

6-2008

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RESEARCH ARTICLE

SEED INVASION FILTERS AND FOREST FIRE SEVERITY

Tom R. Cottrell^{1*}, Paul F. Hessburg², and Jonathan A. Betz¹

¹Department of Biological Sciences, Central Washington University,
400 East University Way, Ellensburg, Washington 98926, USA

²USDA Forest Service, PNW Research Station,
1133 N. Western Ave., Wenatchee, Washington 98801, USA

*Corresponding author: Tel.: 001-509-963-3011; e-mail: cottreLT@cwu.edu

ABSTRACT

Forest seed dispersal is altered after fire. Using seed traps, we studied impacts of fire severity on timing of seed dispersal, total seed rain, and seed rain richness in patches of high and low severity fire and unburned Douglas-fir (*Pseudotsuga menziesii*) forests in the Fischer and Tye fire complexes in the eastern Washington Cascades. Unburned plots had the lowest average seed production. The high severity fire patches in the Fischer Fire Complex had a higher total seed production than low severity fire patches of the same complex. At the Tye Fire Complex, the total seed production for each of the two fire severities was similar, but the period of maximum seed dispersal was later for high severity than low severity fire. Seed rain at the Fischer Fire patches (sampled one year after the fire) was predominantly composed of annual species, while that of the Tye Fire patches (sampled nine years after fire) was predominantly perennial species. Seed rain richness was greater in Tye high severity patches than paired low severity fire patches. In these paired Tye patches the average number of new seed species (species not found in the extant plot vegetation) was greater for high severity than low severity fire. Our results suggest that high severity fire plots are more porous to seed rain than low severity plots. Intact forest canopies may filter seed rain and reduce seed influx, while high severity fires are more open to invasion by seed dispersal.

Keywords: fire, seed dispersal, seed rain, seed rain richness, Washington Cascades

Citation: Cottrell, T.R., P.F. Hessburg, and J.A. Betz. 2008. Seed invasion filters and forest fire severity. *Fire Ecology* 4(1): 87-100. doi: 10.4996/fireecology.0401087

INTRODUCTION

Forest fires and other ecological processes produce complex patterns of vegetation on the landscape. For example, there is large variation in patch sizes of newly regenerated early seral conditions (Hessburg *et al.* 2007), and these patches are interspersed with the

remaining forest canopy, influencing the ease, timing, and type of post-fire colonization. Plants occupy new habitats via sexual reproduction and seed dispersal, and asexual reproduction in close proximity to the parent plant. In annual species, seeds are the perennating organ. Colonization of newly altered sites requires short- to long-distance

seed travel, and the ability of a species to invade a site is largely related to seed traits, including seed mass, and time between seed crop years (Rejmanek and Richardson 1996). Due to a short juvenile period and the small size and ease of seed dispersal, annual species are often favored immediately after fire (Howe and Smallwood 1982).

An increase in seed production following fire in some rhizomatous monocot species has been linked to post-fire colonization of burned sites (Lamont and Runciman 1993). This effect is not limited to monocots. For example, Hartnett and Richardson (1989) found evidence that seed rain from Florida lady's nightcap (*Bonamia grandiflora*) was 10 to 30 times greater after a fire, an increase they ascribed to increased stem densities from both asexual growth and new genet recruitment from seed in the year after fire. Survival of tissue for asexual growth, however, depends in part on fuel size, surrounding fuels, and the season of burn (Monsanto and Agee 2008). Understanding vegetation responses to fire therefore requires understanding propagule dispersal and production, as well as fire conditions.

Seed dispersal mechanisms vary widely, resulting in different patterns of colonization. Species with wind or explosively dispersed seeds show a less clumped distribution than animal dispersed seeds (Levine and Murrell 2003). Some wind dispersed seeds may also travel long distances. Solbreck and Andersson (1987) trapped fireweed (*Epilobium angustifolium*) seeds using a vacuum pump 90 m above the ground in Sweden. They showed that 20 % to 50 % of dispersing fireweed seeds may reach 100 m or more above the ground, suggesting that newly burned sites some distance away may be readily colonized by this species. Shorter distance dispersal by insects is also important. Parr *et al.* (2006) showed that seed dispersal by ants is modified by fire. These authors found that after fire, seed

dispersal distance by ants often increases; a change they relate to the decreased complexity of the foraging surface following fire.

Seed dispersal may vary over time after fire. For example, in the Yellowstone ecosystem, Turner *et al.* (1997) found that most vegetation cover within three years of the 1988 fires was from re-sprouting, followed later by a pulse of seedlings from local seed. This local dispersal might be important in the maintenance of post-fire communities. Levine and Murrell (2003) provided theoretical evidence that local seed dispersal slows extirpation of a dispersing species from a site, but empirical evidence for this conclusion was limited.

Land use history is also important to plant species dispersal (Bossuyt and Hermy 2001). Harper (1977) presented data showing that in some agricultural lands, seed dispersal did not mask the effects of local land use on seed bank composition. Similarly, Devlaeminck *et al.* (2005) found that seed dispersal and colonizing ability could be modified by local forest structure. In that study, forest edges and interiors differed in seed bank composition, suggesting that seed rain filtering occurred in forest canopies. By measuring the seed bank, the authors found that interior forest settings had reduced seed input relative to adjacent fields, suggesting that forest canopies acted as barriers to seeds of the surrounding non-forest.

The remarkably varied dispersal characteristics of plant species has made the link between dispersal and extant vegetation difficult to understand, especially in altered environments. As an example, Salonen (1987), found no relation between the number of dispersing seeds and plant abundance of the same species growing in the pioneer vegetation of abandoned peat harvest areas. However, other workers have found conflicting results and suggest that seed size and number, and nearby vegetation may be tightly linked to early recruitment (Jakobsson and Eriksson 2000).

There are few studies on the effects of fire on seed dispersal and seed rain. In a seed rain study of forest patches interspersed with crops and roads, Honu and Gibson (2008) reported that dispersal richness was lower in forest interiors than in forest edges. In another recent study, Standish *et al.* (2007) found that, in old fields in Australia, seed dispersal limited community recolonization, and seed rain richness was depressed. More commonly, plant community richness has been related to forest fire. For example, Turner *et al.* (1997) showed that severely burned sites five years after fire had lower vascular plant species richness than less severely burned sites. Halpern and Spies (1995) found a similar depression in species richness five years after severe burns in Pacific northwest forests. They noted that post-fire depression in richness was short lived due to rapid recolonization by ruderal species. We note that vegetation richness is not equivalent to seed rain richness.

With increased occurrence of large-scale forest fires, it has become increasingly important to improve understanding of the species that repopulate burned areas and how they arrive there. Knowledge of seed availability and dispersal is critical to understanding forest successional responses after fires. With efficient seed dispersal, a species increases the number of micro-sites it is able to reach, greatly influencing potential colonization opportunities after fires. Seed rain composition provides one avenue for community change following fire.

The purpose of this study was to determine the impacts of fire severity on seed dispersal after fire. We quantified seed production and seed species richness at two fires, in patches of different burn severity and in unburned forest. We hypothesized that seed dispersal into burned forests would be affected by fire severity, and that more dispersal would occur in high severity than low severity fire patches owing to filtering effects of intact canopies.

METHODS

All plots were located in disturbed patches of two recent fires, both on the Wenatchee National Forest, Chelan County, Washington. The Tyee Fire began on July 24, 1994, and burned 56 000 ha (Everett *et al.* 2000), nine years prior to sampling. The Fischer Fire began on August 8, 2004, and burned 6652 ha (Chelan County Conservation District 2005) one year prior to sampling. Sampling took place in two different years: Tyee Fire plots were sampled in 2003; Fischer Fire plots were sampled in 2005. Ignoring year, the month and day of samples were the same. While we acknowledge that plots within a single fire complex can be considered pseudo-replicated, we adopted Monsanto and Agee's view (2008) that the areal and temporal extent of these fire complexes were sufficiently large that the post-fire forests were adequately variable, even within a single fire.

Thirty-two study plots were located in an equal number of patches of the Cool Dry Grass-Douglas-fir Plant Association Group (PAG) (Lillybridge *et al.* 1995). This PAG contains several plant associations; the most common association among our plots was PSME/SPBEL/CARU (*Pseudotsuga menziesii* / *Spirea betulifolia* / *Calamagrostis rubescens*). This association is dominated by Douglas-fir, but ponderosa pine (*Pinus ponderosa*) is also common. Undergrowth in this association is a mixture of graminoids and low and tall shrubs (notably, shiny-leaved spirea [*Spirea densiflora*], Scouler willow [*Salix scouleriana*], and oceanspray [*Holodiscus discolor*]). Tree density in this association averaged 96.3 ha⁻¹. By constraining patches to a single PAG, we attempted to control for environmental influence on seed production and richness. Plot elevation ranged from 430 m to 968 m, and the elevation of a single patch spanned no more than 20 m. Patch aspects were generally NNW, ranging from 257° to 15°.

Plots were classified as having experienced either high severity fire, low severity fire, or no fire (unburned). Control patches with no evidence of fire were sampled in the Fischer Fire Complex. No control patches were sampled in the Tye Fire Complex. One control patch was disturbed by post-fire salvage logging during the study and abandoned, leaving 31 total plots.

Plots were categorized post-hoc as having experienced either a high severity or low severity fire based on survival criteria: high severity is $\leq 30\%$ tree survival, and low severity is $\geq 70\%$ tree survival. In addition to the estimation of tree survival, a spherical densiometer was used in each patch to determine canopy cover (values include both live and dead tree tissue). At the Fischer Fire, some trees still had dead needles in the canopy, which resulted in higher than expected cover values. A visual evaluation of standing and fallen trees was done in an attempt to assure that all patches had similar tree densities prior to the fire.

The areal extent of the large Tye Fire allowed selection of adjacent, paired high severity and low severity fire patches in which we nested our plots. Paired patches were selected to maximize the probability of having similar pre-burn vegetation. Plots of each pair were separated by no more than 30 m and shared the same aspect, elevation, and soils. Average low severity patch size was

approximately 2500 m² (50 m × 50 m), while high severity fire patches were larger, forming the matrix in which the low severity patches were found. Distance from each patch to the nearest unburned patch was determined by aerial photos in order to account for the confounding effects of patch size.

Vegetation of the patches was sampled using a modified Whittaker plot (Stohlgren *et al.* 1998) designed to maximize characterization of plant species richness. In each patch, we randomly located a 10 m × 25 m macro-plot with its long axis perpendicular to the topographic contour. This macro plot was sampled using 10 systematically placed 0.25 m × 1.0 m micro-plots, two 1 m × 2.5 m micro-plots, and one 2.5 m × 10 m micro-plot. The entire macro-plot was then searched for any species not observed in the micro-plots.

In each macro-plot, seed rain was captured by funnel traps (0.0289 m² each) that were placed level and protruded 2 cm above the ground surface (Table 1) (Cottrell 2004). Funnels were placed systematically on four transects parallel to the topographic contour using a random start. Contents of the traps were collected at three-week intervals from mid-April to early October, the period of peak seed dispersal.

Trap samples consisted of all material that fell into the trap between each sampling date and contained seeds, soils, and plant and animal debris. Seeds were removed from the

Table 1. Numbers of sampled seed rain plots and their fire history. Total tree cover indicates the mean values for the plot and includes dead and live overstory. Plot aspects were northerly, ranging from 257° to 15°. Plot sizes were estimated to range between 1800 m² to 2500 m².

Fire complex	Time since burn (yr)	Fire severity	Plots	Elevation range (m)	Tree cover (%)	Traps	Sample dates	Total collections
Tye	9	high	10	474 to 812	10.4	100	9	900
Tye	9	low	10	474 to 812	60.4	100	9	900
Fischer	1	high	4	722 to 968	35.9	32	7	224
Fischer	1	low	4	445 to 914	77.8	32	7	224
non-burn	not burned	none	3	430 to 491	87.2	24	7	168
Total			31			288		2416

samples and counted and identified with the aid of a dissecting microscope and a seed reference collection. The reference collection comprised 120 species of identified plant seeds collected from mature fruits of plants in the study plots. We removed the seeds of each species from its fruit and photographed them for later use in identification of seed trap material.

To standardize detection, we searched each sample until no seed was detected for two minutes, at which point the search of a new sample was begun. This resulted in samples being searched different amounts of time, but with equal intensity (Cottrell 2004). Damaged and apparently nonviable (unfilled, diseased, or parasitized) seeds were not counted. All unknown seeds were preserved and photographed for future identification. Total seeds, species richness, and individual species totals were recorded for each sample.

Analysis

For each sampling date, we determined the average number of seeds m^{-2} by burn severity and patch. This allowed a depiction of seed dispersal timing. Mean species richness per trap was determined for all patches by date. Prior to statistical analysis, all values were normalized using a Johnson transformation (Chou *et al.* 1998, MINITAB Release 14, State College, Pennsylvania).

Separate two-factor fixed effects ANCOVA were performed on the Fischer data using normalized seeds m^{-2} and normalized seed richness as the dependent variables; sample date and fire severity were the independent factors. In both ANCOVAs, we used distance to nearest unburned patch as the covariate. We also ran separate two-factor fixed effects ANOVA with Tukey-Kramer (T-K) multiple comparisons for these same dependent and independent variables, in the event that a significant covariate was lacking.

For the Tye Fire Complex we ran separate one-factor fixed effects ANOVAs with T-K multiple comparisons using the normalized difference between seeds m^{-2} and seed richness for each paired patch, as the dependent variable, and sampling date as the independent factor.

Because species richness depends on area (Rosenzweig 1995, Adler and Lauenroth 2003), and the trapped area of non-burn (control) patches was unequal to either those of the Fischer or Tye fires, control richness data were not included in analyses of richness (Table 1).

Paired Tye Fire patches (low and high severity fires) were analyzed for invasion by novel seed species relative to extant vegetation composition. Pairing assured high similarity of pre-burn vegetation and post-burn seed sources. For each patch, we determined the number of species in the seed rain that were not represented in the extant vegetation. We interpreted these seeds as invaders and tested the hypothesis that the mean number of invaders in high severity fire patches exceeded those in low severity fire patches using a one-tailed paired t-test.

During the three weeks between sampling dates, traps were occasionally dragged away, presumably by animals, and could not be found, or they were overturned by fallen trees. Hence, the count of samples submitted to analysis was 2331; 85 traps (3 %) were missing. Additionally, some traps were found empty; on average, 15 % of traps were empty (lacking any viable seeds) after three weeks in the field. In all calculations, empty traps were included as zeros, while missing traps were not included.

RESULTS

From the 2331 total samples, we recognized 85 seed species and 21 unknowns. The total number of seeds counted, summing all species

and samples, was 45 768. Of these, we were unable to identify 109 individual seeds, the majority of which comprised three unknown species of 29, 21, and 15 seeds. All other unknown seed species had totals less than 10, with most having only one occurrence.

The most numerous seed at a single patch for one sample period was miner's lettuce (*Montia perfoliata*, synonym *Claytonia perfoliata*), which in the June 27, 2005, sample totaled 2945 seeds from 8 traps (12 738 m⁻² per three weeks). The next four largest seed counts for individual patches on a single sampling period were also miner's lettuce. All of these patches were in the Fischer Fire Complex. Of the ten largest seed counts for individual patches, eight were miner's lettuce, all of which occurred in the Fischer Fire. The other two species were flixweed (*Descurainia sophia*), also from the Fischer Fire, and fireweed, from the Tye Fire. Fireweed was the only species in the top ten counts that was a perennial species, and the only one not found in the Fischer Fire.

In the Fischer Fire patches (high and low severity fires), annual species made up the largest percentage of seeds (Table 2). In both fire severity classes at the Tye Fire, the seed rain was predominantly perennial species. The mean number of exotic (non-native) seeds in the seed rain of Fischer high severity fire patches was 14 times greater than Fischer low severity fire patches, and greater than in either Tye fire severity. In the Tye high severity fire patches, exotic seeds made up only 2.5 % of the seed rain.

The covariate used in the analysis of the Fischer data was not significant for seed production nor seed richness ($F_{1,55} = 1.66, p = 0.068$ for seeds m⁻² wk⁻¹; $F_{1,41} = 0.70, p = 0.136$ for seed richness wk⁻¹).

Differences in Seed Totals

At the Fischer Fire Complex, high severity fire patches had a higher average number of seeds (2236 m⁻² per three weeks) than low severity patches (1027 m⁻² per three weeks), (ANOVA, Table 3a, Figure 1,

Table 2. Mean number of seeds m⁻² per three weeks and percent total (in parentheses) for seeds captured in seeds traps from all high severity, low severity, and unburned treatments. Sums differ due to unidentified nativity or biennial habit.

	Fischer Fire Complex			Tye Fire Complex	
	Unburned	Low severity	High severity	Low severity	High severity
Annual species	5 (1.6)	849 (82.5)	2068 (92.4)	132 (33.5)	84 (15.5)
Perennial species	350 (98.4)	178 (17.3)	167 (7.5)	259 (66.0)	455 (84.2)
Native species	353 (99.4)	993 (96.6)	1747 (78.0)	369 (93.9)	535 (97.3)
Non-native species	2 (0.5)	34 (3.3)	489 (21.9)	22 (5.6)	13 (2.5)

Table 3. Analysis of variance (ANOVA) results for a) mean number of seeds m⁻² wk⁻¹ for the Fischer Fire Complex; and b) mean difference between paired high and low burn severity patches at the Tye Fire Complex. Bold font indicates the significant differences.

Source of variation	df	SS	F	p	Power
a) Fire severity	2	15.946	9.15	0.000	0.969
Sampling date	6	37.269	7.13	0.000	0.999
Fire severity x sampling date	12	13.599	1.30	0.244	0.649
Error	56	48.799			
b) Sampling date	8	23.366	3.95	0.000	0.985
Error	81	59.917			

$F_{2,56} = 9.15, p < 0.001$). Dispersal also varied by sampling date ($F_{6,56} = 7.13, p < 0.001$). Most seeds were dispersed early in the summer, while maximum seed output in unburned patches occurred mid-summer (Figure 1). There was no significant interaction between fire severity and sampling date (Table 3a). At the Tye Fire Complex, the difference in the number of seeds between high and low severity fire patches among sample dates was significant (ANOVA, Table 3b, Figure 2, $F_{8,81} = 3.95, p < 0.001$).

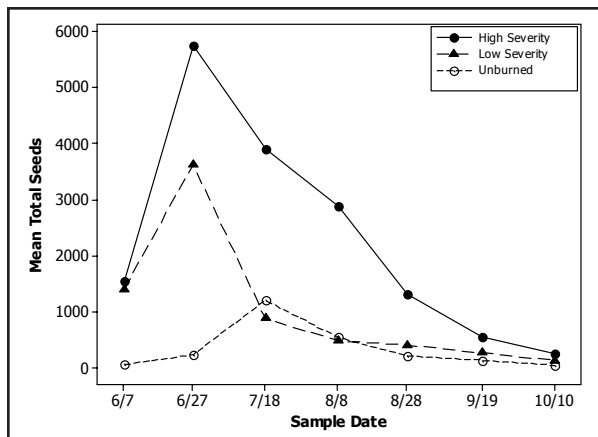


Figure 1. The mean total seeds m^{-2} per three weeks for the Fischer Fire (1 yr post-fire). Lines indicate high and low severity patches, and unburned patches.

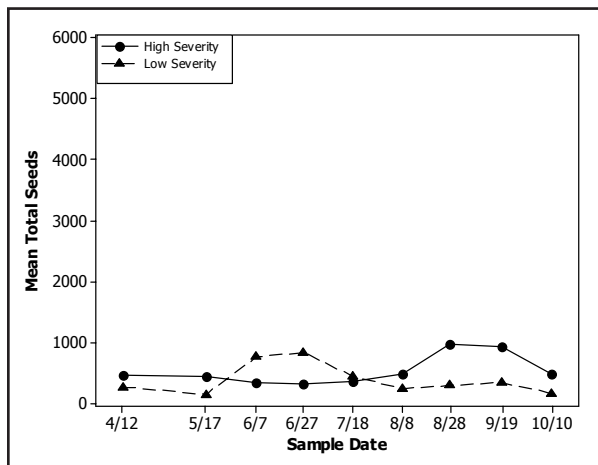


Figure 2. The mean total seeds m^{-2} per three weeks for the Tye Fire (9 yr post-fire). Lines indicate high and low severity patches.

Differences in Seed Species Richness

At the Fischer Fire Complex, seed richness per trap was not significantly different for the two burn severities (1.96 vs. 1.68 for the three week sample period, $F_{1,42} = 1.95, p = 0.170$). Richness by date of sample varied significantly, however, and the highest levels of richness occurred in mid-summer (two-factor ANOVA, Table 4a, Figure 3, $F_{6,42} = 2.44, p = 0.041$). The one-factor ANOVA of the difference in seed richness between paired low and high severity fire patches at the Tye Fire Complex was significant (ANOVA, Table 4b, Figure 4, $F_{8,81} = 4.43, p < 0.001$). The difference in seed richness (over three weeks) varied significantly among dates with the high severity fire patches showing greater richness than low severity fire patches in August and September (T-K multiple comparison, $p < 0.05$). One-tailed paired t-test of the mean number of invading seed species trapped over the summer showed that there were significantly more invading species in high severity fire (11.00 seeds) than low severity fire patches (13.75 seeds), at the Tye sites ($T_7 = 2.252, p = 0.029$; Figure 5).

DISCUSSION

We measured total seed dispersal and seed rain richness in unburned and burned forest patches that had experienced either high or low severity fires. We used distance to the nearest unburned forest as a potential covariate in the Fischer Fire analyses to account for patch size differences and found that the covariate was insignificant. We attempted to control for exogenous factors through placement of all sets of paired high and low severity patches in close proximity and sharing common elevation, slope, and aspect. Further, the plant association group was held constant for all patches, thus reducing variation resulting from community differences. The time since fire, however, was an important difference between the two fires.

Table 4. Analysis of variance (ANOVA) results for a) normalized mean seed richness for the Fischer Fire Complex; and b) normalized seed richness differences between paired high and low burn severity patches at the Tye Fire Complex. Bold font indicates the significant differences.

Source of variation	df	SS	F	<i>p</i>	Power
a) Fire severity	1	1.516	1.95	0.170	0.276
Sampling date	6	11.417	2.44	0.041	0.765
Fire severity x sampling date	6	1.607	0.34	0.909	0.134
Error	42				
b) Sampling date	8	26.610	4.43	0.000	0.993
Error	81	60.850			

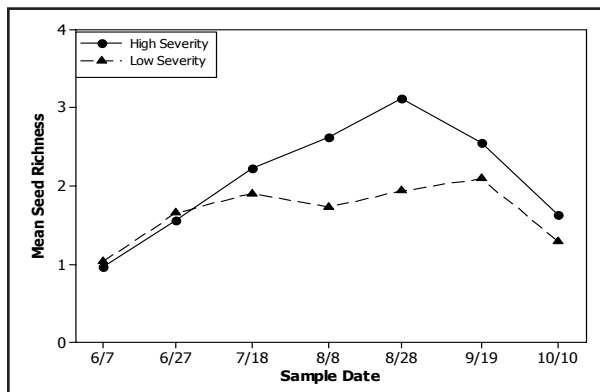


Figure 3. Mean seed richness per trap for each three week sample period, by fire severity treatment and sampling date for Fischer Fire (1 yr post-fire). Lines indicate high and low severity fire patches.

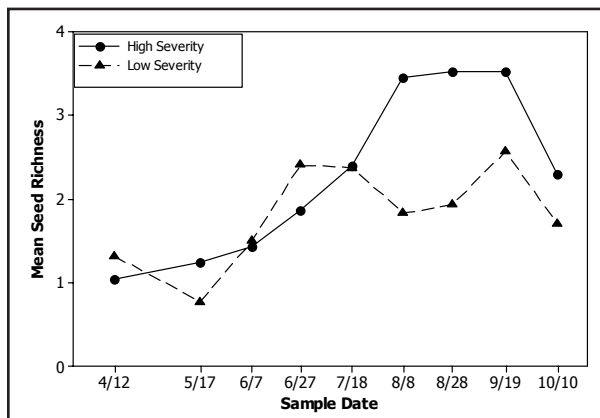


Figure 4. Mean seed richness per trap for each three week sample period, by fire severity and sampling date for the Tye Fire samples (9 yr post-fire).

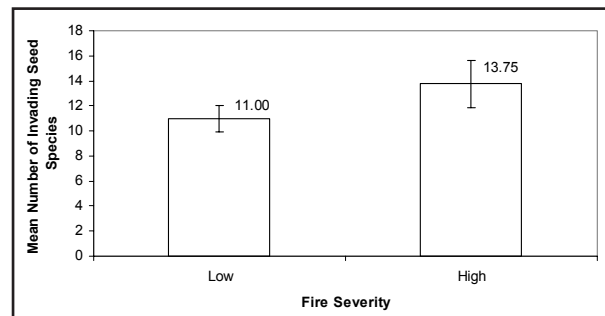


Figure 5. Mean number of invading seed species in the low and high severity burn patches at the Tye Fire patches (9 yr post-fire). Invading seeds were defined as any seed species that was not found in the extent patch vegetation. Test was a one-tailed paired t-test of mean number of seed species represented in the seed rain but not in the vegetation. Error bars are +1 SE. ($t = 2.25$; $p = 0.029$; power at $\alpha = 0.05$ is 0.65)

Fischer Fire patches were sampled one year post-fire, while the Tye Fire patches were sampled nine years post-fire. At the time of our samples for the Tye Fire, the Fischer Fire had not occurred and our samples occurred in different years. While we recognize that we cannot conclude that all differences between the seed rains of these two fires are due to the time since the fire, we believe this is an important driving variable.

The total seed dispersal (seeds m^{-2}) at the Fischer Fire varied significantly with fire

severity and sample date. The Fischer high severity fire patches had their peak seed production in June. In comparison, the seed production of the Fischer low severity fire patches was considerably lower, but also peaked during June. The control (unburned) patches displayed a less varied seed production across the summer, with a small peak in July. Our data show that seed rains for both high and low severity fires at the Fischer Fire were predominantly composed of annual species. The large seed numbers we found support the contention by Stark *et al.* (2006) that seed dispersal in the first year following fire is an important mechanism in vegetation recovery. However, seeds from the seed bank must be important as well, and many of the plants dispersing seeds in the burned Fischer patches must have begun from the existing seed bank.

The early dispersal peak at the Fischer Fire sites (in both fire severities) indicate the predominance of spring flowering annuals in these dry forests, particularly miner's lettuce. The unburned plots, characterized by extensive, intact canopy shading, showed a much less dramatic peak of seed dispersal. This smaller peak occurred in the middle of July and contained fewer annual species. The seed rain of these unburned patches was dominated by two taxa: hawkweed (*Hieracium* spp.) and Tweedy's reedgrass (*Calamagrostis tweedyi*).

At the Tyee Fire, the difference in seed production of closely paired high and low severity burned patches varied significantly by sampling date. High severity patches had peak dispersal in late August and September. This is later than peak production for the Fischer Fire. While these samples were taken in different years and are not directly comparable, it is likely that this difference is ecologically meaningful. Seeds in the Fischer Fire were mostly annuals, and some of this abundance is partially explained by the earlier successional status, in comparison with Tyee Fire patches. The seeds disbursed by the high severity Tyee

Fire patches were predominantly the late-flowering perennial forbs fireweed, yarrow (*Achillea millefolium*), and tall annual willowherb (*Epilobium brachycarpum*). All three of these species are sun-adapted and establish well in areas where the canopy has been removed.

In contrast to the high severity patches, Tyee low severity fire patches, which had an intact canopy, had their peak seed dispersal during June. The principal species contributing to this dispersal peak included miner's lettuce and Sandberg bluegrass (*Poa secunda*). While miner's lettuce did not produce the large seed numbers that occurred in the Fischer Fire, there was an important surge in seed production from this ruderal species in June. It is noteworthy that this annual species played a large role in the Tyee low severity fire patches while the high severity fire patches of the same age had seed rains dominated by perennial natives. While early succession on sunny sites favors annual seed production (Grime 1979), the dominance of miner's lettuce in the low severity Tyee patches requires explanation. Most likely, the shading provided by the unburned canopy maintained adequate soil moisture that allowed the annual miner's lettuce to compete longer in the post-fire succession. The distinction between seed rains dominated by annual or perennial species could not be simply explained by fire severity, but must include reference to the specific taxa involved; miner's lettuce is unlike many annuals, having a greater tolerance for shading.

Clearly, any succession after fire is influenced by seed production, and this production was very different for the Fischer and Tyee fires. At the time of our samples, the Fischer Fire patches had four to six times more seeds than the Tyee Fire patches. One possible explanation for the greater number of seeds at the Fischer Fire than the Tyee Fire is the time since burning. The Fischer Fire was more

recent and these forests were in earlier stages of succession, where annuals, with their large seed output, are favored. Large numbers of seeds produced after fire do not necessarily translate into large changes in plant populations (Lortie and Turkington 2002), though that is certainly one possibility. Keeley (1977) found in the California chaparral that as many as 99 % of seeds stored in the soil did not result in seedlings after fire. Hewitt and Kellman (2002) and Blade and Vallejo (2008) provide evidence that large seeded species have the greatest survival rates as seedlings, perhaps surmounting the advantage in number of seed produced by annual species. Nevertheless, the seed rain can provide an important part of the species pool from which the burned forests may initially develop.

In all our burned plots (Fischer and Tyee), the seed number of exotic (non-native) species, while higher than unburned patches, was still relatively small. This probably says more about the available species pool than the tendencies of non-native species to colonize after a fire. These forests, at least away from roads, are not overwhelmed by non-native species. Nelson *et al.* (2008) agree, but also report that non-native understory plants showed increases in cover and richness after burning and thinning. The authors noted that the cover of non-natives was negatively correlated to basal area. Such correlations may be, in part, driven by a reduction in seed rain filtering whenever stand basal area is reduced. For example, our data suggest an increase in the numbers of non-native seeds after high severity fire. At the Fischer Fire (one year post-fire) the numbers of non-native seeds was 14-fold higher in the high than the low severity patches, suggesting that non-native seeds, as a group, tend to be better dispersers. This supports the Nelson *et al.* (2008) findings. The implications for stand restoration treatments are clear; reducing canopy cover can allow increased seed infiltration and, if there is an

available species pool, perhaps more non-native species.

In addition to production, timing, and the non-native component of a seed rain, the overall richness is also important to post-fire forests. At the Fischer Fire, the bulk of seed rain diversity occurred in mid-summer. Total diversity appeared to be slightly greater for high than low severity fire patches, but the difference was insignificant. Stark *et al.* (2006) found greater seed bank species richness in low severity than high severity burn sites one year after a burn. Because they sampled the seed bank by germination tests, however, their results are not directly comparable to our seed rain data.

At the Tyee Fire in late summer, the seed richness of high severity fire patches was greater than in the paired low severity patches. This greater richness resulted primarily from the addition of perennial native forbs including pearly everlasting (*Anaphalis margaritacea*), grand collomia (*Collomia grandiflora*), fireweed, and a few graminoids, including pinegrass (*Calamagrostis rubescens*) and western fescue (*Festuca occidentalis*). The late season spike in richness corresponded to the late season spike in total seed production in these patches.

Two mechanisms can account for the late season increase in seed species richness observed at the Tyee Fire. First, the late season increase in richness in high severity fire sites may be associated with greater micro-site habitat variability, perhaps from greater sun penetration and soil drying. If other micro-sites of these same high severity patches were more mesic (an intuitive assumption given the number of fallen trees providing shade and moist micro-sites), the effect could be a greater number of available habitats favoring a late maturing species. The Tyee low severity fire patches may lack these dry micro-sites and therefore have lower species richness. The second mechanism is the open canopy

condition of the high severity burn sites. A relatively open canopy in these patches might allow more seed influx than more densely forested sites. This has implications for weed spread after high severity fires. Seed richness was higher in the more severely burned patches and this difference suggests seed dispersal and colonization are influenced by the degree of canopy removal.

The test of paired high vs. low severity fire patches (Tyee) lends support to the idea of dispersal inhibition by an intact forest canopy. Species that occur in the seed rain but not in the extant vegetation can be considered invaders. Significantly more of these invading seeds occurred in high severity fire than low severity fire patches of the Tyee Fire Complex. In this fire, there were three more invading species on average in the high severity patches than in low severity fire patches. Dandelion (*Taraxacum officianalis*) and prickly lettuce (*Lactuca serriola*) were the only frequent non-native invading species in our data; other frequent invaders in our traps were fireweed, oceanspray, and black cottonwood (*Populus trichocarpa*). If a non-native seed source is present, the vegetation of high severity patches may be more easily breached than low severity patches. Our finding provides a second explanation for the Merriam *et al.* (2006) study that showed canopy cover retention during thinning was associated with fewer non-native species in these forests. These authors contend that ground disturbance by thinning crews led to this increase in non-natives. Our findings offer a second, perhaps additive, interpretation that intact forest canopies filter the seed rain, reducing invasion. This is further supported by our finding that more severe fires (at both Fischer and Tyee fires) display more total seeds in the seed rain. Further support for this interpretation comes from Meekins and

McCarthy (2001) who found that mesic forests with more open canopies or with many edges were more vulnerable to invasion than interior forests. Certainly patch attributes in addition to seed availability and establishment are requisite for successful invasion, but seed influx must be a first step.

Researchers have reported that vegetation species richness is depressed following high severity forest fires (Turner *et al.* 1997). Our work suggests that, concomitantly with this depression in local vegetation richness, there is an increase in local and dispersed seed production and seed rain richness. The less rich post-fire vegetation might be faced with a greater influx from the seed rain species pool. In island biogeography terms, immigration rate increases (less filtering by forest canopy) at the very time that forest vegetation richness has been drastically reduced from an equilibrium number, thereby increasing risk of expansion of non-native species.

Certainly, the size of the fire must also matter. For example, Hessburg *et al.* (2007) showed that patch size distributions of low, mixed, and high severity fires in dry forests fit a negative exponential distribution. In their study, patch sizes ranged from 10^{-1} ha to 10^4 ha, with median patch sizes ranging from 50 ha to about 100 ha. Landscape mosaics patterned in this way likely presented fine to broad-scale patterns of patches, which functioned as “fences” and “corridors” to dispersal of processes, including seed dispersal. Interestingly, the seed dispersal gradients of many native species fall within similar ranges (Cain *et al.* 2000, Ness *et al.* 2004). It is likely that the pattern of fire mosaics influenced subsequent tree, shrub, and herb composition indirectly by limiting seed dispersal via burned patch size, and directly by filtering the seed rain.

ACKNOWLEDGEMENTS

We want to thank three anonymous reviewers for suggestions that greatly improved this manuscript, and for GIS analysis assistance from James Dickinson. This work was accomplished with the help of grants from the Center for Invasive Plant Management, Bureau of Land Management, The MJ Murdock Charitable Trust, and Central Washington University Science Honors Program, as well as research funds from the National Fire Plan Research Fund.

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