

Conifer seed predation in harvested and burned dry Douglas-fir forests in southern British Columbia

David J. Huggard and André Arsenault

Abstract: Consumption of seeds of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws.) was measured in dry Douglas-fir forest at the Opax Mountain Silvicultural Systems site and a nearby burned area as one component of understanding limited natural regeneration in these sites. Seeds were placed in plots surrounded by a physical barrier to invertebrates, enclosed in mesh impermeable to small mammals, covered by litter, or unprotected in clear-cut, partially harvested, uncut, and burned areas and monitored for three several-day sessions in 2 years. Daily survival rates of unprotected seeds of both species were equally low: 0.63 in uncut forest, 0.45 in partially harvested and clear-cut sites, and 0.03 in the burned area. Experimental reductions of coarse woody debris reduced seed predation moderately in patch cuts but not in uncut forest. Litter cover or selective enclosure of ground-dwelling invertebrates reduced seed losses only slightly, whereas small mammal enclosures eliminated most seed loss. Deer mice (*Peromyscus maniculatus* Wagner) are likely the most important seed predators. High rates of seed predation in dry Douglas-fir forests likely limit natural regeneration in harvested and burned stands.

Résumé : La consommation de graines de sapin douglas (*Pseudotsuga menziesii* (Mirb.) Franco) et de pin ponderosa (*Pinus ponderosa* Dougl. ex P. & C. Laws.) a été mesurée dans une forêt sèche de douglas de Menzies sur le site expérimental du mont Opax dédié à l'étude des systèmes sylvicoles et dans un brûlis situé à proximité, dans le cadre d'une étude des facteurs qui limitent la régénération naturelle dans ces sites. Les graines ont été placées dans des placettes entourées de barrières physiques contre les invertébrés, enveloppées dans un grillage imperméable aux petits mammifères, recouvertes ou non de litière, dans des coupes à blanc, des coupes partielles, des sites non coupés et des brûlis, et suivies durant trois sessions de plusieurs jours pendant deux ans. Les taux quotidiens de survie des graines non protégées des deux espèces étaient semblables et assez faibles : 0,63 en forêt non coupée, 0,45 dans les coupes partielles et les coupes à blanc et 0,03 dans les brûlis. La réduction expérimentale des débris ligneux grossiers a entraîné une diminution modérée la prédation de graines dans les coupes, mais pas dans la forêt non coupée. Le couvert de litière de même que les exclos à invertébrés hypogés ont à peine réduit les pertes de graines tandis que les exclos à petits mammifères les ont pratiquement éliminées. La souris sylvestre (*Peromyscus maniculatus* Wagner) est probablement le plus important prédateur de graines. Le taux élevé de prédation des graines dans les forêts sèches de douglas de Menzies limite de toute évidence la régénération naturelle dans les peuplements coupés et les brûlis.

[Traduit par la Rédaction]

Introduction

Seed predation influences vegetation patterns and succession at scales ranging from small plots and local edge effects to larger landscape scales in natural and managed systems (Janzen 1971; Whelan et al. 1991; Hulme 1993; Ostfeld et al. 1997; Orrock et al. 2003; Tallmon et al. 2003). In managed forests, seed predators can limit recruitment of preferred crop trees (Spencer et al. 1954; Sullivan and Sullivan 1982; Shepperd et al. 2006). However, in conifer forests, rates of seed predation after dispersal from the cone and its importance as a limiting factor range widely,

even for the same species. Direct measurements have shown nearly complete loss of seeds within days in some studies (Sullivan 1979a; Castro et al. 1999; Plucinski and Hunter 2001; Broncano et al. 2008) and moderate or minor losses in others (Gashwiler 1970; Radvanyi 1970; Stoehr 2000; Côté et al. 2003; Nilson and Hjältjén 2003; Worthy et al. 2006; Gworek et al. 2007). Where conifer seed predation is substantial, small mammals are usually identified as the chief consumers; ants or carabid beetles play a role in some systems (Nilson and Hjältjén 2003; Worthy et al. 2006). Although conifers often produce abundant seed, the effect of predation on reducing recruitment has been demonstrated by increased germinants in rodent exclosures (Stoehr 2000) or, in some older operational trials, by direct reduction of rodent populations (Spencer et al. 1954).

Because of poor historical success with direct seeding of harvested areas (Spencer et al. 1954; Langdon and LeGrande 1965; Sullivan and Sullivan 1982), most forestry operations in western North America now rely on restocking cutblocks by planting nursery-grown seedlings. However, natural regeneration is still important in several situations, including

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partially cut stands and planted stands where natural infill is required to maintain density or stocking distributions when planted trees fail. Natural regeneration can also be favoured by economic values (Zhou 1998) or for promoting genetic and structural variety (Finkeldey and Ziehe 2004). Natural regeneration is also operationally important in management of naturally disturbed areas, such as burns and large insect disturbances, influencing decisions about whether these areas are salvaged and how they are subsequently managed (Kaufmann et al. 2003; Blade and Vallejo 2008).

Ensuring conifer regeneration is an operational concern in the management of dry Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests in the southern interior of British Columbia (Vyse et al. 2006). These forests have been selectively harvested for over a century. Regeneration has historically been poor or in scattered dense patches, reflecting a combination of hot, dry conditions; inadequate site preparation; competition with grass and other vegetation in some sites; and trampling by livestock (Vyse et al. 1991, 2006). Recent increased use of patch-cutting, followed by site preparation and planting with nursery grown trees, has improved regeneration success (Vyse et al. 2006), but multiple-entry uniform partial cutting relying on natural regeneration is still the dominant silvicultural system in these dry forests. Rehabilitation of large burns and extensive areas affected by mountain pine beetle (*Dendroctonus ponderosae* Hopkins) are also pressing management issues (Astrup et al. 2008; Nigh et al. 2008), along with ongoing debate about restoration of these ecosystems formed by a complex interaction of natural disturbances and historical management (Arsenault and Klenner 2005; Metlen and Fiedler 2006; Baker et al. 2007; Klenner et al. 2008). Conifer seed predation is an integral part of these issues of crop-tree production, succession after natural disturbances, and sources of natural variability in the ecosystem.

Studies in dry Douglas-fir forests have shown that seed fall is abundant, with a mean of 17.9 viable conifer seeds·m⁻²·year⁻¹ (at the Opax Mountain Silvicultural Systems research site (Klenner and Vyse 1998); A. Vyse, British Columbia Forest Service, Kamloops, British Columbia, personal communication, 2007). However, natural seedlings are rare, with only 0.13 seedlings·m⁻² on sites with exposed mineral soil and 0.02 seedlings·m⁻² on undisturbed ground (Huggard et al. 2005) and 0.085 larger advanced regeneration trees per hectare in dry sites (Kaipainen et al. 1998), although patches of denser regeneration do occur. Possible explanations for the sparse natural regeneration include consumption of a large portion of the seeds, poor germination, poor survival of new seedlings, or a combination of these factors. Low levels of viable conifer seeds in the seedbank following harvesting of dry forests (Stark et al. 2006) support the importance of seed predators. Determining the importance of seed predation compared with other limitations to regeneration has implications for management tools that could be used to improve natural regeneration: habitat management to avoid promoting seed predators (e.g., Schreiner et al. 2000), mechanical treatments to improve seedbeds, or vegetation and overstory management to enhance seedling survival. Some intensively burned stands in the area also have little or no regeneration after 10 years, creating a management dilemma of whether to invest in planting or to risk

relying on natural regeneration to provide long-term timber production.

Our goal in this study was to measure rates of conifer seed predation in dry Douglas-fir forest managed with different harvest systems and in burned stands using seed protection treatments to distinguish the effects of different groups of potential seed predators, as a contribution to understanding and possibly mitigating poor natural regeneration in managed stands in this ecosystem. We also examined the effect of experimental manipulations of coarse woody debris (CWD), as an option for habitat management that could affect small mammals (Craig et al. 2006) and potentially seed predation rates.

Methods

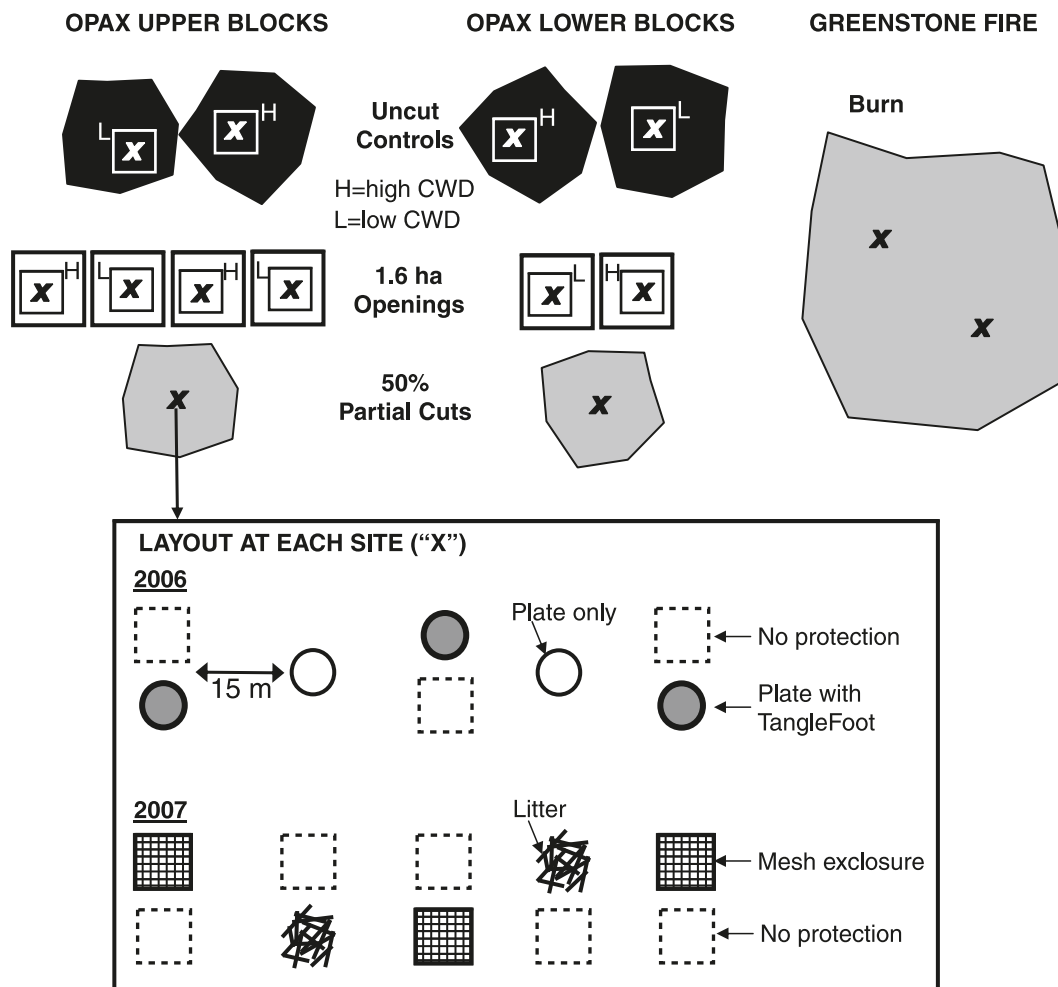
Study area and treatments

The study was conducted at the Opax Mountain Silvicultural Systems site (hereafter referred to as Opax; Klenner and Vyse 1998), 17 km northwest of Kamloops, British Columbia, in the dry Interior Douglas-fir ecosystem. The forest is dominated by Douglas-fir, with lodgepole pine (*Pinus contorta* Dougl. ex Loud.) at higher elevations, some ponderosa pine (*Pinus ponderosa* Dougl. ex C. Laws.) on drier sites, and scattered white spruce (*Picea glauca* (Moench) Voss) and aspen (*Populus tremuloides* Michx.). The patchy understory in forested areas is dominated by pine grass (*Calamagrostis rubescens* Buckl.), low herbs and patchy shrubs, with denser grass and herb cover in openings. In British Columbia's biogeoclimatic system, the Opax site is in the Interior Douglas-fir very dry hot and dry cool sub-zones (IDF_h and IDF_{dk}; Lloyd et al. 1990). Natural grasslands occur at lower elevations immediately adjacent to the Opax site.

The Opax site has been divided into six higher elevation and six lower elevation treatment units of 20–25 ha each (Klenner and Vyse 1998). We sampled in three silvicultural systems treatments: four sites in uncut controls, six sites in 1.6 ha clear-cut openings, and two sites in partial cuts with 50% tree removal (Fig. 1). Additionally, the levels of CWD have been experimentally manipulated within uncut controls and in 1.6 ha square openings in clear-cut treatments, including “high” treatments with natural levels of CWD and “low” treatments in which all wood with a diameter >6 cm was removed (Craig et al. 2006). The four sites in uncut controls included two with high CWD and two with low CWD; the six sites in 1.6 ha openings included three with high CWD and three with low CWD (Fig. 1). Using these CWD treatments allowed us to examine the effect of changing a major habitat component for small mammals, which could be a management option for reducing seed predation. If the CWD differences did not affect predation rates, the manipulated sites simply provided additional replicates of the harvest treatments.

We also worked in a 3400 ha burned area, the “Greenstone fire”, 18 km west of Kamloops, British Columbia, in the same forest type as the Opax site. The severe fire in mature and midseral forest in 1998 and subsequent salvage harvesting left few live trees. Few or no trees have regenerated across most of the burned area 8 or 9 years after the fire, despite abundant exposed mineral soil. We sampled two

Fig. 1. Study design at the Opax Mountain Silvicultural Systems site and the Greenstone fire, and layout of seed protection treatments at each site (X) in 2006 and 2007. The main silvicultural treatment units are 20 ha; coarse woody debris (CWD) treatments (L, low; H, high) are 1 ha. Note that the seed-protection treatments in 2006 also included unsuccessful 12 mm mesh exclosures (not shown and results not included).



sites, separated by 4 km, that were severely burned but not salvaged.

We refer to the control, two harvested treatments, and burns as "disturbance treatments."

Conifer seed treatments

At each study site, we established five sampling stations spaced 15 m apart along a transect (Fig. 1). Stations were ≥ 20 m from a forest-opening edge. Subplots within a station compared seed-protection treatments intended to exclude different potential seed predators. In 2006, seed-protection treatments were control (no exclusion); Tanglefoot plates (16 cm diameter plastic plates set into the ground, with the 1 cm wide rim coated in Tanglefoot, which is a persistently sticky tar used to exclude crawling insects in orchards; Tanglefoot Co., Grand Rapids, Michigan); plate control (plastic plate without Tanglefoot as a control for the effect of the plates themselves). In 2006, we also attempted to exclude small mammals using 20 cm $\times$ 20 cm covers of wire mesh with 12 mm spacing set into the ground. However, field observations showed that mammals were able to enter these covers, either through the openings in the mesh or by exca-

vating under the buried sides. At the end of the 2006 field season, we compared these 12 mm covers with completely enclosed boxes of 6 mm wire mesh. Most invertebrates and the seeds themselves can pass through the 6 mm wire mesh. The 6 mm mesh boxes excluded small mammals successfully, with 205 of 216 seeds surviving in the 8 day pilot study, compared with only 9 of 216 seeds in the paired 12 mm mesh exclosures. The 6 mm mesh boxes were used in 2007; we do not report the results from the unsuccessful 12 mm mesh exclosures. Seed-protection treatments in 2007 were control (no predator exclusion), 6 mm mesh boxes, and litter cover (no exclosure, but seeds covered in a 1–2 cm layer of dry pine and fir needles). Therefore, the 2006 treatments compared unprotected seeds with seeds protected from crawling invertebrates, whereas the 2007 treatments compared unprotected seeds with seeds protected from small mammals and seeds covered by litter.

We examined predation of dinged Douglas-fir and ponderosa pine seeds provided by the BC Tree Seed Centre. In 2006, we used nine seeds of each species in each subplot. Because either all or no seeds were removed in most subplots, we reduced this number to four of each species in

2007. We also used equivalent numbers of coloured plastic beads, which were the same size and similar density as ponderosa pine seeds, in each subplot as a control for seeds removed physically from plots (e.g., by rain, wind, or disturbance by larger mammals) rather than by seed predators. Seeds and beads in all seed-protection treatments were placed on a thin layer of sand, which allowed the small seeds to be detected reliably when checking the plots. One seed of each species and one bead were placed together at the nine or four points spread uniformly across the $\sim 10 \text{ cm} \times 10 \text{ cm}$ area of the sand substrate.

Plots were initially established in late August of each year. In 2006, they were checked 3–4 days later, rechecked 8 or 9 days later and rechecked again 8 or 9 days later. Because seed loss occurred rapidly, we checked the plots 1 day after establishment, 2 days later, and again 2 days later in 2007. Missing seeds and beads were replaced at each field visit.

Analysis

Comparisons of seed-protection treatments, disturbance treatment, and CWD treatment within patch cuts and controls were made separately for each seed species and year using model selection based on Akaike Information Criterion (AIC) corrected for small sample sizes (Burnham and Anderson 1998). Subplots of a particular seed-protection treatment within a site and the three sessions per year were pooled, so that the site was the sample unit for each year. Model selection for the seed-protection treatments used four candidate models for 2006 treatments and three models for 2007 treatments (Table 1). Eight candidate models for the disturbance treatments (Table 2) were defined separately for the species and years using pooled results from the three seed-protection treatments in 2006 and from the control and litter treatments in 2007 (based on the AIC analyses of the seed-protection treatments). The CWD treatments were analysed using two candidate models (separate means for the two treatments vs. one common mean) separately for species, for years, and for patch cut and uncut treatments. The AIC analyses were based on an overdispersed binomial likelihood model for seed survival, where the overdispersion parameter was estimated using the χ^2 goodness of fit of a model with each seed treatment and study block divided by the residual degrees of freedom of this “global” model (Burnham and Anderson 1998). The survival distributions observed with rechecking periods of 1–9 days, S_{OBS} , were standardized to daily values, S_{DAILY} , as $S_{\text{DAILY}} = S_{\text{OBS}}^{1/T_{\text{OBS}}}$, where T_{OBS} is the number of days in the rechecking period. We report the AIC weights of the candidate models, which can be interpreted as the probability that that model is best supported by the data, given the set of candidate models. Results are presented as the maximum likelihood estimate of daily seed survival and the 95 percentiles of the lower and upper tails of the distribution.

Results

All seeds were removed from 49.8% of subplots; no seeds were removed from 36.0% of subplots. Partial removal occurred in only 14.2% of subplots. Removals of Douglas-fir and pine seeds were highly correlated at the subplot level

($r = 0.94$), and the effects of seed-protection, disturbance, and CWD treatments were nearly identical for the two species. Therefore, we only present results for Douglas-fir here. Few beads were removed: one of the four or nine beads was displaced from 8.2% of the subplots and more than one bead from 6.1%. In most cases of bead displacement, we observed extensive digging of unprotected plots by small mammals, rather than rain, wind, or large mammal disturbance.

Seed-protection treatments

The AIC analysis for 2006 supports estimating a single mean daily survival value combining the three main seed-protection treatments within each disturbance treatment (Table 1). That is, within a disturbance treatment, there was no substantial difference among the seed-protection treatments. The one possible effect of the 2006 seed-protection treatments was moderately greater seed survival in the Tanglefoot subplots and slightly reduced survival in the plate-only treatment (Fig. 2a). The latter effect is likely due to flooding and larger mammal disturbance of a few of the plates. Otherwise, the treatments excluding invertebrates had no effect compared with unprotected controls.

For 2007, the AIC results support a survival estimate for the 6 mm mesh boxes separate from the unprotected or litter treatments (Table 1). The best models combined the unprotected and litter-covered subplots in three disturbance treatments but separated these treatments in the patch cuts. Seed survival was much higher (nearly 100%) in the mesh boxes than in the unprotected subplots (Fig. 2b). In the few cases where seeds were lost from the mesh boxes, there was clear evidence in the field that small mammals had burrowed under the boxes until the seeds fell through the mesh floor. In the patch cuts, and less distinctly in the uncut forest, litter cover increased seed survival moderately.

Disturbance treatments

In both years, the best model combined estimates of seed survival for partial cuts and patch cuts, with separate estimates for uncut and burned sites (Table 2). Seed survival was highest in uncut stands, moderately lower in partial cuts and patch cuts, and close to zero in burned sites (Table 3). Survival rates were higher in the partial cuts and patch cuts in 2007 than in 2006. In the burns in 2007, no seeds outside of mesh boxes survived the 1 or 2 day sessions.

CWD treatments

AIC weights were >0.98 for the model with one common mean for the two CWD treatments (i.e., no difference between treatments) for all combinations of year and harvest treatment, except for pine and Douglas-fir seeds in patch cuts in 2007, where the model with different means had >0.999 weight for both species. Seed survival was higher in the low-CWD treatment than the high treatment in the patch cuts in 2007 (Fig. 3).

Discussion

The daily survival rates of unprotected seeds were low enough in both years that few seeds would be expected to

Table 1. Candidate models for comparisons of 2006 and 2007 seed-protection treatments, and Akaike Information Criterion (AIC) weights for Douglas-fir seed survival by disturbance treatment and year.

Year and model ^a	Uncut	Partial cut	Patch cut	Burn
2006				
1. No protection, plate only, Tanglefoot	0.080	0.000	0.029	0.000
2. No protection, plate only = Tanglefoot	0.071	0.008	0.154	0.007
3. No protection = plate only, Tanglefoot	0.408	0.010	0.156	0.008
4. No protection = plate only = Tanglefoot	0.442	0.981	0.661	0.985
2007				
1. No protection, litter, mesh box	0.191	0.000	0.775	0.000
2. No protection = litter, mesh box	0.809	0.992	0.225	1.000
3. No protection = litter = mesh box	0.000	0.008	0.000	0.000

Note: The AIC weight is the probability that the model is the best model, given the data and the set of candidate models being compared. Results were very similar for ponderosa pine.

^aFor the candidate model descriptions, treatments separated by commas have distinct means, and treatments connected by an equal sign share the same mean. For example, model 2 in 2006 fitted a mean to the no-protection treatment, and a mean to the other two treatments combined.

Table 2. Candidate models for comparison of disturbance treatments, and Akaike information criterion (AIC) weights for Douglas-fir seed survival by year.

Model ^a	2006	2007
Uncut, partial cut, patch cut, burn	0.074	0.171
Uncut, partial cut, patch cut = burn	0.000	0.000
Uncut, partial cut = patch cut, burn	0.913	0.685
Uncut = partial cut, patch cut, burn	0.011	0.023
Uncut = partial cut, patch cut = burn	0.000	0.000
Uncut = partial cut = patch cut, burn	0.002	0.121
Uncut, partial cut = patch cut = burn	0.000	0.000
Uncut = partial cut = patch cut = burn	0.000	0.000

Note: The AIC weight is the probability that the model is the best model, given the data and the set of candidate models being compared. Results were very similar for ponderosa pine.

^aFor the candidate model descriptions, treatments separated by commas have distinct means, and treatments connected by an equal sign share the same mean.

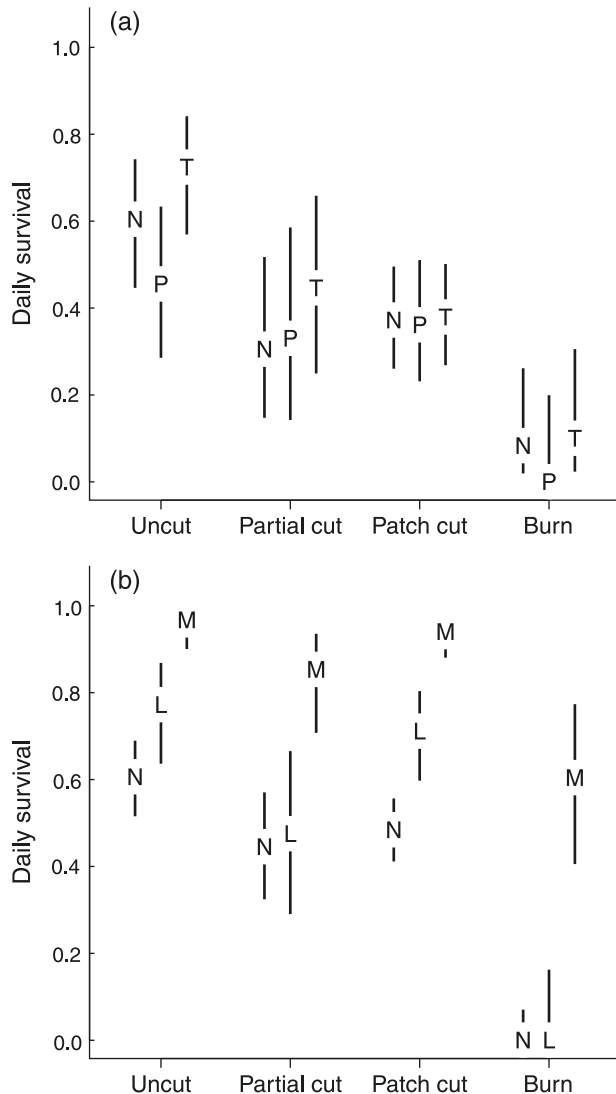
survive on the ground for more than a few days. The mean daily survival in uncut stands of 0.63 corresponds to 4% of seeds surviving for 1 week, whereas the mean survival of 0.45 in harvested stands would allow only 0.4% to survive for 1 week. These high rates of pine and Douglas-fir seed losses are comparable with rates reported elsewhere for these genera. Pine seeds are preferred by seed predators (Ostfeld et al. 1997; Cornett et al. 1998), and high rates of seed loss have been reported for pine in other ecosystems, including 0%–38% survival over 5 months for lodgepole pine in southern and central British Columbia (Sullivan and Sullivan 1982), <1% survival over 2 days for eastern white pine (*Pinus strobus* L.) in oak–pine forests in eastern North America (Plucinski and Hunter 2001), 4% postdispersal survival for Scots pine (*Pinus sylvestris* L.) in southern Spain (Castro et al. 1999), and <1%–20% survival seasonally for Aleppo pine (*Pinus halepensis* Mill.) in burned sites in northern Spain (Broncano et al. 2008). Predation rates reported for Douglas-fir range from 5% survival over 3 days (Sullivan 1979a) or 2 weeks in coastal British Columbia (Sullivan 1979b) to 10% survival in coastal Oregon (Gashwiler 1970). Lower rates are typically reported for

other species, including boreal white spruce (Radvanyi 1970; Peters et al. 2004), boreal black spruce (*Picea mariana* (Mill.) BSP; Côté et al. 2003), western larch (*Larix occidentalis* Nutt.) in south-central British Columbia (Stoechr 2000), or coastal western hemlock (*Tsuga heterophylla* (Raf.) Sarg.; Gashwiler 1970), although seed losses are still considered operationally significant in these systems (Spencer et al. 1954; Sullivan and Sullivan 1982). However, generalizations among genera are uncertain because lower rates have also been reported in some pine studies (Nilson and Hjältén 2003; Worthy et al. 2006; Jeffrey pine, *Pinus jeffreyi* Grev. & Balf., Gworek et al. 2007). Broadly, predation rates are often higher in warmer drier situations across the range of species summarized above and within species, e.g., Scots pine (Castro et al. 1999 compared with Nilson and Hjältén 2003; Worthy et al. 2006), Douglas-fir (this study compared with coastal studies by Gashwiler 1970; Sullivan 1979a, 1979b), and lodgepole pine (three study areas of Sullivan and Sullivan 1982). However, there are exceptions (e.g., higher seed survival at lower elevations; Gworek et al. 2007), which emphasize the need for measurements in particular forest types where seed predation is a management concern.

The plastic bead controls support the assumption that seeds that disappeared had been consumed rather than moved away from the subplots by wind, rain, or large mammal disturbance. The assumption that the daily rates continue to apply over several days is supported by the similar daily rates calculated for 2007, with 1 and 2 day re-checking periods, and 2006, with rechecking periods up to 9 days. Replacement of seeds at each session is unlikely to have artificially increased predation rates because removal rates were as high in the first session as in subsequent sessions in a year. If all seeds accessible to small mammals at a site were eaten in each session, the provision rate would have been 21.6 seeds-day⁻¹ over 20 days in 2006 and 33.6 seeds-day⁻¹ over 5 days in 2007. We do not expect that these small amounts of seed and short periods would have been enough to cause population changes or shifts in small mammal territories.

The seeds in this study were placed on small patches of sand to ensure that they could be recounted accurately,

Fig. 2. Daily survival of Douglas-fir seeds in (a) 2006 and (b) 2007 by disturbance treatment and seed-protection treatment (2006: N, no protection; P, plate only; T, Tanglefoot; 2007: N, no protection; L, litter cover; M, 6 mm mesh box). The symbols are positioned at the maximum likelihood estimates. Error bars are 95 percentiles.



which may have increased their vulnerability to seed predators. More complex ground cover may provide refugia (Johnson and Fryer 1996; Nilson and Hjältén 2003; Reed et al. 2006). The subplots with litter cover showed a modest increase in seed survival in the uncut and patch cut treatments. However, the daily survival rate under the litter cover was still low enough to allow very few surviving seeds if the survival rate applied over weeks or months. We used a 15–20 mm thick uniform mat of dry conifer needles as our litter cover, so that we could reliably count the remaining seeds underneath, including when the litter was disturbed; a more complex substrate might have further protected seeds. However, if surviving seeds were buried in too much litter, this could reduce their germination success and early survival (Hermann and Lavender 1990; Li et al. 1994). The preferred substrate of exposed mineral soil is where seeds are likely most vulnerable to predation.

Small mammals appear to be the dominant seed predators at the Opax and Greenstone sites. The Tanglefoot treatments, which restricted access by ground-dwelling insects but were accessible to small mammals, increased seed survival only slightly and not in all treatments. Only a few individual seeds were removed from the 6 mm mesh boxes, which exclude small mammals but not small and moderate-sized invertebrates (excluding mesh boxes where seeds were removed by mammals excavating underneath the box floor). Husked shells of the conifer seeds and tracks or digging of small mammals were found in many of the subplots from which all seeds had been removed. Despite the abundance of ants at the sites (observed in many subplots), they appear to make a minor contribution to seed predation compared with small mammals, as also found by Brown et al. (1975), Castro et al. (1999), and Broncano et al. (2008) in other dry ecosystems. Large carabid beetles may have been excluded by the 6 mm mesh; however, in studies where carabid beetles have been identified as seed predators, they consumed <10% of seeds (Nystrand and Granström 2000; Worthey et al. 2006).

Deer mice (*Peromyscus maniculatus* Wagner) are likely the most important of the small mammal seed predators at Opax. Their nocturnal activity corresponds to our field observation that seeds often disappeared overnight, whereas few were touched during the day. Deer mice were considered the major seed predators in clearcuts by Sullivan (1979a, 1979b) and Sullivan and Sullivan (1982), and the related white-footed mouse (*Peromyscus leucopus* Raf.) is the main seed predator in eastern North America (Ostfeld et al. 1997; Manson and Stiles 1998; Plucinski and Hunter 2001). In Sullivan's studies, population densities up to 36 mice·ha⁻¹ consumed up to 860 000 seeds·ha⁻¹·year⁻¹, or roughly 24 000 seeds·year⁻¹ for every mouse. Deer mouse densities at Opax over 3 years prior to this study ranged from 1 to 14 mice·ha⁻¹ in nine trapping grids in uncut forest and from 4 to 45 mice·ha⁻¹ in nine grids in clearcuts (Craig et al. 2006). With the same consumption rate as in Sullivan (1979b), this would correspond to 24 000–336 000 seeds·ha⁻¹·year⁻¹ consumed by deer mice in uncut forest at Opax, and from 96 000 to >1 000 000 seeds·ha⁻¹·year⁻¹ in openings. The mean Douglas-fir seedfall density of 179 000 seeds·ha⁻¹ in uncut forest at Opax (Huggard et al. 2005) is in the middle of the range of expected consumption by deer mice in uncut forest. The seedfall rate at the edge of openings was 97 000 seeds·ha⁻¹, the amount that the lowest clear-cut population of deer mice would consume, whereas the highest yearly seedfall at edges in 10 years of measurements was 520 000 seeds·ha⁻¹·year⁻¹, in the middle of the expected range of consumption. Seedfall at Opax decreased by 50% every 15 m into the opening, so that seedfall within openings would only be expected to exceed the amount consumed when high seedfall years corresponded to the lowest populations of deer mice. Seeds are even less likely to escape predation in burned sites, where observed consumption rates were higher, deer mice are typically more abundant (Martel 1983), and conifer seed sources are often sparse and distant.

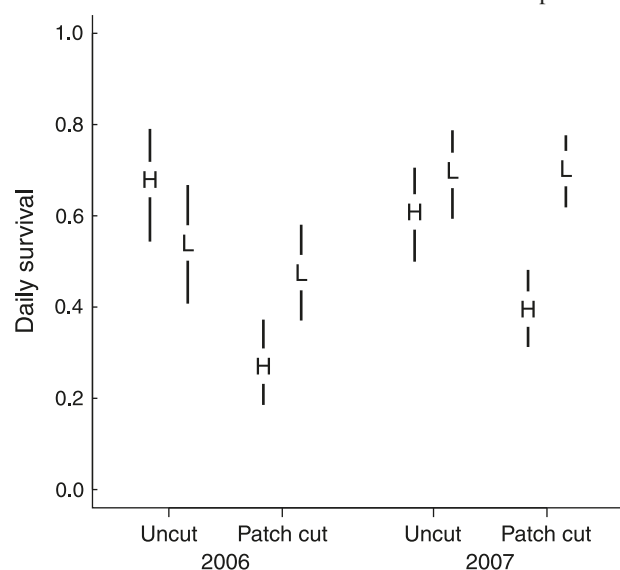
Seeds could escape from predation if they fall into a vacant deer mouse territory. However, deer mice rapidly recolonize areas where the residents have been removed (Sullivan 1979a), and movements of several hundred metres

Table 3. Daily seed survival by disturbance treatment for seeds outside of mesh boxes in 2006 and 2007.

Treatment	2006		2007	
	ML	95 percentiles	ML	95 percentiles
Uncut	0.610	0.513–0.697	0.654	0.579–0.722
Partial cut	0.363	0.246–0.494	0.455	0.351–0.560
Patch cut	0.373	0.302–0.447	0.550	0.487–0.610
Partial + patch cut	0.370	0.308–0.434	0.526	0.472–0.578
Burn	0.069	0.024–0.167	0.000	0.000–0.052

Note: ML, maximum likelihood estimate of daily survival rate.

Fig. 3. Daily survival of Douglas-fir seeds in coarse woody debris treatments (H, high; L, low) in uncut and patch cut sites in 2006 and 2007 for all three seed-protection treatments in 2006 and for no protection and litter treatments in 2007. The symbols are positioned at the maximum likelihood estimates. Error bars are 95 percentiles.



by deer mice at Opax (Craig et al. 2006) suggest that they will readily find open territories. Another possible mechanism to allow seed survival is saturation of the small mammals by alternative foods. Sullivan (1979b) and Sullivan and Sullivan (1982) have shown that providing supplemental food to deer mice improves conifer seed survival in clear-cuts. Grasses and forbs that recolonize harvested openings may provide a similar effect, if productive seed years for these early seral plants correspond with a good year for conifer seeds.

Deer mice are habitat generalists, although they increase in harvested openings in dry forest (Sullivan 1979a; Craig et al. 2006). Deer mice showed less of an increase in partial cuts at Opax than in patch cuts in the 3 years after harvest (Klenner 1998), but we found similar seed survival in the two harvest types. This may reflect changes in the populations in the decade since harvesting or additional seed consumption by other species that are more common in partial cuts at Opax, including red-backed voles (*Myodes gapperi* (Vigors)) (Klenner 1998) or red squirrels (*Tamiasciurus hudsonicus* (Erxleben)) (Herbers and Klenner 2007). Although seedfall is greater in the partial cuts than in the patch cut openings (approximately proportional to tree reten-

tion levels; A. Vyse, B.C. Ministry of Forests, Victoria, B.C., personal communication, 2007), the low survival rates suggest that few seeds are likely to survive to allow extensive natural regeneration in the partial cuts.

Several authors associate deer mice with high levels of downed wood (Carey and Johnson 1995; Manning and Edge 2004; Pearce and Venier 2005), but Craig et al. (2006) found that initial densities were higher in patch cuts with CWD removed. This leaves the higher survival of seeds in the low-CWD patch cuts in 2007 unexplained. The effect of the CWD manipulations on deer mice may have changed with 10 years of succession since the initial small mammal monitoring, other small mammal species may have a bigger role than we believe, or the differences in seed survival may be a chance effect with only three patch cuts at each CWD level. In any case, we do not believe that intentionally reducing CWD levels would be effective in producing more natural regeneration, because seed survival levels were still low in the low-CWD patch cuts.

The two species of seeds examined had nearly identical predation rates in the various treatments, primarily because all or none of the seeds of both species were consumed at a given subplot. Therefore, seed predation by small mammals is not likely to have a major effect on the relative occurrence of Douglas-fir and ponderosa pine. We did note some insects on surviving seeds, particularly the heteropteran *Leptoglossus occidentalis* (Heideman) on ponderosa pine seeds, which reduce seed survival (Bates et al. 2000). However, the silvics of survival and growth of the two tree species is likely a more important determinant of their distributions. Seed predation of the intensity we observed in burns may prevent or delay tree regeneration and help to maintain the community in early seral conditions.

The high rate of seed predation that we observed for unprotected seeds implies that seed loss will often be a limitation for natural regeneration of harvested stands in dry Douglas-fir forests, including in partially cut stands where natural regeneration is more likely to be considered in operational management. Seed predation will certainly compound other limiting factors, such as poor survival of germinants in hot dry conditions and with vegetation competition, and a variety of pests and pathogens. Reducing CWD will likely not be a useful management option for lowering seed losses. In fact, removing CWD could exacerbate regeneration failure due to abundant livestock in this forest type. The extremely high rates of seed predation in burned dry forest implies that natural conifer regeneration in these sites will be very slow, if it occurs at all. Salvage logging that

reduces seed sources will exacerbate the problem. On the other hand, the existence of these forests shows that they have successfully regenerated naturally after fires in the past, demonstrating that there must be some mechanism to allow conifer seeds to escape occasionally from seed predators. Occasional conifer mast years with extraordinary seed production are one possibility, which would only be detected with longer-term monitoring of seedfall.

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