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Seed release in serotinous lodgepole pine forests after mountain pine beetle outbreak

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Abstract. There are concerns that large-scale stand mortality due to mountain pine beetle (MPB) could greatly reduce natural regeneration of serotinous Rocky Mountain (RM) lodgepole pine (*Pinus contorta* var. *latifolia*) because the closed cones are held in place without the fire cue for cone opening. We selected 20 stands (five stands each of live [control], 3 years since MPB [3-yr-MPB], 6 years since MPB [6-yr-MPB], and 9 years since MPB [9-yr-MPB] mortality) in north central British Columbia, Canada. The goal was to determine partial loss of serotiny due to fall of crown-stored cones via breakage of branches and in situ opening of canopy cones throughout the 2008 and 2009 growing seasons. We also quantified seed release by the opening of forest-floor cones, loss of seed from rodent predation, and cone burial. Trees killed by MPB three years earlier dropped ~3.5 times more cones via branch breakage compared to live stands. After six years, MPB-killed stands had released 45% of their canopy seed bank through cone opening, cone fall due to breakage, and squirrel predation. Further losses of canopy seed banks are expected with time since we found 9-yr-MPB stands had 38% more open canopy cones. This was countered by the development of a modest forest-floor seed bank (6% of the original canopy seed bank) from burial of cones; this seed bank may be ecologically important if a fire or anthropogenic disturbance reexposes these cones. If adequate levels of regeneration are to occur, disturbances to create seedbeds must occur shortly after tree mortality, before the seed banks are lost. Our findings also suggest that the sustained seed rain (over at least nine years) after MPB outbreak may be beneficial for population growth of ground-foraging vertebrates. Our study adds insight to the seed ecology of serotinous pines under a potentially continental-wide insect outbreak, threatening vast forests adapted to regeneration after fire.

Key words: biotic disturbance; cone burial; cone opening; Dendroctonus ponderosae; *ground-foraging vertebrates; mountain pine beetle; natural regeneration;* Pinus contorta *var.* latifolia; *Rocky Mountain lodgepole pine; seed banks; serotiny (canopy seed storage);* Tamiasciurus hudsonicus.

INTRODUCTION

Seed release in serotinous plants is the first and arguably the most critical step in regeneration (Nathan and Ne'eman 2000). Serotiny is broadly defined as canopy seed storage (sensu Lamont et al. 1991) in Rocky Mountain (RM) lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) and is thought to be an adaptation to stand-replacing fires (Lotan 1975, Critchfield 1985, Keeley and Zedler 1998). Fire enables seed release (pyriscence sensu Lamont 1991) by producing temperatures that are high enough to break the resin bond that holds the cone scales together. Plant species can range from weakly serotinous (seeds are retained for some time but released spontaneously without fire) to strongly serotinous; however moderate serotiny is favored in environments subject to stochastic fires or when fire intervals are near or longer than the longevity of the species (Enright et al. 1998). Typical populations of RM lodgepole pine in western Canada and northern United States (except in Yellowstone National Park [NP] and more south) are highly serotinous (Lotan and Perry 1983, Koch 1987). As a result an enormous canopy seed bank is present in these mature forests.

Large-scale outbreaks of mountain pine beetle (*Dendroctonus ponderosae* Hopkins) in RM lodgepole pine forests of western Canada has affected over 10 million hectares of forests representing 46% of British Columbia's RM lodgepole pine in 2007 (and predicted to be 76% by 2015) (Walton et al. 2008). The outbreak has recently spread into Alberta and may transfer over to jack pine (*Pinus banksiana* Lamb.), another serotinous species ranging eastward to the Atlantic coast (Logan and Powell 2001, Rice et al. 2008). It is thought that serotiny is a disadvantageous trait in the context of mountain pine beetle (MPB) outbreaks because gradual tree death after MPB does not provide the usual fire cue for cone opening and seed release (Hellum and Wang 1985), thereby jeopardizing seedling establishment in the period after MPB attack. It is still unclear if seeds can be released in the absence of fire and whether seed viability declines after tree death.

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PLATE 1. A 3-yr-MPB stand in black and white infrared with a surviving live codominant Rocky Mountain lodgepole pine (white needles). Photo credit: F. P. Teste.

First, as trees die, seeds may be released as a result of canopy cone opening due to increased canopy temperatures and weathering. A comparable situation has been observed in the serotinous pine *Pinus halepensis* Miller where warm and dry conditions provoked cone opening (xeriscence) and released up to 59% of the canopy seeds (Nathan et al. 1999). Second, cones from the crown will likely be lost in the years following MPB outbreak. We hypothesize a peak in loss of cones to the forest floor early after tree death; the small branches will quickly dry and become brittle while the bole still retains moisture and remains flexible. The sway of the trees and the crown friction (Rudnicki et al. 2003) at this time could cause significant breakage of cone-bearing branches. Third, it remains to be seen if the seeds in these cones are retained or fall onto the forest floor. Fourth, if closed cones are covered by plant matter such as mosses before opening, these cones have the potential to protect the seeds until a secondary disturbance such as fire or logging reexposes these cones to conditions suitable for opening.

Pine squirrels (*Tamiasciurus hudsonicus* Erxleben) are the dominant and often only predator of RM lodgepole pine seed (Smith 1970, Elliott 1974, Benkman et al. 2003). While moderate to high frequency of crown fire favors serotiny (Enright et al. 1998), predation by pine squirrels appears to select against serotiny (Benkman and Siepielski 2004). The seeds in closed cones serve as an all-year food supply in cone caches, resulting in poor dispersal of seeds compared with seed dispersal by birds in pines of subgenus *Strobus* (white pines; Lanner 1998, Steele et al. 2005). If canopy cones open after tree death, the amount of seed-bearing cones available for pine squirrels would be reduced; however, the released seeds may become an important food source for ground-foraging vertebrates. Because new canopy cone crops are not produced after MPB outbreaks (most or all trees are killed), it is unclear if squirrels continue to prey on cones in the years after attack or abandon these stands.

The first set of objectives was to determine if canopy seed release after MPB outbreak in RM lodgepole pine forests occurs, specifically to determine: (1) to what degree is there a greater falling of cones to the forest floor post MPB via breakage of canopy branches; (2) the amounts of canopy cone opening after 3, 6, or 9 years since MPB mortality; (3) the extent that fallen cones found on the forest floor open and release their seeds; and (4) to what degree do squirrels prey on recently fallen cones and if predation is related to cone density. The second objective was to take this newly generated knowledge on seed release and estimate the temporal changes in canopy and forest-floor seed banks in the years after a MPB outbreak. Such estimations are important for decision-makers and managers to plan for

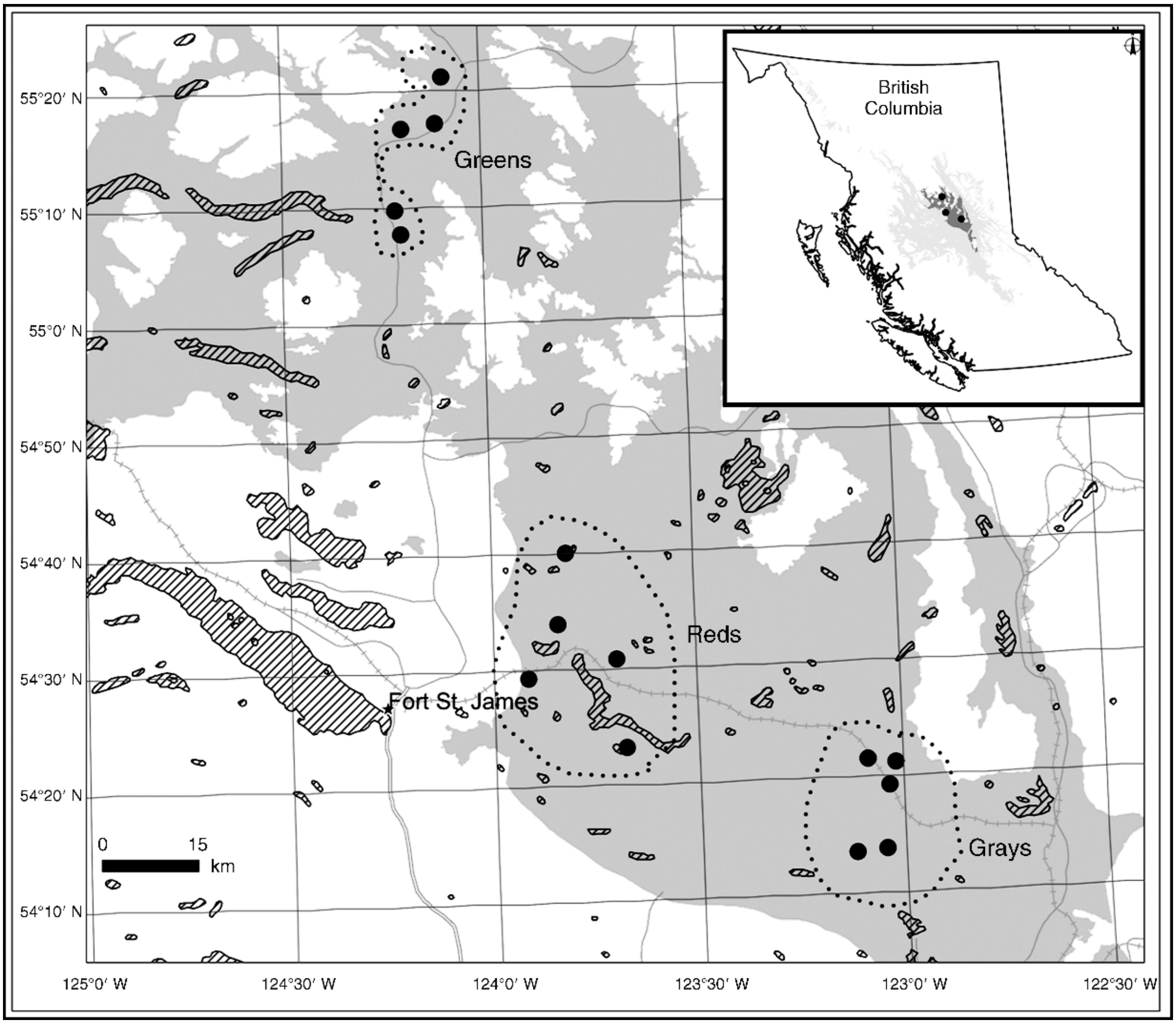

FIG. 1. Maps of study areas showing the general location of the live, 3-yr-MPB, and 6-yr-MPB stands (inset map, British Columbia, Canada) within the Sub-Boreal Spruce (SBS) zone (light gray) and the specific locations of the live, 3-yr-MPB, and 6-yr-MPB stands within the SBS mk1 (Sub-Boreal Spruce moist cool 1) biogeoclimatic subzone (dark gray). Green stands are unattacked or recently attacked stands retaining green needles. Red stands usually occur 1–2 years (occasionally up to 3 years) after mortality; during this period the foliage turns red, and branches become brittle. Gray stands usually occur at 3 years (occasionally 4 years) after death; branches completely lose their needles, and stands appear gray from a distance (British Columbia Ministry of Forests 1995).

natural regeneration in the reforestation of the immense and growing landscape of MPB-attacked stands.

METHODS

Site and stand characteristics

Fifteen stands (>4 ha) were selected in the Sub-Boreal Spruce moist cool 1 (SBSmk1) biogeoclimatic subzone of British Columbia (Meidinger and Pojar 1991; Fig. 1). These stands included five stands with no MPB (live-control), five stands 3 years since MPB mortality (see Plate 1), and five stands 6 years since MPB mortality (referred to as live, 3-yr-MPB and 6-yr-MPB stands hereafter). An additional five stands 9 years since MPB mortality (9-yr-MPB) (of similar structure and composition but 9 years after MPB attack) were examined in 2009. These 9-yr-MPB stands were from the nearby SBSdk (Sub-Boreal Spruce dry cool) biogeoclimatic subzone and used only to determine if partial loss of stand serotiny due to opening of canopy cones continued with time. Color of needles (typically used by forest managers and by MPB researchers) can be used to indicate years since MPB attack and can be associated with mechanisms that promote cone and seed release from the canopy (e.g., trees with red needles can still sway widely and collide into neighboring trees thereby releasing cones via branch breakage). Ground and aerial surveys of the annual spread of MPB conducted by the British Columbia Ministry of Forests and Range and our own cross-dating of tree rings (Table 1) were used to determine the year(s) of the MPB outbreak at each stand. Cross-dating between three to five live trees and five MPB-attacked trees in each stand was done on cross sections cut from the base of the felled trees. Red stands usually occur 1–2 years (occasionally up to 3 years) after mortality: during this period the foliage turns red and branches become brittle. Gray stands usually occur at 3 years (occasionally 4 years) after death; branches completely lose their needles and stands appear gray from a distance (British Columbia Ministry of Forests 1995). The boles in the gray stands become dry and rigid until trees fall 10 to 15 years later.

Stands similar in density, tree height, and understory characteristics, such as low levels of conifer advanced regeneration and suppressed tree cover, were selected. Accessible live stands with similar stand characteristics (stem density and height) as the 3-yr-MPB and 6-yr-MPB stands (in the SBSmk1) were difficult to locate, because of the broad scale of the outbreak, and as a result only five replicate stands were selected. The live stands were located in the northern part of the SBSmk1 where in 2008 the edge of the MPB outbreak was located (Fig. 1) and had slightly lower levels of serotiny (Table 1). This slight difference was attributable to the younger age of the live stands and their location at higher elevations (Koch 1987, Keeley and Zedler 1998). For this reason, we did not use the live stands as a control for measurements of canopy cone opening. Instead, we sampled residual live trees within the 3-yr-MPB and 6-yr-MPB stands to examine changes in cone opening after mortality. Stand and tree characteristics of all measured stands are summarized in Tables 1 and 2. The SBSmk1 is a large subzone (12 910 km^2) typical of the SBS biogeoclimatic zone and similar to the Foothills Natural Region on the east side of the Rocky Mountains (Meidinger and Pojar 1991, Natural Regions Committee 2006). Large fires (>500 ha) with a mean return interval of 175 years are typical for the SBSmk1 zone (Delong and Tanner 1996, Wong et al. 2003); therefore fire frequency was not considered during site selection because under this scenario, strong cone-scale resin bonds (partly responsible for serotiny) would be equally selected for across the whole study region. Given that the stands were all within the SBSmk1, the RM lodgepole pine trees in this study were considered to be from a comparable genetic population (Ying and Yanchuk 2006). Tree canopies were dominated by mature RM lodgepole pine and understory vegetation was dominated by red-stemmed feathermoss (*Pleurozium schreberi* Mitten), bunchberry (*Cornus canadensis* L), and black huckleberry (*Vaccinium membranaceum* Hook).

Canopy seed bank

We defined serotiny as canopy seed storage (sensu Lamont et al. 1991), and it is only used when referring to whole-tree's or stand's ability to retain a certain level of canopy seed. Therefore we avoid using the terms "cone serotiny" or "serotinous cones" because a cone is not strictly a canopy seed storage structure because closed cones with seed can be found on the forest floor. Instead a cone is described as closed, partly open, or open.

Canopy cone fall due to branch breakage.—In each of the 15 stands, 10 (10-m^2) cone-survey plots were randomly established along a 100-m transect during the first week of June 2008. Ground survey of cones (attached to twigs and branches or loose on the ground) in plots started promptly after snowmelt between 5 and 10 June 2008. We assumed that this initial density of cones released from the canopy (referred to as ground cones hereafter) was the result of cone fall that occurred during the winter months (from October 2007 to May 2008), when moss growth is negligible (Frolking et al. 1996). Additional surveys were conducted 15–24 July and 25–29 September in order to estimate release of canopy cones over one year. Fallen branches and ground cones that appeared to have been severed or damaged by squirrels (i.e., showing distinct teeth marks) were excluded from the data related to cone fall from the canopy. Furthermore, the resulting values for cone density for the year were considered underestimates of breakage because they did not account for post-dispersal squirrel predation for the whole period. At each plot, all ground cones lying on top of the moss layer, without signs of moss overgrowth, were counted and marked.

All ground cones and branches were marked with fast-drying, odorless paint (Yolo Colorhouse zero VOC exterior 100% acrylic paint; YOLO Colorhouse, Portland, Oregon, USA) to quantify the input and output (see *Squirrel predation of forest-floor cones*) of ground cones throughout the growing season. Scales at the base of cones were painted with a small brush. At each sampling date a new color was used to mark newly added ground cones and an openness value was assigned to each cone.

All measured cones were assigned a cone-openness value based on visual estimates of the fraction of open scales to total scales. An openness value of 0 was assigned to cones with 0 to ~5% opened scales (a few open scales was tolerated); 25, to cones with ~6% to ~38% opened scales (estimated visually); 50, to cones with 39% to 63% opened scales (estimated visually); 75, to cones with 64% to 95% opened scales (estimated visually); and 100, to cones with ~96% to 100% opened scales (a few closed scales was tolerated). If the cones were wet (causing the scales to close over), cone openness was assessed by a hand-squeeze test (Crossley 1956*a*), where pressure was applied to the cone scales to determine if they had been open.

Opening of canopy-held cones.—In late July, in each stand, 10 dead and 5 live residual dominant or codominant trees were randomly selected and felled along a second transect, at least 25 m away but parallel to the line of cone-survey plots. Cone loss during felling of trees was minimized by dropping trees in clear alleys (reducing branch breakage as the trees fell), in gaps or on roads where cones could easily be collected for

TABLE 1. Stand characteristics of live, 3-yr-MPB (mountain pine beetle), and 6-yr-MPB attacked stands of Rocky Mountain (RM) lodgepole pine, *Pinus contorta* var. *latifolia*, in the Sub-Boreal Spruce moist cool 1 (SBSmk1) biogeoclimatic subzone of British Columbia, Canada in 2008.

Stand and |stand comparisons|	Elevation (m)	Composition (% RM lodgepole pine)	Tree attack class (%)†		
			Green-live	Red-dead	Gray-dead
Live	979 (950 to 1007)	97 (94 to 100)	98 (92 to 100)	2 (0 to 9)	0 (0 to 8)
3-yr-MPB	835 (806 to 864)	99 (96 to 100)	9 (3 to 16)	76 (69 to 83)	15 (7 to 23)
6-yr-MPB	755 (727 to 784)	100 (96 to 100)	6 (0 to 17)	17 (10 to 24)	77 (69 to 85)
|Live − 3-yr-MPB|	143 [94 to 193]	2 [−4 to 8]	89 [77 to 100]	74 [62 to 86]	15 [1 to 29]
|3-yr − 6-yr-MPB|	80 [30 to 129]	1 [−5 to 7]	3 [−8 to 15]	59 [47 to 71]	62 [48 to 75]
|6-yr-MPB − Live|	223 [173 to 273]	3 [−3 to 9]	92 [81 to 100]	15 [3 to 27]	77 [63 to 90]

Notes: Stand values are means with 95% confidence intervals (CIs) in parentheses, and stand comparisons are differences between means with simultaneous 95% CIs in brackets. The simultaneous CIs for the differences in means are based on the studentized range statistic, Tukey's honestly significant difference (hsd) method. If zero is included in the CI then the two means are not considered statistically different.

† Cross-dating revealed that stands were initially attacked between 2004 and 2005 (3-yr-MPB) and 2001 and 2002 (6-yr-MPB). Colors correspond to the shifting colors of the needles in the crowns after an MPB outbreak and can be used to indicate years since death after MPB (British Columbia Ministry of Forests 1995).

tallying. For both live and dead trees, tree-level canopy cone openness was determined by the mean cone-openness value for the first 100 mature cones starting from the top branch. Most of these cones were young but a few ranged up to 20 years old, where 1-yr-old cones were mature in 2007 from the trees in the live stands, in 2004 from the trees in the 3-yr-MPB stands, and in 2001 from the trees in the 6-yr-MPB stands. Stand-level canopy cone openness was determined by calculating the mean tree-level canopy cone openness. The total number of mature cones was counted on three randomly selected felled trees per stand.

At the stand level, we estimated initial canopy cone openness levels by determining the average proportion of open cones on residual live trees found in the MPB-attacked stands. We did not use cone-base asymmetry as a surrogate for estimating persistently open cones because the relationship found by Tinker et al. (1994) did not hold in these forests, based on our observations. Indeed, with the techniques that we used, we could not separate persistently open cones from those that opened since time of maturation. This does not matter; however, because our objective was to determine the incremental degree of cone opening after MPB, we compared the cone openness values from the dead trees to those of the residual live trees within the same stands. This comparison of trees within each stand (as opposed to the comparison with the live stands) was done because variation in serotiny among stands, due to stand age, fire frequency, light transmission, and soil conditions (Crossley 1956*b*, Keeley and Zedler 1998), was considered greater than variation in serotiny within stands (e.g., <1 km; Tinker et al. 1994).

To estimate the number of seeds per cone across all stands, we randomly sampled 30 closed cones (with an openness value 0) evenly distributed among the last 10 annual cohorts of cones from each stand (total of 450 cones). Cones were placed in a kiln at 200°C for 15

TABLE 2. Tree characteristics of live, 3-yr-MPB (mountain pine beetle), and 6-yr-MPB attacked stands of Rocky Mountain lodgepole pine, *Pinus contorta* var. *latifolia*, in the Sub-Boreal Spruce moist cool 1 (SBSmk1) biogeoclimatic subzone of British Columbia, Canada in 2008.

Stand and |stand comparisons|	Age (yr)	Height (m)	dbh (cm)	Crown		Canopy cone openness (%)	Cone density (cones/tree)
				Height (m)	Width (m)		
Live	78 (53 to 103)	17.4 (15.5 to 19.3)	16.1 (13.7 to 18.4)	7.2 (6.0 to 8.4)	2 (1.5 to 2.5)	20 (16 to 24)	182 (5 to 360)
3-yr-MPB	114 (89 to 139)	21.4 (19.5 to 23.2)	19.6 (17.3 to 22.0)	8.0 (6.8 to 9.2)	2.4 (1.9 to 2.9)	8 (3 to 12)†	392 (214 to 569)
6-yr-MPB	92 (67 to 117)	18.2 (16.3 to 20.0)	16.8 (14.5 to 19.2)	8.4 (7.2 to 9.6)	2.3 (1.7 to 2.8)	8 (4 to 12)†	392 (214 to 569)
|Live − 3-yr-MPB|	36 [−7 to 79]	4.0 [0.7 to 7.3]	3.6 [−0.5 to 7.6]	0.8 [−1.3 to 2.9]	0.4 [−0.5 to 1.3]	12 [5 to 20]	209 [−98 to 516]
|3-yr-MPB − 6-yr-MPB|	22 [−21 to 65]	3.2 [−0.1 to 6.4]	2.8 [−1.3 to 6.8]	0.4 [−1.7 to 2.5]	0.1 [−0.8 to 1.1]	0 [−7 to 7]	0 [−307 to 307]
|6-yr-MPB − Live|	14 [−29 to 57]	0.8 [−2.5 to 4.1]	0.8 [−3.3 to 4.8]	1.3 [−0.8 to 3.4]	0.3 [−0.6 to 1.2]	12 [5 to 20]	209 [−98 to 516]

Notes: Stand values are means with 95% confidence intervals (CIs) in parentheses, and stand comparisons are differences between means with simultaneous 95% CIs in brackets. The simultaneous CIs for the differences in means are based on the studentized range statistic, Tukey's honestly significant difference (hsd) method. If zero is included in the CI then the two means are not considered statistically different.

† Predicted canopy cone openness levels of the 3-yr-MPB and 6-yr-MPB stands prior to MPB outbreak based on residual live trees within the site.

Table 1. Extended.

Stand density (trees/ha)	Basal area (m^2/ha)	Moss thickness (cm)
1920 (1310 to 2530)	36.2 (31.3 to 41.0)	2.2 (0.9 to 3.5)
1740 (1130 to 2350)	38.7 (33.8 to 43.6)	3.8 (2.4 to 5.1)
1960 (1350 to 2570)	34.1 (29.2 to 38.9)	4.0 (2.7 to 5.3)
180 [−880 to 1240]	2.5 [−5.9 to 10.9]	1.6 [−0.8 to 3.9]
220 [−840 to 1280]	4.6 [−3.8 to 13.0]	0.2 [−2.1 to 2.6]
40 [−1020 to 1100]	2.1 [−6.3 to 10.5]	1.8 [−0.5 to 4.1]

minutes or until cone scales were completely flexed open. Individual cones were hit on a hard surface and scales pulled apart to extract the seeds. The total number of seeds per cone was adjusted for the average number of nonviable empty (without embryo) seeds (14.5%, 15.2%, 13.9%) associated with each stand type. The percentage of empty seeds was determined by subjecting 500 randomly selected seeds from each MPB-attacked stand (total of 10 000 seeds) to X-rays (25 kV and 750 μA for 30 s) and scoring the number of empty seeds in digital radiographs (Kubtec, Xpert 40; KUB Technologies, Milford, Connecticut, USA).

Forest-floor seed bank

Forest-floor cone opening.—The marking of ground cones and estimation of cone openness allowed us to monitor any changes in ground-cone openness throughout the growing season. We monitored these changes in openness of ground cones between sampling dates (early June and late September). On many occasions, as ground cones were picked up to estimate openness, we observed in situ seed release.

Squirrel predation of forest-floor cones.—We were able to estimate squirrel predation of marked ground cones over the sampling intervals by recounting the ground cones of different colors that had been marked between June and July. It was assumed that a decrease in number of marked cones was the result of squirrel predation on the ground cones over that time period.

Cone burial.—In autumn, another set of 10 1-m^2 subplots were established in each of the 15 sites to excavate cones that had been buried in the forest floor; cones were classified as embedded if part of the cone was embedded in the feathermoss layer, and cones completely buried below the feathermoss were referred to as buried cones. Embedded and buried cones were counted, and their openness was determined.

Data analysis

All statistical analyses were carried out using the R statistical environment for statistical computing and graphics (R Development Core Team 2008). The data were first analyzed using a fixed-effects model with a one-way treatment structure where the sites served as replicates ($n = 5$). Assumptions of normality and homoscedasticity were assessed graphically in R. Analysis of covariance, using canopy cone density as the covariate, was not justified suggesting that the slightly lower (nonsignificant) canopy cone densities in the live stands (Table 1) were not a confounding factor affecting rates of canopy cone fall. Based on the pooled variance from the fixed effects model and the experimental error degrees of freedom, we calculated and used least significant difference (LSD) bars, 95% confidence intervals (CIs), and effect-size estimates as a stand-alone approach for making both statistical and ecological inferences (Kline 2004, Di Stefano et al. 2005, Levine et al. 2008).

In the figures, CIs were accompanied by LSD bars ($\alpha = 0.05$) and used as visual multiple-mean comparison tests (Saville 2003, Crawley 2007). In the tables, unstandardized-effect sizes (i.e., differences between means) with their associated simultaneous CIs based on Tukey's honestly significant difference method (function TukeyHSD in R) were used to detect statistically significant effects and highlight precision and uncertainty in the estimates (Altman et al. 2000, Nakagawa and Cuthill 2007). Graphical use of CIs was also used to suggest ecological importance in the estimated effects (Steidl and Thomas 2001, Di Stefano 2004). Results of null hypothesis significance testing and *P* values were not reported (see Appendix A) because CIs provide all of the necessary information and more (e.g., uncertainty) to make inferences (Cumming 2008).

Temporal estimation of seed banks

Based on our data, we determined the fate of the canopy- and forest-floor seed banks of RM lodgepole pine in annual time steps at the three stand types after MPB outbreak, compiling results for the end of each growing season (October) and using some values from the literature, in order to highlight the number of seeds released from the canopy seed bank and moved to the forest-floor seed bank. We estimated backward in time, starting with the remaining canopy seed bank in the 6-yr-MPB stands (year 6 since MPB attack) and back-calculated up to year 0. Temporal estimates of seed banks were specifically made up of two separate components: (1) the canopy seed bank estimates accounted for canopy cone fall from branch breakage, canopy cone opening, and squirrel predation of canopy cones; and (2) the forest-floor seed bank estimates accounted for the opening of ground cones, fate of dispersed seeds, squirrel predation of ground cones, and cone burial. See Appendix B for details about the calculations of the seed bank estimates.

RESULTS

Canopy cone bank

Partial loss of serotiny due to canopy cone fall.—Three years since MPB mortality stands dropped an estimated 17 800 (CI 12 400 to 23 100) canopy cones·ha^{-1}·yr^{-1} to the forest floor (Fig. 2A); 9200 cones were found on the

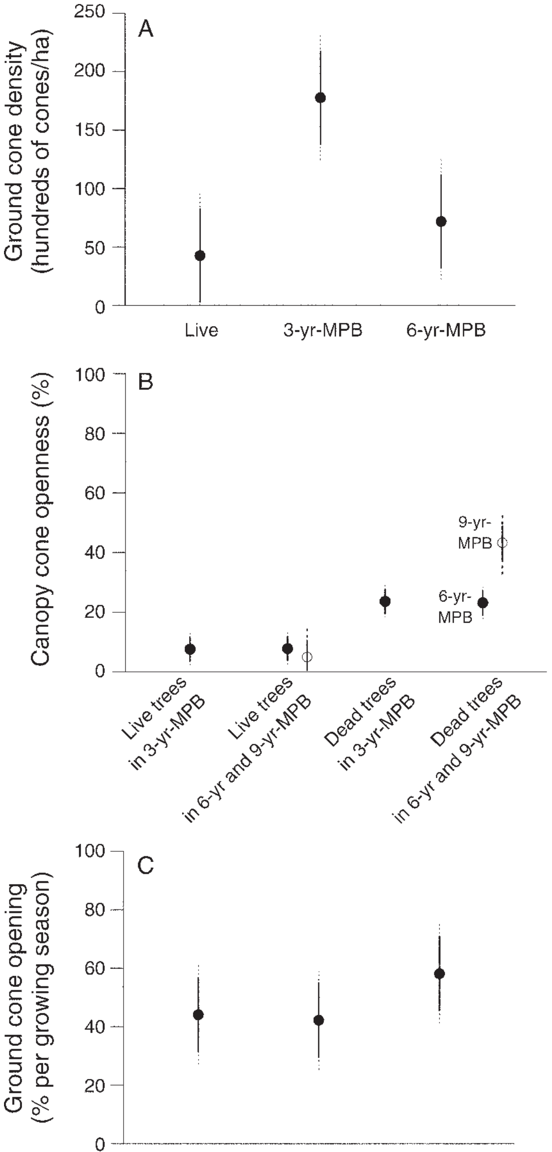

FIG. 2. Seed release from the canopy to the forest floor in MPB-attacked stands. (A) Density of seed-bearing ground cones on top of the moss layer at the end of the 2008 (late September) growing season in MPB-attacked stands (3-yr-MPB and 6-yr-MPB) and unattacked stands (live). (B) Canopy cone openness levels during the 2008 growing season (late July) on dead trees in MPB-attacked stands and on residual unattacked live trees in 3-yr-MPB, 6-yr-MPB, and 9-yr-MPB attacked stands. Open circles correspond to data gathered from an additional series of 9 years since MPB-attacked stands nearby in the SBSdk biogeoclimatic subzone. Openness values represent the percentage of open scales on cones. (C) Opening rate of ground cones on the moss layer (cone openness at the end of September – cone openness in early June). Circles are means with 95% confidence intervals (dotted) and least significant difference (LSD) bars (solid). Means are considered statistically different if the LSD bars do not overlap. If the 95% confidence interval did not overlap the zero line, it was inferred that the rate of cone opening was significantly greater than zero.

ground in the spring and 8600 more were added over the growing season (Table 3). This compares with a total of 4260 cones in the live stands and 7200 cones in the 6-yr-MPB stands (Table 3). The differences in annual seed release due to breakage between 3-yr-MPB and live stands was 13 500 cones·ha^{-1}·yr^{-1} (CI 4300 and 22 700). The 6-yr-MPB stands did not drop more canopy cones than the live stands indicating that the peak release of cones occurred in the 3-yr-MPB stands (Fig. 2A).

Partial loss of serotiny due to opening of canopy cones.—Change in canopy cone openness in the years after MPB (i.e., canopy cone openness of dead trees – canopy cone openness of live trees within the same stands) was 16% (CI 6–26) higher in the 3-yr-MPB stands and 15% (CI 5–25) higher in the 6-yr-MPB stands, suggesting a partial loss of serotiny (Fig. 2B). In the 9-yr-MPB stands, cone openness of the dead trees was 38% (CI 17–59%) higher compared with live trees in the same stands (Fig. 2B). There was no detectable difference in cone openness between the 3-yr-MPB and 6-yr-MPB stands (Fig. 2B) or between the measured cone openness of the 3-yr-MPB and 6-yr-MPB stands prior to MPB (Table 1).

Forest-floor seed bank

Opening of ground cones.—By the end of the growing season, ground cones had partially opened (Fig. 2C). Overall, there was a further 48% (CI 38–58) cone opening over the June to September time interval (Fig. 2C) over the starting openness value of 8% for the canopy cone of the live trees in these stands. This indicates a considerable number of seeds are locally dispersed once cones fall to the forest floor.

Squirrel predation of ground cones.—Squirrel predation was responsible for removal of 1400 (CI 900 to 1800) seed-bearing ground cones·ha^{-1}·yr^{-1} from the plots over the summer and autumn but no statistical differences were found among the three stand types (Table 3). Squirrel predation adjusted for differences in ground-cone density (for the three stand types) was not statistically different despite the greater ground-cone densities found in the 3-yr-MPB stands (Table 3).

Cone burial.—Considerable numbers of cones were embedded and buried (incorporated into and below the moss) in the 3-yr-MPB (209 000 cones/ha) and 6-yr-MPB stands (173 000 cones/ha) (Table 4). Density of embedded cones was greater in the 3-yr-MPB and 6-yr-MPB stands compared with the live stands (Table 4). Furthermore, the 6-yr-MPB stands had 102 000 cones/ha (CI 4000 to 200 000) more cones found below the moss compared with the live stands (Table 4). The overall openness value for these embedded and buried cones, however, was quite high (78%), translating into a small forest-floor seed bank (Fig. 3B).

Temporal estimation of seed banks

Our estimation of the canopy seed bank indicates an accumulated loss of 45% of total canopy seed after six

TABLE 3. Initial density, recruitment, and predation of forest-floor surface cones throughout the 2008 growing season; cones were recruited through branch breakage.

Stand and |stand comparisons|	*n*	Density of ground cones† (hundreds of cones/ha)			Relative predation (%)#
		Initial density‡	Recruitment§	Predation¶	
Live	5	18 (0 to 41)	24 (0 to 63)	9 (2 to 16)	22 (14 to 31)
3-yr-MPB	5	92 (69 to 115)	86 (47 to 124)	20 (12 to 27)	12 (3 to 20)
6-yr-MPB	5	38 (15 to 61)	34 (0 to 72)	12 (5 to 20)	20 (11 to 28)
|Live − 3-yr-MPB|	10	73 [34 to 114]	61 [−6 to 128]	10 [−2 to 23]	11 [−4 to 26]
|3-yr-MPB − 6-yr-MPB|	10	54 [14 to 94]	52 [−15 to 119]	7 [−5 to 20]	8 [−7 to 23]
|6-yr-MPB − Live|	10	20 [−21 to 60]	10 [−57 to 77]	3 [−9 to 16]	3 [−12 to 18]

Notes: Values are means with 95% confidence intervals (CIs) in parentheses, and comparisons are differences in means with simultaneous 95% CIs in brackets. The simultaneous CIs for the differences in means are based on the studentized range statistic (Tukey's hsd method). If zero is included in the CI then the two means were not considered statistically different. Sample size *n* is the number of stands used to calculate means and differences in means; there were 10 1-m^2 plots in each stand.

† Closed and partially opened cones.

‡ After snowmelt in early June.

§ Cones added early June to late September.

¶ Squirrel predation of cones is the cause of cone disappearance in these forests (see *Discussion*) and is likely underestimated because we could not account for the predation of fallen cones between plot survey periods.

Relative predation is = (predation/[initial density + recruitment]) × 100.

years (Fig. 3B). After six years we estimated that the stands had 13 406 400 remaining seed in their canopies (Table 5). Our model results predicted that these stands initially contained 24 395 191 seed (Table 5), equating to a 45% loss of canopy seed due to annual loss of seed from cone fall, canopy cone opening, and squirrel predation. By year 6, partial loss of serotiny due to falling of cones and cone-bearing branches from the canopy was responsible for a 10% loss from the canopy seed bank, increased canopy cone openness accounted for 13% loss, and squirrel predation of canopy cones 22% (Fig. 3B). Peak release of seeds from the canopy occurred in the 3-yr-MPB stands. The falling of canopy cones promoted the development of a modest forest-floor cone bank (Fig. 3B), translating to a small bank of buried seeds due to high openness values of embedded and buried cones. Following opening of canopy cones seeds were dispersed widely and produced an ephemeral forest-floor seed bank (Fig. 3B). The forest-floor seed bank peaked at three years in absolute numbers after MPB outbreak but after six years this seed bank represented 6% of what remained in the canopy seed bank (Fig. 3B, Table 5). The annual and short-lived seed release that is not eaten by squirrels and ground-foraging vertebrates, plus the embedded and buried cones, represents the forest-floor seed bank that could play a role in regeneration after a secondary disturbance.

Model verification

Our estimations back-calculated 24 395 191 seeds/ha as a starting value (Table 5) for the 6-yr-MPB stands when they were alive. This appears to be reasonable; based upon the number of cones per living tree from similar stands and site types (Hellum and Wang 1985, Koch 1987), we calculated that given the stem density of our stands, they would have a mean of 23 366 140 seeds/ha.

DISCUSSION

Serotinous populations of RM lodgepole pine are thought to be dependent upon fire for the release of their seeds (Lamont et al. 1991, Keeley and Zedler 1998). We, however, estimated that after mortality from MPB, 45% of the canopy seed bank is released after six years. While this number needs further verification from other research, it is the first estimate of seed release from serotinous RM lodgepole pine following MPB. This indicates that serotinous pines may be more accurately classified as both pyriscent (sensu Lamont 1991; i.e., release due to high temperatures that melt the resin bonds of closed cones) and xeriscent (i.e., release due to dry-warm conditions not generated by fires), or perhaps partially dependent upon the warming and deteriorating effects of the sun (soliscence; sensu Lamont 1991). A similar response has been described for the serotinous Aleppo pine (*P. halepensis*) that releases 59% of its seeds without fire (Nathan et al. 1999). In the past it has been suggested that cone opening in RM lodgepole pine could potentially occur without fire on xeric sites during hot summers (Cameron 1953), but this remained unsubstantiated until now. Our study demonstrates that seeds are released by a chain reaction of events that follow MPB-killed RM lodgepole pine stands. These findings may also be relevant to jack pine (*P. bansiana*), a closely related serotinous species that is spatially contiguous with lodgepole pine, spreading across the boreal forest.

Our study showed a 3.5-fold increase in the falling of cones from the canopy three years after MPB stand mortality (equivalent to an additional 17 760 cones/ha) compared with the usual falling of 4260 cones/ha in live stands. Over six years, cone fall was estimated to be 10% of the total cones in the canopy and can be viewed as another partial loss of serotiny (i.e., partial loss of the canopy seed store). Also, this is likely to be an underestimate of the loss as some of the cones might have been removed from our plots by squirrels between

TABLE 4. Density and openness of cones embedded and buried in the moss layer.

Stand and |stand comparisons|	n	Density (thousands of cones/ha)	Openness† (%)
A) Embedded cones			
Live	5	25 (−16 to 66)	85.0 (75.0 to 95.0)
3-yr-MPB	5	141 (100 to 182)	80.7 (70.7 to 90.7)
6-yr-MPB	5	55 (14 to 96)	71.7 (61.6 to 81.7)
|Live − 3-yr-MPB|	10	116 [45 to 186]	4.3 [−13.1 to 21.6]
|3-yr-MPB − 6-yr-MPB|	10	86 [15 to 156]	9.0 [−8.3 to 26.4]
|6-yr-MPB − Live|	10	30 [−41 to 100]	13.3 [−4.1 to 30.7]
B) Buried cones			
Live		16 (−41 to 73)	77.3 (69.4 to 85.2)
3-yr-MPB		68 (12 to 125)	72.0 (64.1 to 79.9)
6-yr-MPB		118 (61 to 174)	79.4 (71.5 to 87.3)
|Live − 3-yr-MPB|		52 [−46 to 150]	5.2 [−8.4 to 18.9]
|3-yr-MPB − 6-yr-MPB|		49 [−49 to 147]	7.4 [−6.3 to 21.1]
|6-yr-MPB − Live|		102 [4 to 200]	2.2 [−11.5 to 15.8]

Notes: Values are means with 95% confidence intervals (CI), and comparisons are differences in means with simultaneous 95% CIs in brackets. If zero is included in the CI then the two means were not considered statistically different. Sample size n is the number of stands used to calculate means and differences in means; there were 10 1-m^2 plots in each stand.

† Openness values represent the percentage of open scales on cones.

survey dates. We suggest that crown friction (Meng et al. 2006) is the main driver of cone fall three years since MPB, because these stands still retain their dead foliage, thereby, conveying considerable sway of the still-flexible tree trunks. This allows crowns to collide resulting in breakage of the brittle outer branches holding the cones. We note that branch breakage as a mechanism for cone fall from the canopy is only temporary, as in the six years since MPB mortality stands, the needleless trees provide less sail and the dry stems become more rigid against the force of the wind. Here the additional loss of cones was likely from other mechanisms associated with degradation of crowns of dead trees. As breakage due to snow loading usually removes whole crowns of conifers (Peltola et al. 1997), we think that this was not a factor in our study.

A second mechanism for seed release from the canopy after MPB outbreak is a partial loss of serotiny due to the opening of canopy cones after the trees die (∼15% further loss in serotiny after six years, which increased to ∼38% after nine years). Increased cone weathering or heating due to greater exposure to direct sunlight may have broken down some of the resin bonds that normally keep the cone scales closed. Air temperature at the canopy level (at these latitudes during the warmest days) can reach up to 39°C for a few minutes and can remain at 30°C for up to five hours in RM lodgepole pine stands (P. Pina and U. Silins, *unpublished data*). Under these conditions, cone surface temperature may reach 45°C (Crossley 1956*a*), a minimum temperature necessary to open RM lodgepole pine cones (Perry and Lotan 1977). It is possible that drier and hotter sites may experience greater loss of serotiny after MPB. Instead of the live stands, live residual trees within the MPB-attacked stands were used to assess partial loss of serotiny due to the opening of canopy cones. Younger trees at higher elevation (live stands) growing on nutrient-poorer sites within the same RM lodgepole pine population tend to be less serotinous than older trees at lower elevations on richer sites (Crossley 1956*b*, Koch 1987, Keeley and Zedler 1998). The slight differences in the number of canopy cones and canopy cone openness in the live stands may have also been caused by greater pre-dispersal seed predation due to a greater density of pine squirrels (Elliott 1988, Benkman and Siepielski 2004). In stands with low to moderate levels of serotiny, MPB outbreaks are expected to cue the release of cones and seed similarly to the highly serotinous stands in this study. However, because of the low amount of seed in the canopy of low serotinous stands, natural regeneration of RM lodgepole pine is expected to be even scarcer unless favorable seedbed conditions are created promptly by fires or drag scarifications.

Once cones fell from the canopy to the forest floor, there was a 48% per year increase in cone opening over the summer. Comparatively, opening rates of cones on the ground for serotinous *Banksia* species ranged from 3% to 53% per year (Witkowski et al. 1991). The mechanism for opening ground cones likely is the result of soil-surface heating; on calm and sunny days the conversion of shortwave energy to sensible heat at the ground surface could push cone temperature above 45°C in unshaded microsites as a result of the open canopy after MPB (Oke 1987). With complete loss of foliage in the six years since MPB mortality, a greater degree of solar radiation should be transmitted to the forest floor but this is counterbalanced by an increase in understory vegetation. Seed released from ground cones is concentrated around the cones and would therefore be more prone to predation by ground-foraging vertebrates than the more widely dispersed seed released from the canopy.

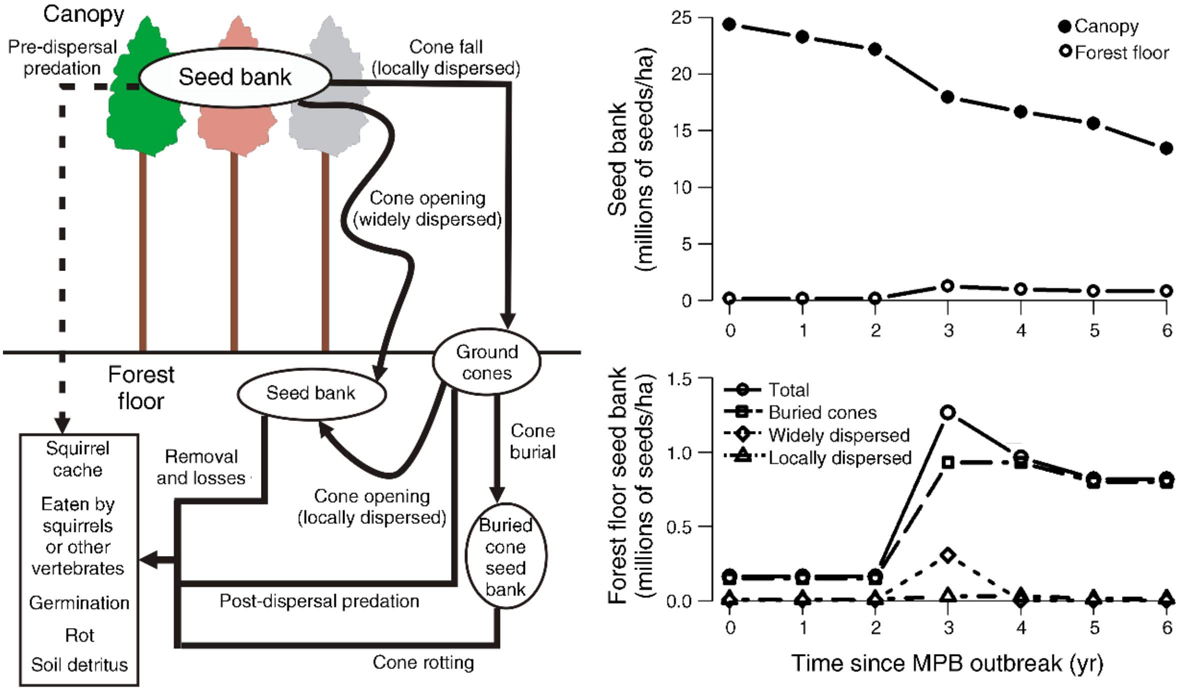

FIG. 3. (A) Conceptual model of seed-release pathways of Rocky Mountain lodgepole pine in stands after a mountain pine beetle outbreak. The pathway marked as a dashed line was estimated with data from the literature. Canopy cone fall, cone opening, and squirrel predation cumulatively resulted in release of 10%, 13%, and 22% of the initial canopy seed bank, respectively, six years after MPB outbreak. Diagrammed trees represent the green, red, and gray phases associated with the discoloration of needles that occurs after MPB outbreak. (B) Fate of seed banks was estimated temporally (see Table 5 and Appendix B for equations and details).

We estimated that over the six years, pine squirrels removed a modest number of cones (total of 29% from MPB-attacked forests; 22% from the canopy and 7% forest floor). In other studies, squirrel predation was estimated to consume 46% of total canopy cones$\cdot$ha$^{-1}\cdot$yr^{-1} (e.g., Steele et al. 2005). However, it has been argued that these rates of predation by squirrels could be overestimations (Despain 2001) because live healthy stands of RM lodgepole pine incrementally increase their canopy seed bank. Nevertheless, we acknowledge that pine squirrel predation represents a continuous reduction in the number of seed-bearing cones (even with our modest predation rates). That squirrels are a keystone selective agent against serotiny (Benkman and Siepielski 2004) was not supported by (1) our field observations of high squirrel predation activity in our highly serotinous stands, or (2) by the squirrel density estimates in highly serotinous stands presented in Wheatley et al. (2002).

It can be expected that the widely dispersed seeds (via canopy cone opening) and the locally dispersed seeds (via ground-cone opening) on the forest floor are quickly eaten by ground-foraging vertebrates (89.5% per year; Vander Wall 2008). Predation and the lack of an appropriate seedbed are likely the main reasons for the very low numbers of RM lodgepole pine germinants at our sites (casual observations) and in other RM lodgepole pines stands even 10 years after a MPB outbreak (Astrup et al. 2008). We also suggest that the sustained seed rain (mostly via cone opening) occurring over at

TABLE 5. Modeled seed bank estimates used in Fig. 3B.

Years since MPB attack	Seed banks (seed/ha)				
	Canopy	Forest floor (FF)	Locally dispersed to FF	Widely dispersed to FF	Embedded and buried cones
0	24 395 191	139 014	10 514	6404	122 097
1	23 285 827	170 143	10 514	6113	153 517
2	22 179 229	189 962	10 514	5822	173 626
3	17 981 815	994 709	29 793	306 815	658 102
4	16 664 784	1 002 334	29 793	4375	968 167
5	15 628 544	950 847	14 261	4102	932 483
6	13 406 400	927 426	14 261	3519	909 646

least nine years after MPB outbreak may bolster population growth of ground-foraging vertebrates.

A modest-sized forest-floor seed bank (6% of what is left in the canopy after six years) is likely to develop in these MPB-attacked stands. First, the burial of partially open and closed cones by growth of moss or coverage of litter, builds a forest-floor seed bank. Seeds in these embedded and buried cones retained moderate viability based on our standard germination trials (F. P. Teste, V. J. Lieffers, and S. M. Landhäusser, *unpublished manuscript*). Four years after MPB outbreak the forest-floor seed bank reached its peak at an estimated 1 002 234 seeds/ha, considerably less than ephemeral soil seed bank densities (2 330 000–14 350 000 seeds/ha) found in other ecosystems dominated by serotinous plants (Enright et al. 2007). Contrary to our findings, these serotinous plants in fire-prone shrublands have no capacity for soil storage once released because they perish quickly (Enright et al. 2007). The annual cone fall from the canopy was ~10% of the embedded and buried cones, suggesting cones last a long time before they decompose. Nevertheless, this estimate should be considered preliminary and needs to be confirmed with a study of long-term survival of seeds in embedded and buried cones. The second and smaller transitory seed bank comes from dispersed seeds, some of which might fall at the end of the growing season and will survive the winter. It is possible that our estimates (Fig. 3B) may be exaggerated based upon the low numbers of pine germinants that we recorded from controlled germination tests of these forest-floor substrates at the end of the 2008 growing season (Teste et al., *unpublished manuscript*).

The forest-floor seed bank has ecological relevance if secondary disturbances reexposed these embedded and buried cones. If a ground fire or salvage logging occurs 3+ years since MPB, then some regeneration can be expected given that the embedded and buried-cone seed bank is exposed and favorable seedbeds are created (Landhäusser 2009). Some non-serotinous pine species (*P. nigra* J. F. Arnold and *P. pinea* L.) appear to have evolved in response to low intensity ground fires (Tapias et al. 2001) unless non-serotiny is the ancestral condition in pines (Schwilk and Ackerly 2001). During evolutionary times, ground fires may have occurred regularly after MPB outbreaks (Parker et al. 2006), and these events would favor the release of seeds (via the mechanisms outlined previously) and promote regeneration. It is clear that many events, including preparation of a suitable seedbed, need to be synchronized to favor successful regeneration.

Important conditions leading to the evolutionary success of serotiny is that seed release occurs quickly, extensively, and be cued with the onset of favorable seedbed conditions for seedling establishment (Lamont et al. 1991). Although it appears that both xeriscence (seed release due to dry warm winds in Aleppo pine; Nathan et al. 1999) and seed release indirectly caused by MPB (in RM lodgepole pine) are alternative cues that favor seed release in the absence of fire, these disturbances do not create favorable seedbed conditions for regeneration, suggesting that RM lodgepole pine is poorly adapted to MPB outbreaks.

We estimated that after six years, the number of seeds released reached 45% of the original canopy seed bank in stands after MPB outbreak. We anticipate that the proposed release of seed will be even greater in younger or denser stands as most of the cones are held on the outer edge of the crown. We also expect very little seed to remain in the canopy in stands with low serotiny (e.g., in Yellowstone NP). The seeds lost from the canopy were related to cone fall via breakage, increased cone opening, and squirrel predation. There is a considerable amount of seed released three years since MPB, but the canopy continues to release seed nine years since MPB stands via cone opening. Canopy seed retained high viability in dead trees (9-yr-MPB) based on standard germination trials (F. P. Teste, V. J. Lieffers, and S. M. Landhäusser, *unpublished manuscript*); hence released seed of RM lodgepole pine are available for germination but most are rapidly eaten by rodents (likely promoting their population growth) or fall on unsuitable microsites and perish. Some of the fallen cones remain closed and are gradually covered by moss; thus a small forest-floor seed bank develops. Consequently, if normal levels of regeneration are to occur, either fire or anthropogenic disturbances must occur shortly after tree mortality.

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APPENDIX A

ANOVA tables and unstandardized effect sizes (*Ecological Archives* A021-008-A1).

APPENDIX B

Equations and development of the temporal seed bank model (*Ecological Archives* A021-008-A2).