Seedfall and Seed Viability Within Artificial Canopy Gaps in a Western Washington Douglas-Fir Forest

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Abstract

Seedfall of coast Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco var. *menziesii*) has been studied at the forest edge-clearcut interface and in small canopy gaps, but it has not been evaluated in gap sizes that would be typical of a group-selection method of regeneration. In a mature Douglas-fir forest in the Puget Sound lowlands of western Washington, seedfall was measured by month in artificially created circular gaps 0.1, 0.2, 0.3, and 0.4 ha (0.25, 0.5, 0.75, and 1.0 ac, respectively) in size and in the forest matrix. Seedfall was assessed 1 year before and 2 years after gap creation, and a germination trial was used to detect potential gap and seasonal effects on seed viability. Seedfall density was not significantly affected by the presence of gaps up to 0.4 ha (1.0 ac). Germination percentage and germination rate did not differ between seed collected in gaps and that collected in the forest matrix. Seed weight and germination percentage both were highest for fall collections and declined for collections taken throughout winter and spring. We found no evidence that seed dispersal or viability would be a limiting factor in natural regeneration of Douglas-fir under a group-selection system that created gaps up to 0.4 ha (1.0 ac) in size.

Introduction

In recent decades, increasing attention has been focused on silvicultural systems for public lands that promote multiple age classes and structural diversity in production forests that traditionally have been managed under single-age systems (Aubry et al. 2009, Guldin 1996, Malcolm et al. 2001, Reutebuch et al. 2004). For tree species of low or moderate shade tolerance, including many of the important conifer timber species in North America, single-tree-selection systems do not create an understory environment with sufficient light for successful regeneration (Harrington 2006, Miller and Emmingham 2001). By contrast, a silvicultural system, such as group selection, which harvests and regenerates areas typically 0.04 to 0.8 ha (0.1 to 2.0 ac), creates gaps with sufficient light to potentially regenerate species that are less shade tolerant (Smith 1986).

Whereas economic or regulatory reasons often spur the planting of seedlings following group-selection harvests, natural regeneration of the canopy species is sometimes a viable alternative, owing, in part, to the close proximity of seed-producing trees bordering the small gaps. If the dominant canopy tree species are shade intolerant, it is unlikely that significant advance regeneration of these species will be present at the time of gap creation, leaving coppice regeneration or seed as the primary source of natural regeneration for the canopy species. Natural regeneration has been studied in group-selection silvicultural systems in a variety of forest types worldwide (Gagnon et al. 2004, Kinny et al. 2012, Stephens et al. 1999); however, much remains unknown about seedfall within the harvested patches. Although many studies have investigated seedfall in canopy gaps of tropical forests (Augspurger and Franson 1988, Connell 1989, Denslow and Gomez Diaz 1990), only a few have measured seedfall under a group-selection system in temperate forests (Gray 1995, McDonald and Abbott 1994).

In the case of coast Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco var. *menziesii*), one of the world's most important timber species and the subject of the present study, seed does not retain viability in the forest floor or soil past the year in which it falls (Isaac 1935). Therefore, under a group-selection system, seedfall rate in gaps—and seed viability—during the initial years following gap creation is of key importance, particularly because vegetative competition grows rapidly in newly created gaps (Spies and Franklin 1989). The small, single-winged seeds of Douglas-fir are dispersed by gravity and wind, with dispersal distance influenced by parent tree height and cone position, wind velocity, and other factors (Isaac 1930, Willson 1993). The seed shadow of Douglas-fir was quantified based on all existing dispersal distance data (Willson 1993); however, all these data were derived from virgin forests bordering clearcuts. Seed dispersal in smaller openings and in younger stands may differ, given potential differences in tree height and wind currents.

This 3-year study examined seedfall in a western Washington Douglas-fir forest to assess seedfall in harvested gaps 0.1 to 0.4 ha (0.25 to 1.0 ac) in size and to compare these values with seedfall within the forest matrix. A germination trial was conducted to assess potential gap and seasonal effects on seed viability. Hypotheses were (1) seedfall in gaps is negatively associated with gap size owing to proximity to seed source; and (2) seed viability is negatively associated with gap size because lighter seeds, including unfilled seeds (i.e., without a developed embryo), are expected to travel greater distances.

Methods

Study Area

The study was located on Joint Base Lewis-McChord, a U.S. military base in the Puget Trough physiographic province of southwestern Washington at an elevation of 106 to 139 m (350 to 460 ft) above sea level. The study area was anthropogenically maintained prairie and savanna before European settlement, which occurred in the mid-1800s. After settlement, Douglas-fir density increased in waves from 1878 to 1938 associated with low-intensity fires with fire return intervals of 10 to 91 years (Peter and Harrington 2014). The study area includes six forest stands, each characterized by a Douglas-fir overstory. Although these stands had been subjected to low-intensity thinning (15 to 20 percent of basal area removed per entry) two or three times, the overstory consisted of the original cohort of trees that colonized the area. The understory in the study area consists largely of western swordfern (*Polystichum munitum* [Kaulf.] C. Presl) and salal (*Gaultheria shallon Pursh*), with a lesser amount of Oregon grape (*Mahonia nervosa* [Pursh] Nutt.), California hazel (*Corylus cornuta* Marshall), oceanspray (*Holodiscus discolor* [Pursh] Maxim.), and common snowberry (*Symphoricarpos albus* [L.] S.F. Blake).

The soils in the study area are Spanaway and Everett gravelly and very gravelly sandy loams (Typic Humixerepts and Humic Dystroxerepts, respectively), mapped as Humic Cambisols by the Food and Agriculture Organization of the United Nations (FAO 1995). These soils are formed in glacial outwash and are very deep and somewhat excessively drained (Soil Survey Staff 2006). The climate is characterized by warm, dry summers and mild, wet winters, owing to a maritime influence. In Tacoma, WA (15 to 25 km [9 to 16 mi] from study plots), mean annual precipitation is 1,008 mm (39.7 in), although cumulative precipitation from May 1 through September 30 averages only 166 mm (6.5 in) (WRCC 2015). Mean air temperatures in January and July are 6 and 19 °C (43 and 66 °F), respectively.

Overstory characteristics of each stand were assessed using prism sampling (5 m^2 ha^{-1} [21.78 ft^2 ac^{-1}] basal-area factor), with 28 grid points per stand sampled. Diameter at breast height (measured at 1.3 m [4.3 ft] above ground) was recorded for every "in" tree and total height and crown height were recorded for one typical dominant or codominant tree per plot. With the exception of a single ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson), all overstory trees inventoried were Douglas-fir.

Study Design and Data Collection

To assess seedfall in stands without gap creation, 24 sample locations (8 in each of three similar forest stands) were established on predetermined grid points during the study's "pretreatment" season (September 2008 to March 2009). In September 2008, a 73.2-m (240-ft) transect was established at each sample location, running northeast-southwest and centered on the sample location. Seven seedtraps were installed along each transect at a 12.2-m (40-ft) spacing. Each circular seedtrap consisted of a shallow fiberglass screen cone, with a 1.0-m^2 (10.8-ft^2) opening at the top, suspended approximately 0.75 m (2.5 ft) above the ground on metal rods (figure 1).

Figure 1. Each seedtrap contained a circular frame, 1.0 m^2 (10.8 ft^2) in area, constructed of flexible plastic tubing. A semicircle of fiberglass screen was stapled to the frame to create a conical trap for collecting Douglas-fir seeds, cones, and other forest litter. The trap was suspended on rods approximately 0.75 m (2.5 ft) above the ground. (Photo by Timothy B. Harrington, 2008)

Owing to operational constraints associated with the timing of overstory treatments (i.e., gap creation and thinning), it was not possible to measure posttreatment seedfall in the same three stands assessed for pretreatment seedfall. Instead, seedfall data were collected during two posttreatment seasons (September 2009 to March 2010 and September 2010 to March 2011), following the same sampling protocol, in three other similar stands that were part of the same study area (table 1). For this reason, we interpret pretreatment data with the caveat that they were collected in different stands from the posttreatment data. It should be noted, however, that pretreatment and posttreatment stand characteristics differed very little (table 1).

Table 1. Characteristics (mean ± standard error) of two groups of stands used in the Douglas-fir seedfall study. Three stands were assessed before any treatment (pretreatment stands), and three stands were assessed 2 years after a treatment that consisted of gap creation and thinning (treated stands).

Variable	Pretreatment stands	Treated stands
Height (m)	47.3 ± 2.3	48.9 ± 1.8
Crown base height (m)	24.9 ± 2.1	27.8 ± 1.9
Quadratic mean DBH (cm)	69.5 ± 4.5	68.9 ± 6.2
Stem density (trees ha^{-1})	141.1 ± 29.8	147.6 ± 40.5
Stand basal area (m^2 ha^{-1})	34.4 ± 3.5	32.9 ± 4.1
Stand density index (percent of maximum)	31.8 ± 2.9	30.4 ± 2.6

DBH = diameter at breast height.

Conversions: 1 m = 3.281 ft; 1 cm = 0.394 in; 1 tree ha-1 = 0.405 tree ac^{-1}; 1 m^2 ha^{-1} = 4.356 ft^2 ac^{-1}.

Treatments consisted of circular canopy gaps, 0.1, 0.2, 0.3, and 0.4 ha (0.25, 0.5, 0.75, and 1.0 ac) in size (figure 2). Gaps were created at the same time as a stand-level operational thinning having a target residual density of 30 percent of maximum Stand Density Index for Douglas-fir (Reineke 1933). Of the eight transect locations in each stand, four were centered in gaps of each of the four sizes ("gap locations") and four were located in nongap locations within the thinned forest matrix ("matrix locations").

For both pretreatment and posttreatment transects, the content of each seedtrap was collected at an approximate 1-month interval during each season. Contents (needles, cones, seeds, and other materials) from the 7 seedtraps at each transect location were composited in the field (figure 3). A total of 432 seedtrap samples were collected (18 sample dates [6 per year] x 3 stands x 8 locations). At the laboratory, cones were separated from other sampled materials, and both of these portions from each composite sample were air-dried in separate paper bags for 6 to 8 weeks. After drying, seeds were removed from cones and the total number of cone seeds per sample was recorded.

Seeds that fell individually (i.e., not in cones) were separated from all other materials in the seedtrap by handsorting and

Figure 2. Example of a 0.4-ha (1.0-acre) circular canopy gap that was created by harvesting trees within a mature stand of Douglas-fir at Joint Base Lewis-McChord. Seven seedtraps were placed within each gap at 12.2-m (40-ft) spacing along a northeast-southwest transect that intersected the gap center. (Photo by Timothy B. Harrington, 2009)

Figure 3. The contents of each seedtrap (Douglas-fir seeds, cones, and other forest litter) were collected monthly from September to March during the year before gap creation (2008 to 2009) and during the 2 years after gap creation (2009 to 2010 and 2010 to 2011). (Photo by Timothy B. Harrington, 2010)

were counted for six sample locations in each season. For the individually fallen seed samples in the posttreatment, a stratified random selection procedure was used to select one transect location from each of the four gap sizes and two from the forest matrix locations, with a total of two selected locations in each of the three stands. Thus, a total of 108 samples of individually fallen seeds were collected (18 sample dates [6 per year] x 3 stands x 2 locations). After sorting and counting, all seeds were placed in storage at -18 °C (0 °F) until the germination trial.

To achieve adequate sample sizes for the germination trial, all seeds (i.e., cone-origin and individual) from each sample date during the pretreatment collection were composited by stand. For the posttreatment samples, all seeds collected at each sample date within each stand were composited into two groups based on treatment: (1) forest matrix and (2) the four gap treatments. Samples were combined for the first two sample dates in posttreatment season 2 because an insufficient number of seeds were collected on those dates for separate germination tests; thus, the total number of samples in the germination test was 102 (17 sample dates x 3 stands x 2 treatment groups). Each sample was weighed (nearest 0.1 mg [0.000004 oz]) and counted to calculate average seed weight.

Before the germination trial, 100 seeds from the pretreatment season, 100 seeds from the posttreatment season 1, and 50 seeds from the posttreatment season 2 samples (owing to a limited number of seeds collected during that season) were randomly selected from each sample, soaked in deionized water for 24 hours, and then cold stratified (>0 °C [32 °F]) for 40 days. Following stratification, seeds were placed on moistened filter paper within a plastic germination box and placed in a germinator with 20/25 °C (68/77 °F) night/day (14 hr/10 hr) temperatures and observed for germination during a 30-day period. Observations were daily for the first 5 days and every 2 days thereafter.

Data Analyses

For each of the three sample seasons, seedfall data (number of cone seeds and individual seeds collected per sample) were analyzed using repeated measures analysis of variance (ANOVA), with sample date (i.e., days since beginning of study) as the repeated unit (Proc MIXED, SAS Institute Inc. 2008). For the two posttreatment sample seasons, the effect of gap treatment was included in the model, using gap size as a continuous variable (range = 0 ha [0 ac] in the forest matrix treatment to 0.4 ha [1.0 ac] in the largest gap treatment).

Average seed weight per sample and total germination percentage after 30 days were also analyzed with repeated-measures ANOVA. In posttreatment models, gap treatment was included as a fixed effect with two levels (presence of a gap of any size vs. absence).

Cumulative distribution of germination over time was modeled for each sample using a four-parameter Weibull cumulative distribution function, as described by Brown (1987) (Proc NLIN, SAS Institute Inc. 2008):

$$F(t) = M(1–\exp[–\{k(t–l)\}^c])$$

where F(t) is cumulative germination at time t (days), M is the maximum germination for the sample (germination at day 30), k is the rate of germination, l is the lag until germination initiates (days), and c is the shape parameter. After a function was fit for each sample, the k, l, and c parameters were analyzed using the same ANOVA model described for analysis of total germination percentage.

Residuals produced by ANOVA models were examined graphically and were tested using PROC REG and PROC UNIVARIATE (White's and Shapiro-Wilk tests) for variance and normality assumptions (SAS Institute Inc. 2008); no transformations were deemed necessary. Mean separation was performed using Tukey's HSD test. Significance was judged at a confidence level of 95 percent throughout the analyses.

Results and Discussion

Seedfall

Total seedfall varied tenfold among the three study seasons, from 211,000 ha^{-1} (85,400 ac^{-1}) to more than 2,165,000 ha^{-1} (876,100 ac^{-1}) (table 2). The proportion of seed dropped individually was 54 percent of the seed crop in the pretreatment season and 93 and 36 percent in posttreatment seasons 1 and 2, respectively. The number of seeds that fell individually varied widely among seasons, whereas seed extracted from dropped cones did not vary appreciably (table 2).

Douglas-fir seed production varies substantially among years, with heavy seed crops occurring every 2 to 11 years; at least some seed is produced in 75 to 80 percent of years (McDonald 1992, Stein and Owston 2008). An average of 800,000 seeds ha^{-1} (320,000 seeds ac^{-1}) has been suggested as necessary to produce an adequately stocked stand of Douglas-fir (Isaac 1943); however, this estimate varies

Table 2. Total estimated seedfall in 3 years (mean ± standard error). Estimates for posttreatment seasons 1 and 2 are an average across five treatments: forest matrix (thinned) and 0.1-, 0.2-, 0.3-, and 0.4-ha canopy gaps.

Year	Seedfall (thousand seeds ha^{-1} yr^{-1})		
	Individual seed	Seed in cones	Total crop
Pretreatment	182 ± 62	158 ± 89	340
Posttreatment season 1	2,017 ± 563	148 ± 178	2,165
Posttreatment season 2	76 ± 24	135 ± 91	211

Conversions: 1 ha = 2.47 ac; 1,000 seeds ha^{-1} = 405 seeds ac^{-1}

widely by site and may be significantly lower for favorable seedbeds (Isaac 1943, Minore 1986). Germination and subsequent seedling establishment success vary substantially among sites; success is highest on mineral soil with germinants protected from direct sunlight and where seed predation and vegetation competition are low (Gray and Spies 1996, Minore 1986). Thinning increases stand-level seed production (Reukema 1961), and it is possible that gap creation would increase seed production of bordering trees. Such an increase in seed production, however, would likely not lead to increased seedling establishment in gaps unless the increase occurred before substantial growth of competing vegetation.

Seedfall rate differed among sample periods for individually dropped seeds during the pretreatment season and posttreatment season 2 (table 3; figure 4). Where significant differences occurred among sampling periods, seedfall was lowest in late fall/early winter and greatest in late winter/early spring. The number of seeds dropped in cones varied among sample periods in all 3 years, with the greatest number of seeds dropped during November or December in all years, likely coinciding with significant fall and winter storms (table 3; figure 5). Previous studies reported seed

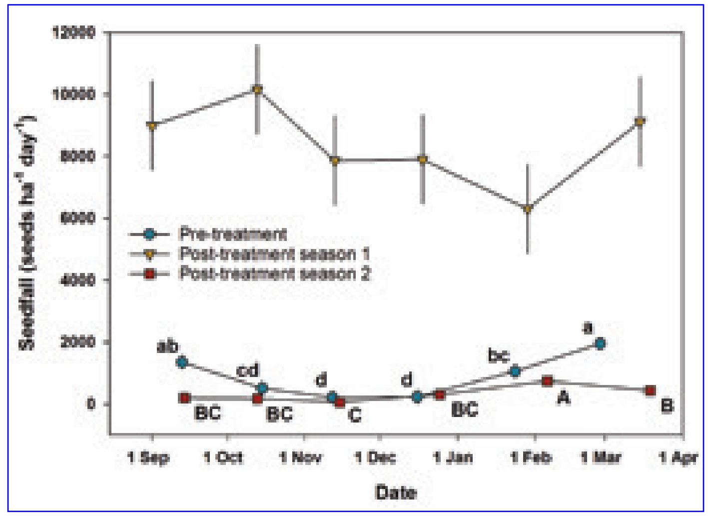

Figure 4. Mean Douglas-fir seedfall rate (± standard error) for seeds dropped individually (i.e., not in cones) by sample period in three seasons. Means accompanied by the same lowercase letter (pretreatment season) or uppercase letter (posttreatment season 2) do not differ significantly by sampling period (alpha = 0.05). No differences were observed among sampling periods for posttreatment season 1. Conversion: 1,000 seeds ha-1 day-1 = 405 seeds ac^{-1} day^{-1}

dispersal for Douglas-fir beginning around September, with most seed usually falling by early December and seedfall virtually completed by the end of March (Gashwiler 1969, Isaac 1943, Pickford 1929, Reukema 1982). Periods of warm temperatures are associated with the opening of cones and an increase in the release of seeds (Stein and Owston 2008). Unlike these previous studies, we observed no obvious seasonal decline in seedfall rate for individually dropped seeds. Although seedfall declined in winter in the pretreatment measurement, it increased again at the final sample period in March (figure 4).

No significant gap effect on the number of individually dropped seeds in either posttreatment season was

Table 3. Significance (Pr > F) of treatment effects from ANOVA models evaluating seedfall (individual seeds and seeds in dropped cones) analyzed during one season pretreatment (no thinning or gaps created) and during two posttreatment seasons (with thinning and canopy gaps of varying sizes). Sampling period was September through March each season.

Variable	Effect[a]	d.f.	Pretreatment	Posttreatment season 1	Posttreatment season 2
Individual seeds (seeds ha^{-1} day^{-1})	Sample period	5[b]	< 0.001	0.387	0.014
	Gap size	1	—	0.284	0.713
	Sample period × gap size	5[b]	—	0.269	0.939
Seeds in cones (seeds ha^{-1} day^{-1})	Sample period	5[b]	< 0.001	0.002	< 0.001
	Gap size	1	—	< 0.001	< 0.001
	Sample period × gap size	5[b]	—	0.541	< 0.001

ANOVA = analysis of variance; d.f. = degrees of freedom; Pr > F = the p-value associated with the F statistic.

[a] Gap size was analyzed as a continuous variable (0 to 0.4 ha).
Conversion: 1 seed ha^{-1} day^{-1} = 0.405 seeds ac^{-1} day^{-1}.

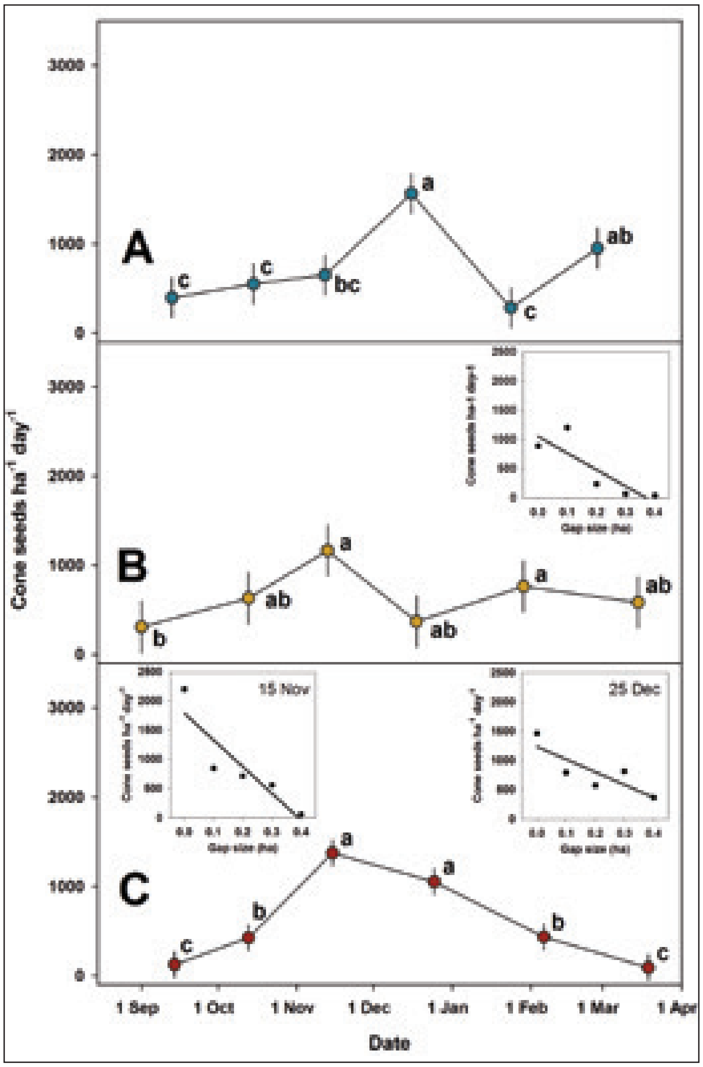

Figure 5. Mean Douglas-fir seedfall rate (± standard error) for seeds dropped in cones by sample period in three seasons: (A) pretreatment season, (B) posttreatment season 1, and (C) posttreatment season 2. In each season, seedfall differed among sample periods; points accompanied by the same lowercase letter do not differ significantly (alpha = 0.05). In posttreatment season 1, seedfall rate also differed significantly by gap size (table 3; inset in B). In posttreatment season 2, a sample period × gap size interaction resulted from significant gap size effects for 15 Nov and 25 Dec sample periods (table 3; insets in C) but not in the other sample periods. Conversion: 1,000 seeds ha^{-1} day^{-1} = 405 seeds ac^{-1} day^{-1}.

observed. A significant negative relationship existed, however, between gap size and cone seeds in posttreatment season 1, and a significant interaction existed between sample period and gap size in posttreatment season 2. This interaction resulted from a negative relationship between gap size and cone seed number in the November and December sample periods, when the overall number of cone seeds was highest. The number of cone seeds decreased linearly as gap area increased from 0 (forest matrix) to 0.4 ha (1.0 ac), probably because of associated increases in the distance from seed-bearing trees. We are not aware of any previous studies that separately assessed Douglas-fir seed that fell still attached to cones from seed that fell individually; however, it is clear that the dispersal distance of cones is less than that of individual seeds. In a heavy seed year, only a small proportion (7 percent) of total seedfall consisted of seeds in cones, and thus the lack of cones falling into larger gaps may not have a meaningful impact on regeneration. It remains unclear what fraction of the seeds that are dropped in cones germinate and establish as seedlings compared with that of individually dropped seeds.

Because no gap-size effect was observed on seedfall density for individually dropped seeds, in posttreatment season 1, even our largest gaps (0.4 ha [1.0 ac]) had seedfall densities well in excess of the densities suggested for successful stocking (355 seeds per seedling [Isaac 1943] and 75 to 190 seeds per seedling [Minore 1986]). We are not aware of any studies that have assessed Douglas-fir seedfall in larger gaps. One study examined smaller gaps in a mixed conifer-hardwood forest in northern California and found that seedfall did not vary significantly among gaps ranging from 9 to 27 m (30 to 90 ft) in diameter (0.007 to 0.059 ha [0.016 to 0.15 ac]) (McDonald and Abbott 1994). Several early studies measured seedfall in large clearcuts bordered by virgin forest (Isaac 1930, 1943; Pickford 1929). Seedfall in western Oregon clearcuts declined at a ratio of 5:2:1 at distances of 23, 69, and 114 m (75, 225, and 375 ft) from the forest edge, respectively (Gashwiler 1969). In another clearcut study, 44 percent of seed fell within 30 m (100 ft) of the forest edge and 83 percent fell within 152 m (500 ft) (Isaac 1943).

Seed Weight and Germination

Seed weight was approximately twice as great in the season of heavy production (posttreatment season 1) compared with the other seasons (figure 6). Seed weight in the year of heavy production was comparable or slightly less than values reported previously, whereas seed weight in the two light-production seasons was substantially lower (Stein and Owston 2008). Germination percentage was also substantially higher in the season of heavy seed production than in the other seasons, averaging more than 50 percent during the first four sample periods (table 4; figure 7). Germination was 10 percent or less throughout the other two seasons. The proportion of filled seed (i.e., seed with a normal embryo that is potentially viable) has been shown in several other studies to be positively correlated with the size of the

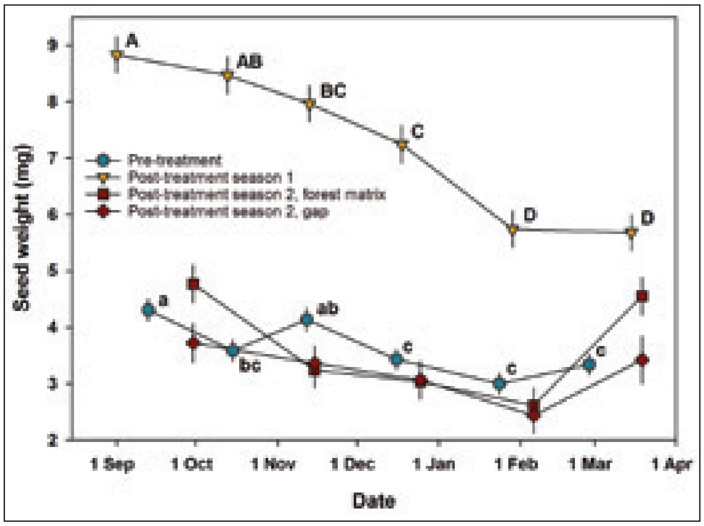

Figure 6. Mean Douglas-fir seed weight (± standard error) by sample period during three seasons. Sample periods differed significantly pretreatment and during posttreatment season 1 (table 4); means accompanied by the same lowercase letter (pretreatment season) or uppercase letter (posttreatment season 1) do not differ significantly by sampling period (alpha = 0.05). During posttreatment season 2, a significant sample period × gap treatment interaction was observed: seed weight was significantly greater in the forest matrix treatment during the first and last sample periods only. Conversion: 1 mg = 0.00004 oz.

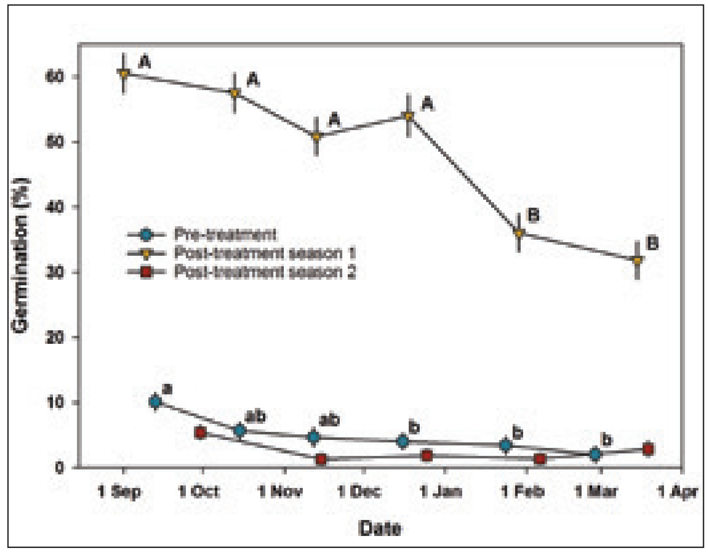

Figure 7. Germination percentage (± standard error) for Douglas-fir seed by sample period during three seasons. Germination differed within season pretreatment and within season during posttreatment season 1 (table 4). Means accompanied by the same lowercase letter (pretreatment season) or uppercase letter (posttreatment season 1) do not differ significantly by sampling period (alpha = 0.05).

annual seed crop, ranging from 1 to 54 percent (Garman 1951; Gashwiler 1969; Reukema 1961, 1982)

Seed weight followed a declining trend during each of the three seasons, with the exception of posttreatment season 2, when seed weight increased in the final sample period (table 4; figure 6). Within each season, seed germination percentage also declined for seeds collected later in the season, although the significance of this effect was marginal in posttreatment season 2. A similar trend was shown in two previous Douglas-fir seedfall studies, in which the seed that fell earliest had the highest viability (Gashwiler 1969, Reukema 1982). Within the year of heavy seed production (posttreatment season 1), a significant positive correlation between seed weight and total germination percentage was observed (figure 8), owing to the fact that both variables decreased similarly during the season.

Germination percentage did not differ between seeds collected in gaps and those collected in the forest matrix (table 4). No effect of gap presence on seed weight in posttreatment season 1 was observed, but, in posttreatment season 2, seed weight in the first and last sample periods in the forest matrix treatment was more than that of seeds dropped in

Table 4. Significance (Pr > F) of treatment effects from ANOVA models evaluating seed weight and total germination for seed collected in one season pretreatment (no thinning or gaps created) and during two seasons posttreatment (with thinning and canopy gaps of varying sizes). Sampling period was September through March each season. The gap presence effect compares forest matrix (thinned only) with a composite sample of seed collected in gaps of 0.1, 0.2, 0.3, and 0.4 ha.

Variable	Effect	d.f.	Pretreatment	Posttreatment season 1	Posttreatment season 2
Seed weight	Sample period	5[a]	0.001	< 0.001	< 0.001
	Gap presence	1	—	0.850	0.006
	Sample period × gap presence	5[a]	—	0.532	0.032
Total Germination (percent)	Sample period	5[a]	0.008	< 0.001	0.054
	Gap presence	1	—	0.616	0.252
	Sample period × gap presence	5[a]	—	0.137	0.276

ANOVA = analysis of variance; d.f. = degrees of freedom; Pr > F = the p-value associated with the F statistic.

[a] Degrees of freedom was 4 in posttreatment season 2.

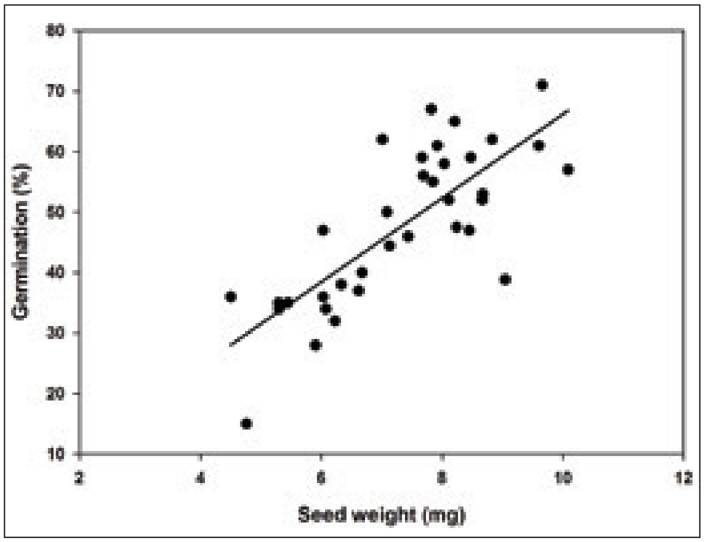

Figure 8. Relationship between germination percentage and seed weight for samples collected on three sites in posttreatment season 1 during six sample periods from September through March. Regression line equation is y = 6.93x – 3.16 (R^2 = 0.60). Conversion: 1 mg = 0.00004 oz.

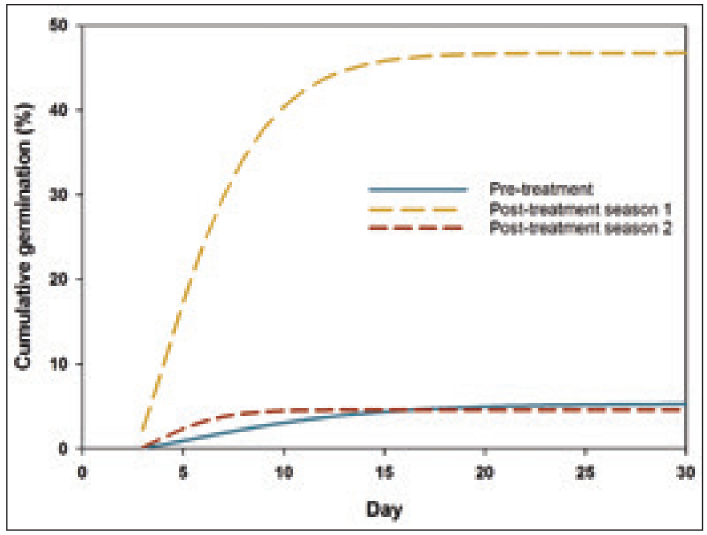

Figure 9. Germination functions for Douglas-fir seed collected during three seasons. Sample period and gap presence did not significantly affect the functions' germination rate, lag, or shape parameters; thus, the functions shown here are for the pooled germination data from each season.

gaps (figure 6). An initial concern with natural regeneration in larger gaps was that heavier seed—presumably the seed with higher viability—would be less likely to fall near the center of the gaps owing to greater distance from the parent tree. Because seed weight and germination percentages of seed collected in gaps were generally similar to that of the forest matrix, however, gaps of the size range in this study are not likely to incur that problem.

Within each season, the parameters describing the Weibull distribution did not differ significantly by sample period or gap presence. Thus, overall cumulative distribution curves describing germination in each season are shown in figure 9. Germination reached an asymptotic level around day 15 during each season.

Conclusions

Our findings, in general, do not support our hypothesis that seedfall in gaps is negatively associated with gap size. The only negative effect of gap size on seedfall occurred for seed dropped in cones. The impact of this phenomenon on total seedfall may be meaningful in a light seed production year, but, in a year of heavy seed production, its relative impact is minor. We found no evidence to support our hypothesis that seed viability is negatively associated with gap size. Although germination was correlated with seed weight, this relationship was a function of sample period rather than of gap presence.

We found no evidence that seed dispersal or viability would be limiting factors in natural regeneration of Douglas-fir in circular gaps up to 0.4 ha (1.0 ac) in size, assuming an adequate seed crop was produced soon after gap creation (i.e., before significant growth of competing vegetation). Thus, with sufficient seedfall and seed viability, establishment of natural regeneration in created gaps is more likely to be limited by other factors, such as light availability, seedbed conditions, seed predation, desiccation of germinants, and vegetative competition (Gray and Spies 1996, Isaac 1943, Minore 1986). Success of Douglas-fir seedlings and saplings as a future canopy cohort will likely require relatively large gaps; 2-year-old Douglas-fir seedlings regenerated from seed were significantly larger near the center of 0.2-ha (0.5-ac) gaps compared with seedlings in smaller gaps (Gray and Spies 1996). Measurements of photosynthetically active radiation (PAR) in this study (unpublished data) showed that PAR was similarly high in gaps from 0.2 to 0.4 ha (0.5 to 1.0 ac) but decreased sharply in the 0.1-ha (0.25-ac) gaps and in the forest matrix. Whereas the present study shows propagules are not limiting in any of the gap sizes tested, 0.2 ha (0.5 ac) may be a realistic minimum gap size for successful natural regeneration of Douglas-fir under a group-selection system.

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