Volume 46 | Number 4 Article 15

10-31-1986

Understory seed rain in harvested pinyon-juniper woodlands

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UNDERSTORY SEED RAIN IN HARVESTED PINYON-JUNIPER WOODLANDS

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ABSTRACT.—Seed rain was collected on six paired tree harvest and undisturbed plots in singleleaf pinyon (*Pinus monophylla*)–Utah juniper (*Juniperus osteosperma*) stands. Approximately 14,600 seeds were collected during four years. Seed rain in undisturbed plots was similar to levels in mixed forest communities. Seed rain on harvest plots was similar to disturbed sites and grasslands. Seed rain levels reflect the current successional stage rather than the climax community type for the site. Seed rain increased in numbers and seed production per unit of plant cover following tree removal and especially on transition soil microsites. Only three to four of the plant species present on a site contributed greater than 10% of the total seed rain. Seed rain composition was similar on harvest and undisturbed plots (Jaccard Similarity Index Values = 47% to 67%) and explains in part the rapid reestablishment of predisturbance understory communities.

Understory response to tree harvesting is dependent upon remnant plants (Dyrness 1973, Lyon and Stickney 1976), soil seed reserves (Oosting and Humphreys 1940), and seed rain (Rice et al. 1960). Seed rain, the dissemination of seed and its dispersal, varies among species and plant communities (Harper 1977). Plant strategies in part control the amount of resources a plant commits to seed production and the impact the species has on community seed rain (Grime 1977, Everett and Sharrow 1983).

Seed rain declines exponentially with distance from the parent plant (Werner 1975, Harper 1977). But seeds are often transported across the soil surface until they lodge against protuberances or depressions (Knipe and Springfield 1972). Nelson and Chew (1977) found greatest concentrations of soil seed reserves in the Mojave Desert, adjacent to shrub canopies, and hypothesized that shrub litter areas acted as seed rain catchments. In pinyon-juniper woodlands soil seed reserves were greatest at the edge of the tree crown (Koniak and Everett 1982).

Seed rain composition changes abruptly from one year to the next in forests. This in part is due to the abrupt appearance and disappearance of species during forest succession (Oosting and Humphreys 1940) and variable annual precipitation (Duba and Norton 1976).

This paper reports on a four-year study of seed rain following tree harvesting in singleleaf pinyon (*Pinus monophylla* Torr. & Frem.)–Utah juniper (*Juniperus osteosperma* [Torr.] Little) woodlands. Seed rain was observed on three grass and annual forb understory sites for four years and three shrub and annual forb understory sites for two years. The null hypotheses to be tested were: (1) there are no differences in seed rain numbers or composition between harvest and undisturbed plots or soil microsites, (2) seed rain is evenly distributed among plant forms and reflects species composition, and (3) seed rain production per unit of cover remains constant following tree harvest. Increased seed rain following tree harvest would promote rapid establishment of understory and if related to floristic composition would increase predictability of plant response.

FIELD METHODS AND DATA ANALYSIS

Previous study sites in stands of singleleaf pinyon–Utah juniper on the Sweetwater and Shoshone mountain ranges were selected for study. The Sweetwater site lies above alluvial fans that are dominated by mountain big sagebrush (*Artemisia tridentata* Nutt. ssp. *vaseyana*) and below a ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) community. The site has an average annual precipitation of 266 mm. Fully stocked stands have a remnant mountain big sagebrush–annual forb understory. The three plots used for the study had a similar east exposure (N 70° E) but varied in elevation from 2,040 to 2,280 m.

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The Shoshone site lies between communities of higher elevation mountain big sagebrush and lower elevation Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis*). The site has an annual precipitation of 330 mm. The three study plots are on north- (N 20° E), west- (S 84° W), and south-facing (S 16° E) aspects at approximately the same elevation (2,300 m). Understory is sparse but includes perennial grasses: Idaho fescue (*Festuca idahoensis* Elmer), Sandberg bluegrass (*Poa sandbergii* Vasey), bottlebrush squirreltail (*Sitanion hystrix* Nutt.); perennial forbs: Hood's phlox (*Phlox hoodii* Rich.), hollyleaf clover (*Trifolium gymnocarpum* Nutt.); and an array of annual forbs.

The soil surface in both woodland study areas is a mosaic of soil microsites: a dense needle duff under the tree, scattered needle cover in a transition zone at the crown edge, and bare ground in the interspace between trees. These soil microsites vary in species composition and productivity (Everett 1984).

Three 30 by 30 m square plots previously clear-cut of all trees greater than 1 m in height were used at Shoshone and Sweetwater sites. Sweetwater plots were cut in 1977 and Shoshone plots in 1979. Trees and slash were removed from the sites by hand with minimal disturbance to the plots. Areas of similar floristic and topographic appearance were selected adjacent to cut areas to serve as undisturbed controls.

Shoshone plots were sampled for seed rain in the first and second years following harvest (1980 and 1981) using 12 seed traps randomly placed on four duff, four transition, and four interspace soil microsites at each of the three harvest and control plots. The study was expanded in 1982 and 1983 to include three paired harvest and control plots at the Sweetwater site (five and six years following harvest). Sampling intensity was increased to 24 seed traps in each harvest and undisturbed plot at Sweetwater and Shoshone sites in 1982.

Seed traps were emptied of seed every 2 to 3 weeks from May to October. Traps were left in the field during the winter months and inspected the following spring. A seed voucher was made for all plant species encountered on the sites. Seeds collected in the traps were compared with voucher specimens for correct identification.

Seed traps consisted of 90 mm dia. petri dishes coated inside with an adhesive (Tanglefoot[2]), as suggested by Werner (1975). Each dish had a central hole (3 mm dia.). We placed a screen (5 mm mesh) over the traps to prevent predation by rodents and inserted a nail through the screen and dish to hold the trap on the soil surface.

Differences in seed rain among harvest and undisturbed plots and among soil microsites were compared in analysis of variance tests using Hartley's Sequential method of testing to identify significant differences between means (Snedecor and Cochran 1978).

To measure plot understory cover, five permanent transects (20 m) were established in each plot. Shrub cover was estimated by line intercept (Canfield 1941). Herbaceous species cover was estimated by the Daubenmire (1959) canopy coverage method using sampling frames (50 x 50 cm) laid down at each meter mark. In addition, we centered circular sampling frames (50 cm dia.) over each seed trap and estimated plant cover of seed producing species.

Relationships between seed rain and plant cover of seed-producing species were evaluated by linear regression. Similarity between plot seed rain and floristic composition was evaluated using Jaccard Similarity Index Value (SIV) (Mueller-Dombois and Ellenberg 1974).

$$SIV = \frac{CS \times 100}{(CS + SSR + SFC)}$$

Where: CS = species common to seed rain and floristic composition
SSR = species in seed rain only
SFC = species in floristic composition only

Similarities in seed rain and floristic composition between harvest and undisturbed plots were also compared.

RESULTS AND DISCUSSION

We collected 14,676 seeds in seed traps from 1980 to 1983. Understory seed rain was

[2]The use of trade, firm, or corporation names in this paper is for the information and convenience of the reader. Such use does not constitute an official endorsement or approval by the U.S. Department of Agriculture of any product or service to the exclusion of others that may be suitable.

TABLE 1. Mean seed rain (seeds/dm²) on tree harvest and undisturbed plots.

Year	Shoshone		Sweetwater	
	Harvest	Undisturbed	Harvest	Undisturbed
	(seeds/dm²)			
1980	20.3 .05[1]	2.9	—	—
1981	35.0 .05	1.6	—	—
1982	23.9 .05	5.0	10.4 .05	1.6
1983	98.3 .05	3.9	61.9 .05	19.9

[1]Significant difference (p = 0.05) between harvest and undisturbed plots.

TABLE 2. Seed rain (seed/dm²) by community types

Seed rain	Plant community	Citation
1,000	Meadow	Mortimer 1974
115–500	Alien annuals	Duba and Norton 1976
20–98	Disturbed woodland	(this study)
24–42	Mine waste–prairie	Archibold 1980a
22	Grassland	Knipe and Springfield 1972
2–20	Woodland	(this study)
3–9	Mixed forest	Archibold 1980b

TABLE 3. Mean proportion of seed rain by plant form for Shoshone and Sweetwater sites for the study period.

	Shoshone		Sweetwater	
	Harvest	Undisturbed	Harvest	Undisturbed
	(percent)			
Annual grass	0.0	0.5^b	0.0	0.0
Perennial grass	36.8^b	59.3^a	$.9^b$	3.0^b
Annual forb	63.2^a	39.5^a	99.1^a	97.0^a

Values in the same column with different superscripts are significantly different (p = 0.05).

estimated at 1.6 to 20 seed/dm² in undisturbed stands and from 10 to 98 seeds/dm² in harvested plots (Table 1). Seed rain was always greater on harvested than on undisturbed stands. This in part explains previous findings that soil seed reserves decline rapidly from early to late successional stages (Koniak and Everett 1983). Seeds/dm² equates to millions of seeds per hectare. Undisturbed pinyon-juniper woodlands had seed rain totals similar to mixed forest communities in Canada (Archibold 1980a). These levels are lower than in other community types (Table 2). Seed rain on tree harvest sites approximates seed rain levels reported for disturbed sites and grasslands.

On the Shoshone site, plant-form composition of seed rain on harvested sites was grass 37% and forbs 63%, and on the undisturbed sites grass 59% and forbs 39% (Table 3). Seed rain on Sweetwater sites was composed almost entirely of annual forb seeds (97% to 99%) on harvested and undisturbed sites. Annual forbs produce copious amounts of seed (Biswell and Graham 1956, Archibold 1980a, b), but populations of annuals change dramatically from one year to the next (Treshow and Allan 1979). Although shrub and perennial forb species were present on both sites, their seed made up less than 1% of the seed rain. Lodging of mountain sagebrush seed stalks by snow was observed and seed dissemination may not have occurred. At both Shoshone and Sweetwater sites the proportion of annuals in seed rain declined in undisturbed stands.

Only three to five species made greater than 10% contribution to total seed rain on any site. On Shoshone plots squirreltail bottlebrush and Sandberg bluegrass each contributed 10% to 50% of the total seed rain. The annual forb *Cryptantha watsonii* (A. Gray) Greene made up 16% to 25% of total seed rain on harvest plots but only 1% on undisturbed sites. *Microsteris gracilis* (Hook.) Greene contributed to the seed rain (11% to 21%) on both harvested and undisturbed plots.

Seed rain on the Sweetwater site was dominated by an array of annual species including *Collinsia parviflora* Dougl. (7% to 54%), *Cryptantha watsonii* (0% to 22%), *Gayophytum ramosissimum* Nutt. (5% to 32%), *Gilia gilioides* (Benth.) Greene (1% to 17%), *Microsteris gracilis* (1% to 23%), and *Phacelia humulis* Torr. and Gray (2% to 20%). Archibold (1980a,b) previously reported the dominance of seed rain by annual forb species on disturbed sites.

Seed rain composition does not mirror floristic composition. Shoshone and Sweetwater sites had Jaccard Similarity Index Values (SIV) of 23% to 78% between floristic composition and seed rain (Table 4). The proportion of perennial species that contributed to seed rain (58%) was significantly less (p=0.05) than the proportion of annual species (80%). Annuals must set seed crops frequently, whereas perennials can forego seed production and still maintain a position in the plant community. SIV values were somewhat lower on the Shoshone site because of a greater proportion of perennial species (55% to 59%) than occurred on Sweetwater sites (26% to 48%).

TABLE 4. Similarity index values between seed rain and plant composition on harvest and undisturbed plots.

	1982		1983	
	Harvest	Undisturbed	Harvest	Undisturbed
		(percent)		
Sweetwater	78	71	23	65
Shoshone	29	31	39	33

Jaccard's Similarity Index Values (Mueller-Dombois and Ellenberg 1974). Maximum SIV = 100.

TABLE 5. Seed rain per dm^2 cover of seed-producing species by soil microsite.

Duff		Transition		Interspace	
Harvest	Undisturbed	Harvest	Undisturbed	Harvest	Undisturbed
		Shoshone			
$3.5^{.05}$[1]	.57	$4.18^{.05}$	.57	$3.95^{.05}$	.97
		Sweetwater			
$5.11^{.05}$	1.43	$9.14^{.05}$	.65	1.56	.27

[1]Slope (b) from regression of species seed rain on species cover significantly different ($p = 0.05$) than 0 based on t-values.

TABLE 6. Proportion of seed rain by soil microsites on harvest and undisturbed plots.

Harvested			Undisturbed		
Duff	Transition	Interspace	Duff	Transition	Interspace
		Shoshone			
28.0^b	45.0^a	26.8^b	17.0	40.5	42.8
		Sweetwater			
25.5^b	51.5^a	23.5^b	22.0	34.0	44.0

Site values in the same row with different superscripts are significantly different ($p = 0.05$).

Cover of seed-producing species adjacent to the seed traps was significantly (regression slope greater than 0) related to seed rain on harvest plot soil microsites (Table 5). Seed rain per unit area of plant cover was greater on harvested than on undisturbed plots for all soil microsites. Cover on harvested plots produced 1.56 to 9.14 seeds per dm^2 of cover, whereas undisturbed plots produced 0.27 to 1.47 seeds per dm^2 of cover. In 1983 understory cover on harvest plots (mean = 24.4%) was significantly greater ($p = 0.05$) than that on undisturbed plots (mean = 7.7%) (five of six plots). Both the quantity of understory and its ability to produce seed increased following tree removal.

Seed rain was greater on the transition soil microsite than duff or interspace in the Shoshone and Sweetwater harvest plots (Table 6). Differences in seed production among microsites were less apparent in undisturbed stands. Tree competition in undisturbed stands may reduce differences in potential understory seed production among microsites. Differences in seed rain among microsites may reflect and maintain previously described differences in understory species distribution (Everett 1984).

Similarity values for seed rain between harvested and undisturbed plots ranged from 47% to 67% for both sites in 1982 and 1983. Similarity values for floristic composition ranged from 43% to 68% during this time. Tree harvest alters understory composition, but the similarity in seed rain is likely to be a contributing factor to the rapid reestablishment of predisturbance woodland communities following tree harvest and burning (Everett 1984, Everett and Ward 1984).

CONCLUSIONS

Seed rain increased following tree harvesting. Seed rain of 10 million to 98 million seeds per hectare fell to the soil surface in harvested pinyon-juniper woodlands. On undisturbed plots seed rain was less than 20 million seeds per hectare. Increased seed rain was a result of increased plant cover and increased seed production per unit of cover. Seed rain on pinyon-juniper harvested plots had a large annual forb component as reported for other disturbed areas. Seed rain reflects the current successional stage and vigor of plants more than the climax community type.

Prediction of seed rain composition from general species floristics would be difficult. Seed rain and floristic composition were not in close agreement (SIV = 20% to 70%). The character of seed rain was determined by the relative cover of a few species producing a majority of the seed. A significant linear relationship existed for seed-producing species cover and its seed rain. But the proportion of perennial species contributing to seed rain was less than the proportion of annual species. The variability in annual populations reduces predictability of seed rain numbers and composition.

Similar seed rain composition on harvest and undisturbed plots (SIV = 47% to 70%) may in part explain the rapid reestablishment of predisturbance understory in the woodland. Reduced seed rain in undisturbed stands in part explains the previously reported decline in soil seed reserves as succession proceeds. Increased seed rain in the transition microsite reflects and perhaps maintains differences in understory distribution among soil microsites.

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