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Scott R. Abella
University of Nevada, Las Vegas, scott.abella@unlv.edu

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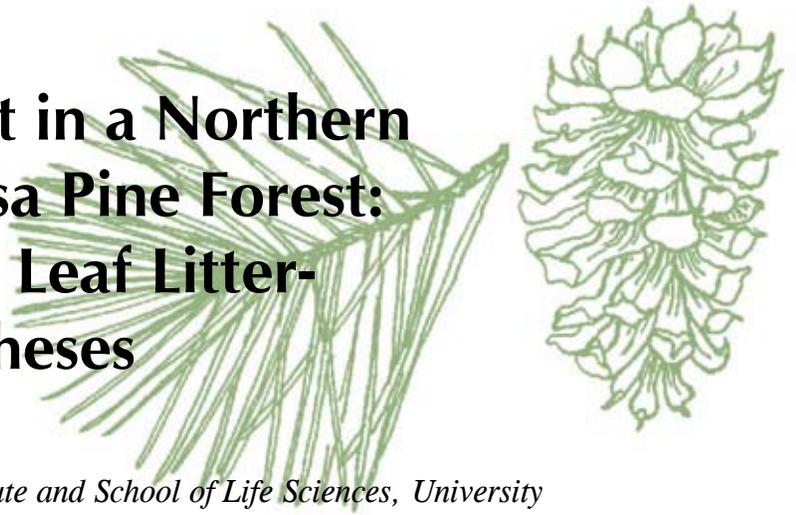
Plant Recruitment in a Northern Arizona Ponderosa Pine Forest: Testing Seed- and Leaf Litter-Limitation Hypotheses

Scott R. Abella, *Public Lands Institute and School of Life Sciences, University of Nevada Las Vegas, Las Vegas, NV*

***Abstract**—Seed availability and leaf litter limit plant establishment in some ecosystems. To evaluate the hypothesis that these factors limit understory plant recruitment in* Pinus ponderosa *forests, I conducted a seeding and litter removal experiment at six thinned sites in the Fort Valley Experimental Forest, northern Arizona. Experimental seeding of four native species (*Penstemon virgatus, Erigeron formosissimus, Elymus elymoides, *and* Festuca arizonica*) and raking of litter occurred in 2005. Seeding resulted in a substantial recruitment of 14 to 103 seedlings/m² (1 to 10/ft²) one month after seeding for two species (*P. virgatus *and* E. elymoides*), but these densities subsequently declined by 13 and 27 months after treatment to near control densities. No* P. virgatus *adults established, and seeding also did not significantly increase densities of* E. elymoides *adults. Litter removal and seeding did not interact, as seedling density on raked + seeded plots did not differ from density on seed-only plots. Consistent with a previous experiment in these forests, litter removal also had no effect on plant richness or cover. Results suggest that (i) factors other than seed availability limited recruitment of adult plants of the four seeded species, and (ii) leaf litter did not limit plant recruitment.*

Introduction

Seed availability affects many ecological processes, such as granivory (consumption of seeds by animals and insects), plant regeneration, and many processes affected by seed-based plants. Just as nutrients or other factors can limit plant growth or recruitment, seeds can be a limiting resource in plant communities. Turnbull and others (2000) define seed limitation as an increase in population sizes following seed addition. Seed limitation occurred in half of the 40 studies Turnbull and others (2000) reviewed, most of which occurred in temperate ecosystems.

Leaf litter is another factor that can limit plant establishment in some communities through several possible mechanisms. For example, litter can intercept light or interact with seeds by trapping them or forming a physical barrier to germination for seeds buried in soil (Facelli and Pickett 1991). Reducing litter can increase plant populations, possibly by stimulating germination in the soil seed bank, allowing seed rain to reach the soil, or altering microclimate.

Western United States ponderosa pine (*Pinus ponderosa*) forests, especially after disturbance, meet criteria of communities predicted to be particularly seed- and leaf litter-limited. Seed limitation is common in early successional communities (Turnbull and others 2000), which characterize these forests following tree thinning or burning. Furthermore, Vose and White (1987) found that soil seed banks at a northern Arizona ponderosa pine site were sparse (< 25 seeds/m^2 [2/ft^2]) in both burned and unburned areas. In a synthesis of 35 leaf-litter studies, Xiong and Nilsson (1999) found that effects of litter removal on plant establishment were greater in coniferous compared to deciduous forests (possibly due to differences in litter type) and in communities with large amounts of litter. Litter thickness and weight in ponderosa pine forests, particularly in densely treed forests, equal or exceed those of many world forests (Vogt and others 1986). These observations also suggest that seed addition and leaf litter could interact. Seed addition may increase plant recruitment only when litter is reduced, and litter reduction may increase recruitment only when seeds are available.

Identifying factors limiting plant recruitment can be useful for understanding the development of plant communities and their management. If seeds are a primary limiting factor, for example, seeding is likely to be a successful revegetation tool, and unsuccessful if seeds are not limiting. I conducted a seed-addition and litter-reduction experiment in a ponderosa pine forest to evaluate the following hypotheses: (1) plant population sizes are seed limited and seed addition will increase population sizes, and (2) litter removal and seeding interact, with litter removal increasing plant population sizes.

Methods

This experiment was conducted in six experimental blocks in a ponderosa pine forest in the Fort Valley Experimental Forest, 15 km (9 miles) north of the city of Flagstaff in northern Arizona, at elevations of 2,243 to 2,311 m (7,357 to 7,580 ft). The blocks, ranging in size from 13 to 16 ha (32 to 40 acres), were physically separated from one another by 0.5 to 3 km (0.3 to 2 miles). These blocks are part of an existing (1998-1999) thinning and burning ecological restoration project, with three blocks thinned by 85 percent ("1.5-3 treatment") and three blocks by 89 percent ("2-4 treatment") of pre-thinning densities detailed in Fulé and others (2001).

One site in each block was located by randomly selecting coordinates using a Geographic Information System, with the constraint that sites avoid overlying existing monitoring plots from the restoration project. At each site, four 2 × 2 m (7 × 7 ft) plots were established in a square pattern. Each plot was separated by 3 m (10 ft) from the nearest plot. One of four treatments was randomly assigned to each plot at each site: control, raking of leaf litter (Oi horizon), seeding, and raking + seeding. I performed raking treatments using a 75-cm (30 inch) wide plastic rake, removing approximately 500 to 700 g/m^2 (70 ºC oven-dry weight) of litter. The seeding treatment, performed after raking, was hand broadcast seeding of 300 seeds/m^2 (28/ft^2) of each of four native perennial species. The species included the forbs upright blue beardtongue (*Penstemon virgatus*) and beautiful fleabane (*Erigeron formosissimus*), and the C$_3$ (cool season) grasses squirreltail (*Elymus elymoides*) and Arizona fescue (*Festuca arizonica*). I standardized seeding rate by total seeds (rather than a measure like pure live seed) to avoid confounding viability and germinability of seeds with absolute total seed limitation. Emergence was 61 (beardtongue), 64 (fleabane), 88 (squirreltail), and 79 percent (fescue) after two months in greenhouse conditions described in Abella and others (2007). Turnbull and others (2000) classify this experiment as seed augmentation, because the four seeded species inhabit the study sites. With the exception of squirreltail at 51 seeds/ m^2 (5/ft^2), Korb and others (2005) found that species seeded in this experiment were sparse or absent in mineral soil seed banks at 0 to 5 cm (0 to 2 inch) depths in the study area.

I established plots, collected pre-treatment data, performed treatments, and installed granivory deterrents on August 7, 2005. Granivory deterrents (designed to reduce seed loss) were 0.5 × 0.5 m (0.25 m^2 [3 ft^2]) wooden squares, with mesh screen (7 mm [0.3 inch] openings) on top (Figure 1). I installed these deterrents in the southwestern corner of each plot and established an equally sized control area adjacent to the east. Seedling and adult (well-developed or fruiting) plants of the four seeded species were counted in granivory deterrents, controls, and whole plots 1 (September 14, 2005), 13 (September 10, 2006), and 27 months (October 28, 2007) after treatment. On whole plots before treatment and during the 2006 and 2007 post-treatment sampling, I recorded the number of species (richness) and total areal plant cover (visually categorized at 1 percent intervals to 10 percent cover, and at 5 percent intervals beyond).

Plant counts for each species were analyzed as a repeated measure, mixed model analysis of variance. Random effects were site-nested within the ecological restoration treatment (either the "1.5-3" or "2-4" thinnings) and its interactions with sample date, rake × date, and seed × date. Treatments, date, and all of their interactions were modeled as fixed effects. Cover and richness were analyzed in a mixed model analysis of covariance, with pre-treatment cover or richness as a covariate. Plant counts and percent cover were log10 transformed to meet model assumptions. Analyses were conducted using SAS (PROC MIXED; SAS Institute 1999).

Figure 1. Views at three of six sites of 2 × 2 m experimental plots containing 0.5 × 0.5 m granivory deterrents in a ponderosa pine forest, northern Arizona. The plot in the bottom right corner of (a) shows leaf litter removed by raking. Even in areas illustrated in (b) where tree canopies were open, removal of litter had no effect on recruitment of seeded species or on resident species. In (c), the densely treed area in the top of the photo represents the edge of the thinned restoration area (which covers the rest of the photo) where plots are located. *Photos by S.R. Abella, September 10, 2006 (a), and October 28, 2007 (b-c).*

Results

Plant density of seeded species averaged among sample dates was similar inside (35/m² [3/ft²]) and outside (34/m² [3/ft²]) of granivory deterrents, so density was analyzed on a whole-plot basis. Few seedlings of fleabane and fescue were detected during the experiment (0 for fleabane and 2 for fescue), so the analysis focused on beardtongue and squirreltail. Raking did not significantly affect beardtongue density or squirreltail adults and was only marginally significant for squirreltail seedlings (Table 1). In contrast, seeding strongly affected seedling density of both species. Seeding and time interacted, however, with significant declines in seedling density through time from 2005 to 2007 (Figure 2). In September 2005, one month after seeding, average density of seedlings (which were about 5 cm [2 inches] tall) on seeded plots ranged from 14 to 16/m² (1/ft²) for beardtongue and 85 to 103/m² (8 to 10/ft²) for squirreltail. However, density subsequently decreased by 6- to 8-fold (beardtongue) and 4- to 18-fold (squirreltail) to levels that did not differ from unseeded plots. No adult beardtongue plants were observed during the experiment. Adult squirreltail density did not differ among treatments.

At the plant community level, treatments had no effect on species richness (Table 1). Seeding was a significant main effect that increased cover in both posttreatment years, but there were no significant differences within the rake × seed × time level (Figure 3).

Table 1. Summary of analysis of variance results for the effects of raking and seeding treatments on seeded species recruitment and plant community characteristics in a ponderosa pine forest, northern Arizona.

Effect[a]	Plant establishment[b]				Community measures		
	df	PV sl	EE sl	EE ad	df	Richness	Cover
	——— *P > F* ———				—— *P > F* ——		
Rake	1,12	0.50	**0.04**	0.68	1,8	0.41	0.06
Seed	1,12	**<0.01**	**<0.01**	0.08	1,7	0.79	**<0.01**
Rake×seed	1,12	0.25	**0.01**	0.39	1,3	0.97	0.24
ER tmt	1,12	0.26	0.80	0.36	1,3	0.31	**0.04**
Rake×ER tmt	1,12	0.62	0.99	0.70	1,3	0.44	0.51
Seed×ER tmt	1,12	0.23	0.98	0.77	1,3	0.23	0.15
Rake×seed×ER tmt	1,12	0.99	0.46	0.29	1,3	0.97	0.09
Time	2,8	**<0.01**	**<0.01**	0.66	1,4	0.13	0.07
Rake×time	2,12	0.81	0.29	0.33	1,8	0.47	0.23
Seed×time	2,12	**<0.01**	**<0.01**	0.59	1,7	0.73	0.50
Rake×seed×time	2,12	0.97	0.86	0.93	1,3	0.76	0.69
Time×ER tmt	2,12	0.92	0.25	0.95	1,3	0.81	0.47
Rake×time×ER tmt	2,12	0.36	0.35	0.53	1,3	0.47	0.44
Seed×time×ER tmt	2,12	0.67	0.78	0.75	1,3	0.79	0.93
Rake×seed×time×ER tmt	2,12	0.42	0.21	0.88	1,3	0.23	0.67
Covariate	–	–	–	–	1,3	**<0.01**	**<0.01**

[a]ER tmt = ecological restoration treatment, serving as a blocking effect.
[b]df = degrees of freedom, PV sl = *Penstemon virgatus* (upright blue beardtongue) seedling density, EE sl = *Elymus elymoides* (squirreltail) seedling density, and EE ad = *Elymus elymoides* adult density.
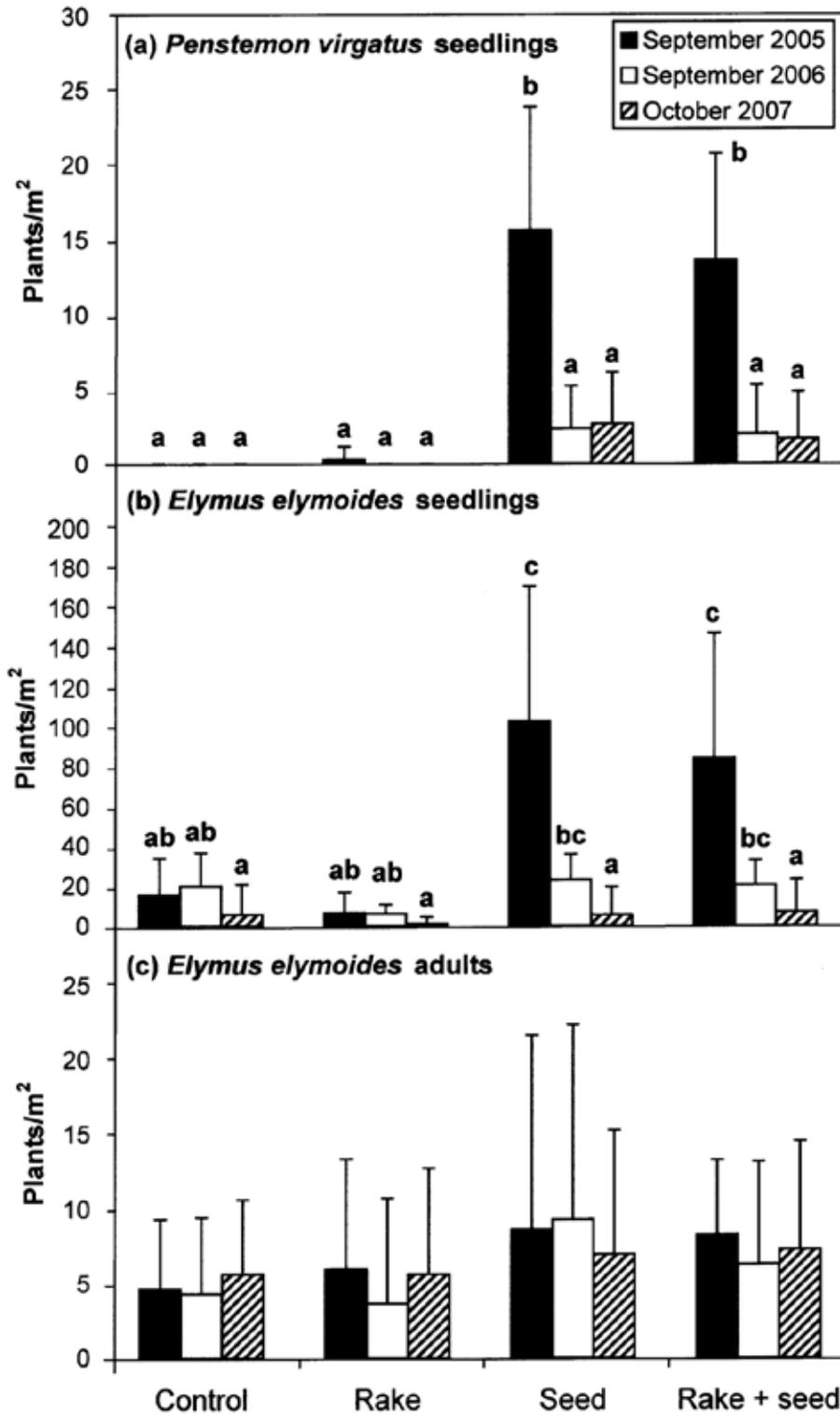
Figure 2. Mean plant densities among raking and seeding treatments 1, 13, and 27 months after treatment in a ponderosa pine forest, northern Arizona. Error bars are one standard deviation. Means without shared letters differ at $P < 0.05$ (Tukey's test).
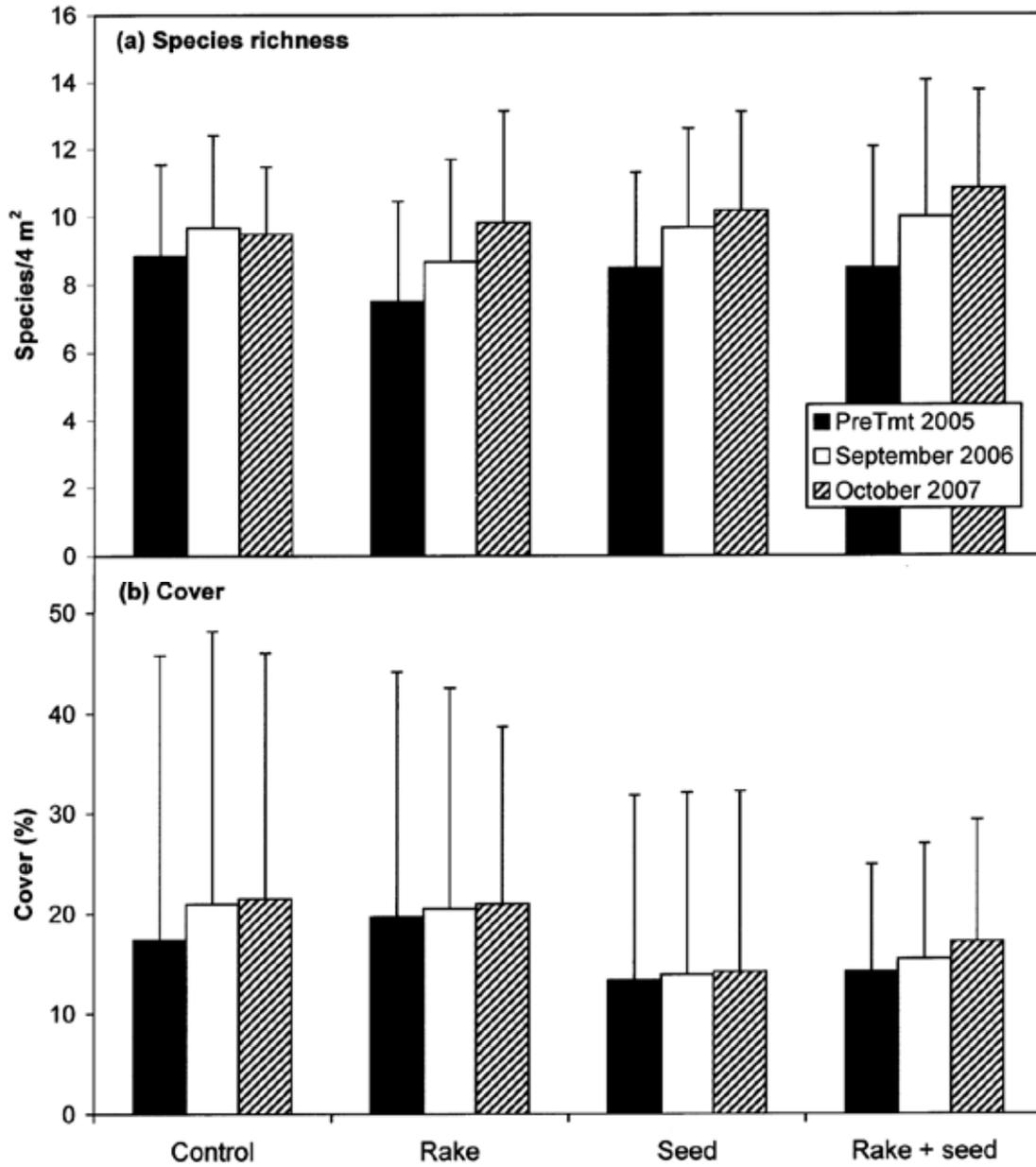
Figure 3. Mean plant community measures among raking and seeding treatments before treatment and 13 and 27 months after treatment in a ponderosa pine forest, northern Arizona. Error bars are one standard deviation.

Discussion

If plant recruitment is seed limited at either the seedling or adult stages, population sizes in these stages should increase with seed addition (Turnbull and others 2000). In this experiment, two species (fleabane and fescue) showed no evidence of seed limitation because neither seedling nor adult density increased after seeding. The remaining two species (beardtongue and squirreltail) had seed-limited recruitment at the seedling but not adult stage, as increased seedling density arising from seed addition did not increase adult density (Figure 2). The findings for beardtongue and squirreltail support the generalization that conditions for establishment of adults are stricter than those for germination (Harper 1977). However, the prediction that understories in these thinned and burned forests should be seed limited was not supported, at least for the four studied species. These species include different growth forms, and dominant (the grasses) and subordinate (the forbs) species, theoretically representing a range of potential responses to seed addition (Turnbull and others 2000). Seeding and leaf litter removal also did not interact as hypothesized, with litter removal having no effect in concordance with a previous study in these forests (Abella and Covington 2007).

Several factors associated with the experimental conditions could have affected results. Although seeds were acquired from a local northern Arizona vendor, the exact genetic origin of the seeds was not available. Seeding in August was timed to correspond with monsoon rains, but it is not known if this seeding time was optimal. However, at least some seeds probably remained on site to germinate at other times, a contention supported by the appearance of new beardtongue seedlings each year (Figure 2). Precipitation during the seeding month of August 2005 was 152 percent of normal (Fort Valley Station, Western Regional Climate Center, Reno, NV). In the summer monsoon months of July, August, and September, precipitation also was above normal in 2006 (158 percent) and 2007 (124 percent). Snowfall was below normal, however, which resulted in annual precipitation being 91 to 86 percent of normal in these years. This could have particularly affected establishment of the cool-season grasses (Clary and Kruse 1979).

Repeating the seeding with different seed sources, additional species, at different times, and within the context of a site seed budget (Vose and White 1987) may be useful for further evaluating seed availability as a potential limiting factor relative to other factors (for example, tree density, root competition). For instance, Springer and Laughlin (2004) monitored an operational seeding in northwestern Arizona ponderosa pine forests and found that 6 of 19 (32 percent) seeded species increased. This supports contentions that seed limitation is species specific, and conclusions from seed-addition studies depend on the included species (Turnbull and others 2000). An additional consideration is that I initiated my experiment six to seven years after tree thinning, and it is unclear if seed limitation changes with time since disturbance.

Acknowledgments

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