

Fire and mice: Seed predation moderates fire's influence on conifer recruitment

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Abstract. In fire-adapted ecosystems, fire is presumed to be the dominant ecological force, and little is known about how consumer interactions influence forest regeneration. Here, we investigated seed predation by deer mice (*Peromyscus maniculatus*) and its effects on recruitment of ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) seedlings in unburned and recently burned fire-adapted montane forests in west-central Montana, USA. Deer mice were almost twice as abundant in burned than unburned stands. Deer mouse removal of seeds from petri dishes was two times higher in burned than in unburned stands, and seed removal levels were 8% higher for ponderosa pine than for the smaller Douglas-fir seeds. In seed-addition experiments, emergence of seedlings in deer mouse-exclusion cages was almost six times higher in burned compared to unburned forest. In both burned and unburned forest, emergence was lower for ponderosa pine than for Douglas-fir. Seedling survival to establishment did not differ between conifer species but was considerably higher in burned than in unburned forest. However, effects of seed predation on recruitment prevailed over fire effects: in cages allowing access by deer mice, emergence and establishment were extremely rare for both conifer species in both burned and unburned forest. This research suggests that consumer interactions can substantially influence recruitment even in fire-adapted forest ecosystems.

Key words: deer mouse; disturbance; Douglas-fir; *Peromyscus maniculatus*; *Pinus ponderosa*; ponderosa pine; *Pseudotsuga menziesii*; seedling establishment; seed predation; wildfire.

INTRODUCTION

Wildfires are among the most important factors determining distribution, structure, and dynamics of plant communities worldwide (Whelan 1995, Bond et al. 2005). In western North America, the influence of recurring wildfires on tree communities is a focus of intense research (e.g., Kulakowski et al. 2004, MacKenzie et al. 2004, Brown and Wu 2005, Franklin et al. 2006, Keyser et al. 2008). Nonetheless, the majority of studies that investigate the effects of this disturbance on plant communities implicitly assume “bottom-up” control (reviewed in Agee 1993, Whelan 1995, Brown and Smith 2000, Rood et al. 2007, Buhk et al. 2007). In other words, changes in plant communities following wildfire are typically explained by direct effects of the physical environment on plant performance and competition, ignoring how vertebrates may mediate bottom-up effects.

Seed predation is recognized as one of the most important factors influencing plant recruitment (Louda

1982, Maron and Simms 1997, Silman et al. 2003), and in many parts of the world, rodents are the primary granivores (Brown et al. 1979, Hulme and Kollmann 2002). In North America, rodent predation of large vs. small seeds has been demonstrated to control the transition between desert and grassland in the southern United States (Brown and Heske 1990); in northeastern hardwood forests, similar processes influence the rate and species composition of tree invasion in old fields (Ostfeld et al. 1997). However, in coniferous forests of western North America, wildfire is believed to drive vegetation patterns (Agee 1993), and researchers have primarily studied rodents in the context of their response to disturbances, including wildfire (Stout et al. 1971, Roppe and Hein 1978, Pearson 1999, Clayton 2003, Zwolak and Foresman 2007, 2008). Deer mice (*Peromyscus maniculatus*) are known to be voracious seed predators in these forests, particularly in disturbed stands where their abundance is often elevated (Gashwiler 1967, Sullivan 1979, Sullivan and Sullivan 1982, 2004, Tallmon et al. 2003), yet their impact on natural forest regeneration remains largely unknown. Thus, in western forests, wildfires not only provide the primary form of disturbance that initiates secondary succession, they also directly affect granivore populations in ways that could greatly influence consumer pressures. Moreover, because the biological signifi-

Manuscript received 26 February 2009; revised 15 July 2009; accepted 24 July 2009. Corresponding Editor: B. J. Danielson.

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cance of seed predation depends on the extent to which plants are seed limited, and the degree of seed limitation is influenced by disturbance (Andersen 1989, Crawley 1992, Hulme 1998, Clark et al. 2007), fire may affect tree recruitment in western forests in a variety of ways.

In this study, we experimentally examined the magnitude of seed predation by deer mice and its impact on conifer recruitment in wildfire-burned and unburned forest stands in western Montana. We focused on two tree species that dominate many forests of western North America: ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*). In both burned and unburned forest, we (1) quantified deer mouse abundance and seed removal, (2) determined whether removal rates were higher for larger ponderosa pine seeds than for smaller Douglas-fir seeds, and (3) investigated the effects of seed removal on seedling recruitment. Together, these analyses assess and compare the effects of fire and mice on the composition and rate of conifer recruitment.

MATERIALS AND METHODS

Study site

We conducted this research within montane forest on the Lolo National Forest in west-central Montana, USA, ~50 km west of Missoula. The dominant species was Douglas-fir, followed by ponderosa pine, lodgepole pine (*Pinus contorta*), and western larch (*Larix occidentalis*). In the summer of 2005, the I-90 wildfire burned 4550 ha of the forest. In the spring of 2006, we selected three pairs of study sites, each pair consisting of one stand that was burned with a stand-replacement fire (100% tree mortality and removal of litter layer) and one located in an unburned forest stand of similar elevation (1600–1900 m) and aspect (south- to west-facing). Distances among all stands ranged from 0.9 to 5.5 km.

Deer mouse trapping

We conducted trapping in 2006 and 2007 from June to August in monthly sessions, each consisting of four consecutive nights of trapping (with minor adjustments of this schedule due to adverse weather). Each sampling grid was located at least 50 m from the edge of burn or the forest edge and consisted of 169 trapping stations, spaced 10 m apart and arranged in a 13 by 13 square (grid area = 1.44 ha). We placed one folding Sherman live trap (H. B. Sherman Traps, Tallahassee, Florida, USA), baited with rolled oats and supplied with polypropylene batting, at each trapping station. To target deer mice, which are nocturnal, we set traps in the evening (~18:00) and closed them upon checking in the morning each day before 10:00. We identified captured rodents to species, weighed them, determined their sex, individually marked them using ear tags, and released them at the trap station.

Seed removal experiments

In 2006 and 2007, we used seed removal experiments to estimate relative levels of seed predation. We conducted the experiments in September, after trapping had ceased, to avoid confounding effects due to the presence of baited traps. In 2007, we delayed experiments at the last pair of sites due to intense rainfall, and eventually conducted them under adverse weather conditions (very low temperature and overnight snowfall) and therefore did not include the results in the analysis of seed removal. Within each trapping grid, we put out 40 seed offerings, each consisting of a petri dish (150 × 33 mm) filled with a mixture of 125 mL of sand and 20 locally collected seeds. Dishes were spaced at 20-m intervals at locations corresponding to every other trap station. At each grid, one-half of the dishes contained ponderosa pine seeds, and one-half contained Douglas-fir seeds, with dishes arranged in an alternating, checkerboard pattern by seed species. We presented seed offerings for two days and two nights. This duration was based on a pilot study conducted in 2006 and on our previous experience (Pearson and Callaway 2008). We examined seed offerings shortly after sunrise (~06:30) and before sunset (~19:30) each day. This way, we could differentiate removal by nocturnal deer mice and diurnal granivores such as chipmunks (*Tamias* spp.) and red squirrels (*Tamiasciurus hudsonicus*). If a seed offering had signs of foraging (disturbed sand surface, broken seed shells, feces), we counted the remaining intact seeds and filled the dish with fresh sand and new seeds. When feces were found, we recorded their presence and identified them as “deer mouse” or “other” rodents. Of the latter species, red-backed vole (*Myodes gapperi*) feces were distinct due to the higher proportion of green plants in their diet, while feces of granivores such as chipmunks or red squirrels were larger than those of deer mice.

Seedling recruitment trials

To address the effects of deer mouse seed predation vs. fire on seedling recruitment (gauged by seedling emergence and establishment) of ponderosa pine and Douglas-fir, we sowed seeds in 20 × 20 × 20 cm wire mesh cages (mesh size 0.5 cm). One-half of the cages had 3 × 6 cm holes cut in each side to allow access of small rodents (primarily deer mice, as captures of similarly sized rodents were uncommon; Zwolak 2008), while the other half remained enclosed to prevent access. We spaced cages 0.5–1.5 m apart in sets of two (one enclosed and one allowing access), and added 10 locally collected seeds to each cage, with seed species randomly assigned to each pair. Cages were buried 10 cm into the ground. To minimize presence of an ambient seedbank, we removed topsoil inside the cages and replaced it with mineral soil, dug out from a depth of 0.25–0.5 m. In unburned forest, the soil was then covered with litter of the same thickness as that found adjacent to the cages. In burned forest, there was no litter present.

TABLE 1. Monthly estimates (\pm SE) of deer mouse (*Peromyscus maniculatus*) abundance in burned (F1–F3) and unburned (C1–C3) sites in Lolo National Forest, Montana, USA.

Site	2006			2007		
	June	July	August	June	July	August
F1	18.4 \pm 2.0	10.3 \pm 1.9	13.5 \pm 2.0	55.5 \pm 13.9	40.7 \pm 3.6	29.7 \pm 2.4
F2	15.4 \pm 2.0	23.5 \pm 2.8	44.9 \pm 4.5	49.8 \pm 13.5	70.6 \pm 5.0	107.4 \pm 6.1
F3	20.0 \pm 2.7	26.9 \pm 3.4	30.3 \pm 3.2	45.4 \pm 12.1	44.9 \pm 3.7	44.0 \pm 4.3
C1	10.6 \pm 1.5	26.8 \pm 3.1	31.3 \pm 3.3	50.6 \pm 15.3	39.3 \pm 3.5	33.3 \pm 2.7
C2	3.4 \pm 0.8	2.2 \pm 0.6	11.4 \pm 1.4	8.3 \pm 3.3	9.8 \pm 1.6	16.1 \pm 1.7
C3	9.6 \pm 1.5	14.9 \pm 2.2	18.5 \pm 2.4	57.7 \pm 18.0	36.8 \pm 3.4	14.0 \pm 2.2

Note: The estimates were derived from program MARK, using Huggins-type robust design models; associated standard errors were unconditional.

We set out eight pairs of cages at 40-m intervals along two transects parallel to and located \sim 10 m from the opposites edges of each trapping grid. In 2006, we added seeds to the surface during September when natural seed rain occurs. We quantified seedlings the following June when emergence was complete (i.e., no new seedlings were found subsequently), and again in September to determine survival. We defined establishment as the proportion of seeds that emerged and survived until September. We then repeated the experiment for another year by pulling seedlings, replacing the soil, and adding new seeds.

Statistical analysis

We estimated abundance of deer mice per site per month using program MARK (White and Burnham 1999). We used Huggins closed robust design (Huggins 1989, 1991) because of its good performance given sparse data (Conn et al. 2006). We determined the most parsimonious models with Akaike's information criterion corrected for small sample size (AIC_c). Estimation of parameters followed Zwolak and Foresman (2008). Briefly, we modeled apparent survival, capture, and recapture probabilities as constant, differing between burned and unburned sites, changing among months, or changing both between burned and unburned areas and in time. We varied the parameters independently, thus there were 64 candidate models ($4 \times 4 \times 4$) for each year (Zwolak 2008; R. Zwolak, D. E. Pearson, Y. K. Ortega, and E. E. Crone, *unpublished manuscript*). The effective sampling area of trapping grids (estimated with mean maximum distance moved; White et al. 1982) did not differ between burned and unburned forest. We model-averaged abundance estimates according to Akaike weights (w_i ; Burnham and Anderson 2002). To derive overall deer mouse abundance in burned and unburned forest for each month, we averaged estimates from respective trapping sites. For yearly estimates, we averaged abundance across months, with standard error reflecting sample variance derived using the Delta method (Seber 1982:138, Zwolak and Foresman 2008).

We analyzed seed removal, seedling emergence, and seedling survival with logistic regression models (function "lmer") in R (R Development Core Team 2006). Fixed effects included fire (burned vs. unburned), seed

species, rodent access (open vs. closed cages, seedling emergence models only), and day (first or second, seed removal models only). Random effects included study site and, to account for the correlation among subsamples, either cage pairing (in seedling emergence and survival models) or trap station (in seed removal trials). We analyzed daytime and nighttime seed removal separately. In each case, we began with a model containing all the above-mentioned variables and their interactions, and determined the structure of the final model through stepwise regression with backward elimination of nonsignificant ($P > 0.05$) variables.

RESULTS

Deer mouse abundance

Estimated abundance of deer mice was 1.6 times higher in burned compared to unburned forest in 2006 (22.6 ± 0.9 vs. 14.3 ± 0.5 mice/grid, mean \pm SE), and 1.8 times higher in burned compared to unburned forest in 2007 (54.2 ± 2.8 vs. 29.5 ± 2.7 mice/grid; Table 1). However, there was considerable variation in deer mouse abundance among grids and sampling months, particularly in unburned forest (Table 1).

Seed removal

Seed removal at night was higher in burned vs. unburned forest, particularly in 2006 (fire and fire \times year effects; Table 2a, Fig. 1a). In addition, more ponderosa pine than Douglas-fir seeds were removed at night (species effect; Table 2a, Fig. 1a).

During the day, overall differences in removal between burned and unburned forest were not significant. However, in contrast to nighttime removal, daytime removal was less intense in burned vs. unburned forest in 2007 (fire \times year effect; Table 2b, Fig. 1b). As in nighttime trials, removal was greater for ponderosa pine seeds compared to Douglas-fir seeds, though this was only significant in 2007 (species \times year effect; Table 2b, Fig. 1b).

We found deer mouse feces in 66% and 30% of trays with missing seeds in burned and unburned stands, respectively. Feces of other species (red squirrels and chipmunks) were found in only a few trays. Although not quantified, most seed appeared to be eaten at the

TABLE 2. Results of logistic regression for (a) nighttime and (b) daytime seed removal trials.

Variable†	Regression coefficient (±SE)	z	P
a) Overnight seed removal			
Intercept	-4.44 ± 0.192	-4.80	<0.0001
Fire	5.59 ± 1.28	4.38	<0.0001
Day	0.73 ± 0.05	13.45	<0.0001
Species	1.16 ± 0.32	3.70	0.0002
Year2007	2.60 ± 0.08	34.92	<0.0001
Fire × year2007	-0.82 ± 0.15	5.56	<0.0001
b) Seed removal during daytime			
Intercept	-6.85 ± 1.50	-4.55	<0.0001
Fire	-2.92 ± 2.11	-1.38	0.167
Day	0.87 ± 0.06	14.01	<0.0001
Species	0.91 ± 0.54	1.70	0.090
Year2007	4.02 ± 0.13	30.23	<0.0001
Fire × year2007	-2.84 ± 0.15	-18.70	<0.0001
Species × year2007	0.62 ± 0.15	4.17	<0.0001

† Fire indicates burned vs. unburned forest; day denotes the change in seed removal rates during the second day of the trials; species is the removal of ponderosa pine (*Pinus ponderosa*), relative to Douglas-fir (*Pseudotsuga menziesii*); and year2007 is the seed removal in 2007 relative to that in 2006. See *Methods: Seed removal experiments* and *Statistical analysis* for further explanation.

trays, as evidenced by broken seed shells left in the vicinity of a substantial proportion of seed trays.

Seedling recruitment

Seedling emergence in cages without rodent access was considerably higher in burned vs. unburned stands (fire effect; Table 3), but this effect disappeared in cages with rodent access (rodent access × fire effect; Table 3). In cages without rodent access, 39% of seedlings emerged in burned forest vs. 7% in unburned forest, while in cages with access, 0% of seedlings emerged in burned forest vs. 0.9% in unburned forest (Fig. 2a). Overall, seedling emergence was lower for ponderosa pine compared to Douglas-fir (species effect; Table 3). The difference between conifer species was not affected by fire or by mice (fire × species and rodent access × species interactions were nonsignificant and eliminated from the final model).

Seedling survival also differed strongly between burned and unburned forest ($z = 2.72, P = 0.006$; Fig. 2b). In 2007, 75% (55 out of 73) of seedlings in burned forest survived until September, whereas survival observed in unburned forest was only 30% (eight out of 27 seedlings survived). In 2008, the overall pattern of higher survival in burned forest remained unchanged, but survival in both burned (30%, 23 out of 76 seedlings) and unburned (0 out of 10 seedlings) forest was lower than in 2007 ($z = -5.48, P < 0.0001$). Besides fire and year, no other factors were significant predictors of seedling survival.

The ultimate impact of mice on conifer recruitment can be gauged by multiplying the probabilities of

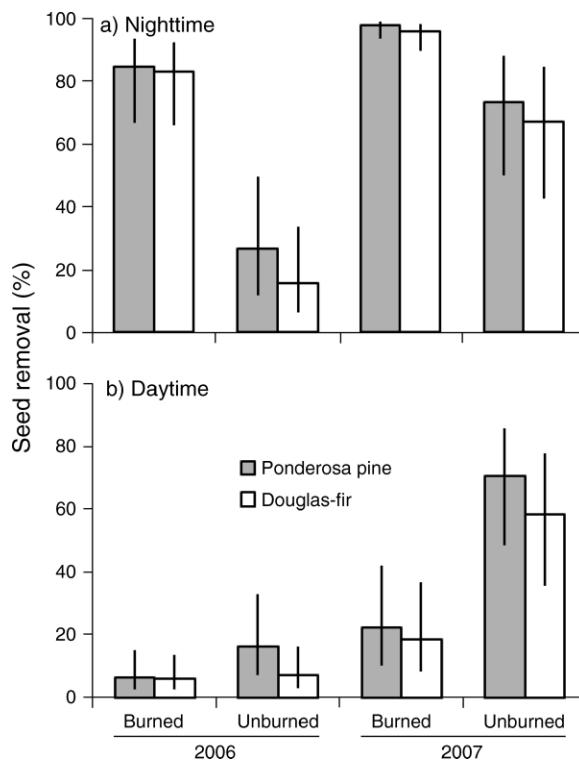


FIG. 1. Seed removal in burned and unburned forest in Lolo National Forest, Montana, USA. Error bars denote standard errors, estimated by setting each group, in turn, to be the reference (intercept) group in function lmer in R. (a) Nighttime seed removal: standard errors for seed removal of ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) overlap, suggesting that statistically significant differences among species (Table 2a) reflect consistent species differences across treatments. (b) Daytime seed removal.

emergence and survival. In 2007, the proportion of seeds sown that reached the establishment stage when mice were excluded was ~26% for ponderosa pine and 34% for Douglas-fir in burned stands, compared to 1% and 4%, respectively, in unburned stands; mouse access

TABLE 3. Results of logistic regression for seedling emergence trials.

Variable†	Regression coefficient (±SE)	z	P
Intercept	-2.28 ± 0.37	-6.08	<0.0001
Fire	2.01 ± 0.45	4.47	<0.0001
Rodent access	-2.23 ± 0.74	-3.01	0.0026
Species	-0.87 ± 0.44	-2.00	0.046
Year2007	-0.82 ± 0.42	-1.94	0.053
Fire × year2007	2.27 ± 0.53	4.28	<0.0001
Fire × rodent access	-3.82 ± 1.22	-3.12	0.0018
Species × year2007	-3.59 ± 0.61	-5.87	<0.0001

† Fire indicates burned vs. unburned forest; rodent access denotes emergence in open cages; species is the emergence of ponderosa pine (*Pinus ponderosa*) seedlings relative to those of Douglas-fir (*Pseudotsuga menziesii*); and year2007 is the emergence during the second year of the cage germination trials. See *Methods: Seedling recruitment trials* and *Statistical analysis* for further explanation.

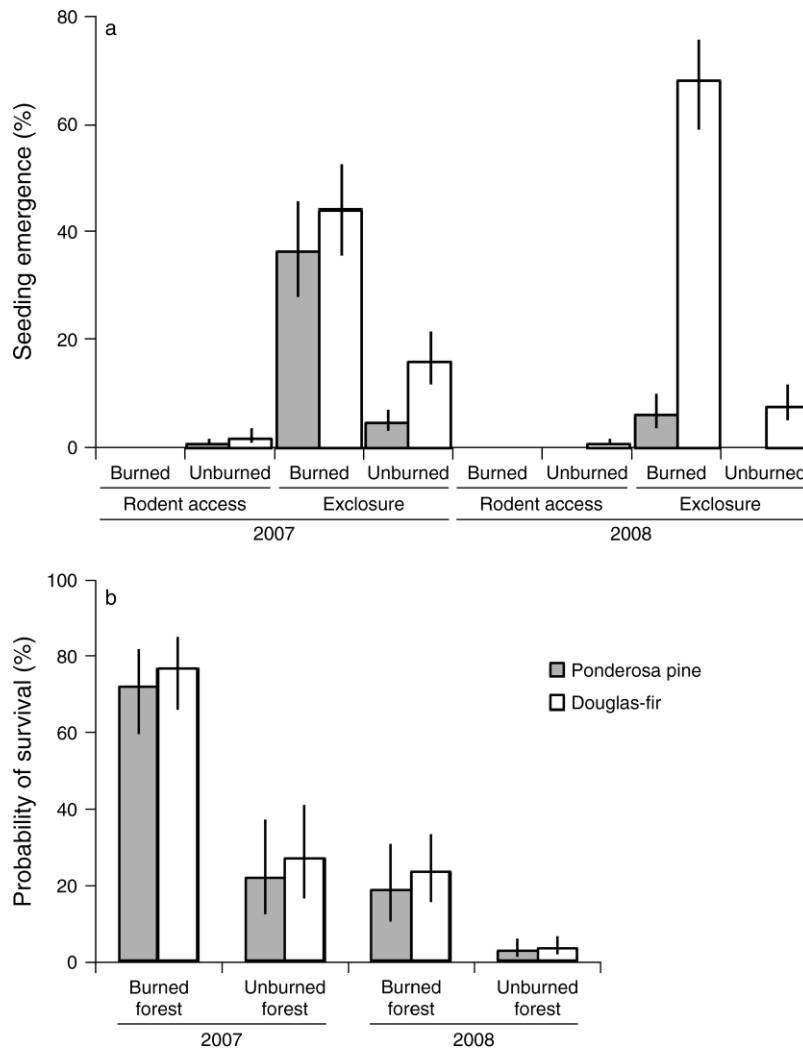


FIG. 2. Demography of ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) seedlings in burned and unburned forest. Error bars denote standard errors, estimated by setting each group, in turn, to be the reference (intercept) group in function lmer in R. (a) Seedling emergence. "Rodent access" indicates emergence in germination cages with openings and "exclosure" denotes emergence in closed germination cages. Seedlings were not found in rodent access cages in burned forest. (b) Seedling survival.

reduced these values to 0% in burned stands and <1% in unburned forest. In 2008, establishment without mice was ~1% for ponderosa pine and 16% for Douglas-fir in burned stands, compared to <1% for both species in unburned stands; mouse access reduced these proportions to 0.

DISCUSSION

Our results demonstrate that wildfire creates highly favorable conditions for seedling recruitment, but intense seed predation by elevated deer mouse populations greatly reduces this effect. Deer mice were probably responsible for most seed loss in burned forest because deer mice accounted for 86% of individuals captured on the study areas (Zwolak 2008; R. Zwolak, D. E. Pearson, Y. K. Ortega, and E. E. Crone,

unpublished manuscript). In addition, seed removal in burned forest was intense only at night, when chipmunks, the only other rodents that were regularly captured in burned forest (Zwolak 2008; R. Zwolak, D. E. Pearson, Y. K. Ortega, and E. E. Crone, *unpublished manuscript*), are inactive. Moreover, in one of our burned sites, chipmunks were absent in 2006 and rare in 2007 (Zwolak 2008; R. Zwolak, D. E. Pearson, Y. K. Ortega, and E. E. Crone, *unpublished manuscript*), but seed predation at that site was as intense as at other burned sites, where more chipmunks were captured. Finally, signs of foraging and feces left on most depredated seed trays indicated seed removal by mice. When deer mice were excluded from seed cages, seedling emergence and survival were high in burned forest, yet very low in unburned stands. However, when mice could

access seeds, emergence virtually ceased, negating the differences between burned and unburned environments. The striking disparity between seedling establishment in open and closed cages in burned stands suggests strong seed limitation (Clark et al. 2007) for these species as they reestablish following wildfire, and indicates that seed predation by deer mice might mediate the process of postfire forest succession. In seed predation trials, deer mice demonstrated slight but significant preference for larger ponderosa pine over smaller Douglas-fir seeds. However, seed removal in burned forest was so intense that no seedlings were found in open germination cages, regardless of sown species. Therefore, mice are more likely to slow the rate of reestablishment than alter seedling composition within this system.

Mice are known to increase in abundance after forest disturbances, including wildfire (Pearson 1999, Fisher and Wilkinson 2005, Zwolak 2009) and for their ability to control plant populations through intense seed consumption (Kauffman and Maron 2006, Pearson and Callaway 2008; Bricker et al. 2010). However, our study is the first to demonstrate that mice reduce seedling recruitment in burned forest, thereby counteracting otherwise positive effects of fire on conifer regeneration. This ecological effect may be unique to the postfire succession in western North America. For example, in *Pinus coulteri* woodlands in coastal California, where the small-mammal community is dominated by kangaroo rats (*Dipodomys agilis*), rodents substantially contributed to postfire seed dispersal and seedling establishment (Borchert et al. 2003). In *Pinus halepensis* forests in Spain, seed predation in burned areas was lower than in unburned areas, and exclusion of rodents (probably *Apodemus* spp.) resulted in only moderate increases in seedling density (Broncano et al. 2008). In another study conducted in Spain, only the simultaneous exclusion of all seed predator guilds (ants, rodents, and birds) increased germination of *Pinus nigra* after a recent fire (Ordóñez and Retana 2004).

It is possible that some of the seeds removed from the seed trays and germination cages were cached rather than eaten (Vander Wall et al. 2005, Moore and Swihart 2008). Even though deer mice are thought to act as seed predators rather than seed dispersers (Sullivan 1978), some individuals do cache seeds (Vander Wall 1992, Vander Wall et al. 2001). Therefore, our estimates of seed removal may be considered the upper boundary of seed mortality caused by deer mice. However, naturally occurring seedlings in burned forest were rare and seedling clumps, a telltale sign of germination from rodent caches (Vander Wall 1992, Borchert et al. 2003), were never found. Deer mice appeared to serve mostly as seed predators in burned forest.

Seed predation often varies both in time and space (Whelan et al. 1991). Such changes in consumer pressure may provide opportunities for successful plant recruitment. In montane and boreal forests, most postfire

conifer recruitment occurs before the depletion of aerial seed banks, i.e., within the first 2–3 years after fire (Turner et al. 1997, Charron and Greene 2002), coinciding with the elevated abundance of deer mice in burned areas (Zwolak 2009). However, populations of deer mice fluctuate from year to year (e.g., Zwolak and Foresman 2008); thus some years may be better for conifer recruitment than others. Spatially, mice quickly colonize even large wildfires (R. Zwolak, *personal observation*). Their high abundance in burned forest reflects elevated fecundity, possibly due to improved foraging efficiency in burned, structurally simplified, habitat (Zwolak 2008, Zwolak and Foresman 2008; R. Zwolak, D. E. Pearson, Y. K. Ortega, and E. E. Crone, *unpublished manuscript*) However, some seeds may escape detection, for example when buried in cracks or crevices (our experiments could not capture this phenomenon), and successfully germinate. Still, severe fires sometimes lead to the development of persistent grass and shrub-dominated communities (Savage and Mast 2005, Lentile et al. 2006, Tappeiner et al. 2007, Keyser et al. 2008). The slow rate or changed trajectory of postfire regeneration is usually attributed to the lack of near seed sources (Keyser et al. 2008). This study suggests that intense seed predation may also play a role.

Our results serve as a prominent example of how vertebrates mediate the effects of the physical environment on plant communities. Deer mice alter seedling recruitment and may act as drivers of postfire succession in western forests. Because fires elevate deer mouse densities, this situation represents an unforeseen, indirect effect of forest fires, and a disturbance-mediated “top-down” effect of rodents on plant communities.

ACKNOWLEDGMENTS

We thank Richard L. Hutto, L. Scott Mills, and two anonymous reviewers for comments on the manuscript. Leigh Ann Reynolds and many other University of Montana students provided invaluable help with data collection. Montana Conservation Seedling Nursery supplied seeds that were used in seedling germination trials. This project was funded by grants from the USFS Rocky Mountain Research Station, Bitterroot Ecosystem Management Research Project, and McIntire-Stennis Cooperative Research Program, and work was conducted while E. Crone was supported by NSF DEB 05-15756.

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