past. The recent MPB outbreak has caused high mortality rates of lodgepole pine in the canopy, but the regeneration response to the outbreak has accelerated MPB-affected stands toward succession by shade-tolerant species.

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Fire Name	Site Name	Elevation (m)	Slope (degrees)	Aspect (degrees)
Big Fish	BF1	2955.0	8.0	159
-	BF2	2671.0	25.5	47
	BF3	2729.0	11.0	34
	BF4	2724.5	6.0	132
	BF5	2932.5	4.5	180
Burn Ridge	BR1	2723.5	9.5	74
	BR2	2669.0	19.0	16
	BR3	2717.5	11.5	183
	BR4	2661.0	12.5	111
	BR5	2547.5	0.0	0
Green Creek	GC1	2789.0	8.0	118
	GC2	2831.0	6.5	61
	GC3	2867.5	12.0	239
	GC4	2821.5	4.0	116
	GC5	2916.5	6.5	215
	GC6	2946.5	3.0	178
	GC7	2879.0	23.5	28
Hinman	H1	2718.5	3.0	194
	H2	2615.5	3.0	53
	H3	2704.5	13.5	284
	H4	2568.5	5.0	165
	H5	2630.5	10.0	260

Table 1Physiographic Characteristics by Site

Notes: Elevation, slope, and aspect measurements recorded from the beginning of each transect and averaged by site

	Tree Density (trees/ha)			Species Composition (%)					
Site Name	LPP	SF	ES	QA	Total	LPP	SF	ES	QA
BF1	1100	225	200	0	1525	72.13	14.75	13.11	0
BF2	600	700	325	50	1675	35.82	41.79	19.40	2.99
BF3	625	500	375	25	1525	40.98	32.79	24.59	1.64
BF4	725	1175	225	125	2275	31.87	51.65	9.89	5.49
BF5	850	825	1025	125	2825	30.09	29.20	36.28	4.42
BR1	1175	650	25	75	1925	61.04	33.77	1.30	3.90
BR2	1525	25	0	0	1550	98.39	1.61	0	0
BR3	2900	525	0	0	3425	84.67	15.33	0	0
BR4	2175	200	0	25	2400	90.63	8.33	0	1.04
BR5	1525	25	0	0	1550	98.39	1.61	0	0
GC1	775	25	0	325	1125	68.89	2.22	0	28.89
GC2	560	680	80	0	1320	42.42	51.52	6.06	0
GC3	1150	525	0	0	1675	68.66	31.34	0	0
GC4	2050	375	850	0	3275	62.60	11.45	25.95	0
GC5	500	900	125	0	1525	32.79	59.02	8.20	0
GC6	550	1250	75	0	1875	29.33	66.67	4.00	0
GC7	625	2075	275	0	2975	21.01	69.75	9.24	0
H1	420	1220	1420	0	3060	13.73	39.87	46.41	0
H2	850	125	50	175	1200	70.83	10.42	4.17	14.58
H3	1200	1650	125	500	3475	34.53	47.48	3.60	14.39
H4	620	580	20	640	1860	33.33	31.13	1.08	34.41
H5	750	1250	500	0	2500	30	50	20.00	0

Table 2
Canopy Composition by Site

Notes: Lodgepole pine (LPP), subalpine fir (SF), Englemann spruce (ES), quaking aspen (QA).

Table 3		
Seedling	Composition	by Site

	Seedling Density (seedlings/ha)				
Site Name	LPP	SF	ES	QA	Total
BF1	0	1950	150	0	2100
BF2	0	10350	200	500	11050
BF3	0	18450	500	650	19600
BF4	0	7800	50	950	8800
BF5	50	5250	500	350	6150
BR1	250	10250	200	200	10900
BR2	1100	3600	0	100	4800
BR3	50	11700	1000	0	11850
BR4	0	2850	0	100	2950
BR5	1050	600	0	0	1650
GC1	500	1400	0	2750	4650
GC2	700	12900	1050	0	14650
GC3	550	1250	100	0	1900
GC4	0	12050	200	0	12250
GC5	250	2800	400	0	3450
GC6	200	9550	150	0	9900
GC7	100	7600	1100	0	8800
H1	0	4600	300	0	4900
H2	0	20950	50	50	21050
H3	0	11250	550	250	12050
H4	0	9850	0	1050	10900
H5	50	6750	950	150	7900

Notes: Lodgepole pine (LPP), subalpine fir (SF), Englemann spruce (ES), quaking aspen (QA).



Figure 1 Lodgepole Pine "Pitch" – A Pine's Defense to Bark Beetles

Notes: Lodgepole Pine can "pitch out" mountain pine beetles in the tree's phloem by exuding resin.

Figure 2

Study Sites within Routt and White River National Forests



Figure 3 Transect and Microplot Diagram



Notes: Yellow line represents the tape measure used to measure length of transect (50 m). Measuring sticks were used to measure one meter on each side of the tape so that transects were 100 m^2 . Transects were extended to two or three meters on each side of the tape measure for the tree census; tree densities were calculated accordingly to account for varying tree census areas.

Figure 4

Relationship between Average Percent of Lodgepole Pine (LPP) Attacked by MPB and the Average LPP Diameter at Breast Height



Average LPP Diameter at Breast Height (cm)



Notes: Notice the difference in scale for seedling densities; the range of subalpine fir seedling densities is near 20,000 seedlings/ha, whereas the other seedling density ranges are near 2,500 seedlings/ha.





Notes: On the Y-axis, 1.0 indicates lodgepole pine seedling presence and 0.0 indicated lodgepole pine seedling absence. Thus, as canopy openness increases, the data suggests that lodgepole pine seedling presence also increases. On the contrary, as litter depth increases, the presence of lodgepole pine seedlings decreases.

LODGEPOLE PINE REGENERATION



Figure 7 Distribution of Lodgepole Pine Seedling Whorls from all 22 Study Sites

Notes: This boxplot illustrates the distribution of lodgepole pine whorls among all 22 study sites. Assuming lodgepole pine seedlings grow one whorl per year, this data suggests that 50% of lodgepole pine seedlings throughout all 22 sites established in the last four to six years. Population = 1640, Mean = 5.71; Median = 5; Q1 = 4; Q3 = 6; Minimum = 0; Maximum = 78. Fifty percent of the data, between Q1 and Q3, are between four and six whorls.