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Invasive potential of ashe juniper after mechanical disturbance

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Abstract

Reinvasion of mechanically disturbed juniper communities is possible through contributions from the soil seedbank, seed rain, and the juvenile seedling bank. We compared spatial distribution of the seedbank and seed rain of undisturbed communities to sites where trees were deliberately left as single trees, small mottes of less than 5 trees per group, or large mottes of 5–10 trees per group. Seed density in the litter layer ranged from 1,197 to 1,436 seeds m^{-2} and in the soil layer from 318 to 617 seeds m^{-2}. Seed rain ranged from 275 to 366 seeds m^{-2} over all tree arrangements. The treatment associated with single trees caused the litter layer to be removed resulting in the removal of that portion of the seedbank, consequently most seeds (>80%) were found under the canopy of mature, seed-producing trees. Soil disturbance was less severe in small and large motte arrangements, so only 65% of the soil seed bank was under mature trees. In undisturbed communities, the seed population was distributed evenly under tree canopies and in interspaces. Viability and germinability within the seedbank were low (4% and 0%, respectively). Viability of new seed was 47% and germinability was approximately 5%. The juvenile seedling bank contained a sufficient number of seedlings (408 seedlings ha^{-1}) for ashe juniper to regain dominance on the site through growth. There was no advantage to any spatial pattern of tree distribution in terms of invasive potential when fewer than 10 trees ha^{-1} were left on a site. However, when 20–50 trees ha^{-1} are left on a site, tree spatial arrangement has a significant effect on reinvasion rates.

Key Words: *Juniperus*, seed bank, seed rain, mechanical control, seedlings

The ecological and economic importance of shrub and tree dominance on semiarid rangelands in western North America is illustrated by the number of recent symposia and textbooks on the subject (Scifres and Hamilton 1993, Everett 1987). Equally evident is interest in controlling or limiting the spread and growth of "problem" trees and shrubs (MacDonald and Wissel 1991, Gonzalez 1990). One of the primary genera affecting semiarid rangelands is *Juniperus*. Roughly 16.6 million ha have been affected by the increasing range and density of *Juniperus* species in the Intermountain West (Buckman and Wolters 1987) and an additional 8.9 million ha have been affected in Texas. Mechanical (Van Pelt et al. 1990, Bozzo et al. 1992), chemical (Scifres 1980), and fire (Bryant et al. 1983, Engle and Stritzke 1992) prescriptions have been developed to control or manage *Juniperus* species but their effects typically last for only 1 or 2 decades.

Reestablishment of *Juniperus* on manipulated communities is possible from a limited number of sources. New juniper trees must originate from residual seed in the seed bank, seed rain or input after the treatment, and/or the seedling bank of juvenile trees. Episodic establishment is common in semiarid communities and a long-lived, viable seed bank may be important to allow a population to respond to episodic precipitation and other favorable establishment conditions. In light of this, considerable effort has been made to determine the effects of management strategies on the seed bank of some invasive shrub species (Zammit and Zedler 1987, Morgan and Neuenschwander 1988, Holmes 1989, Lamont et al. 1993). Seed rain from trees remaining after land clearing or from adjacent communities may direct the path of secondary succession (Olsson 1987) and is often a consideration in silviculture and revegetation plans (Smith 1962, McClanahan 1986). Many small to intermediate size islands of vegetation may be more effective at revegetating adjacent land than a few large islands (McClanahan 1986, Moody and Mack 1988, Skogland 1992) and mechanical disturbance of juniper communities typically results in a mosaic of single trees and tree mottes within a grassland. Lastly, seedling banks represent not a reinvasion but rather a population of trees or shrubs already present on the site (Harper 1977).

To better understand the reestablishment of junipers in native ecosystems, Whisenant (1991) developed a theoretical population model of ashe juniper to identify critical transition stages during the life cycle. Sensitivity analysis of his model indicated seed and seedling mortality, and seed production were the 3 most critical transition periods during the recruitment process. The objectives of our study were: 1) to identify and quantify the major source (or sources) of potential reestablishment by ashe juniper into treated juniper communities, and 2) to determine the effect of tree arrangement on the seed bank, seed production, and seed rain of ashe juniper.

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Methods

The study was conducted on the Silver Lake Ranch, (29°19'N 100°25'W; maximum elevation 730 m) located 60 km northwest of Uvalde, Texas. The research site was located on the southwestern edge of the Balcones Escarpment that forms the south and east margins of the Edwards Plateau physiographic region. The primary soils were Tarrant series which consist of very shallow dark grayish-brown to black stony soils over hard, fractured limestone. Approximately one-third to one-half of the soil surface was covered by limestone rock. Slopes were generally less than 5%. Temperatures range from a mean daily maximum in July of 36°C to a mean daily minimum in January of 4°C. Mean annual rainfall is 500 mm, with maximum rainfall occurring in May–June and September–October (Owens et al. 1995).

Ashe juniper, liveoak (*Quercus virginiana* Mill.), Texas persimmon (*Diospyros texana* Scheele), mescal bean (*Sophora secundiflora* (Ort.)DC), agarita (*Berberis trifoliolata* Moric.), catclaw (*Acacia greggii* Gray), coyotillo (*Karwinskia humboldtiana* (R.&S.) Zucc.), leatherstem (*Jatropha dioica* Cerv.), pricklypear (*Opuntia lindheimeri*), and Lindheimer senna (*Cassia lindheimeriana* Scheele) were the dominant trees and shrubs on the sites. Dominant grasses included threeawns (*Aristida wrightii L.*), red grama (*Bouteloua trifida* Thurb.), Texas wintergrass (*Stipa leucotricha* Trim. & Rupr.), and curly mesquite (*Hilaria belangeri* (Steud.)Nash).

Two study sites approximately 9 km apart were selected as replications. Both sites were mechanically treated using a combination of one-way chaining and bulldozing in March 1987. Three common tree arrangements including single juniper trees scattered across the landscape, small mottes with 5 or fewer neighbors in a group, and large mottes with 10 or more neighbors were identified within each site. Two years later in July 1989, 5 repetitions of each tree arrangement and an additional 5 repetitions of undisturbed trees in adjacent communities were located on each study site. Mottes were located on a topographic map and an individual target tree within each motte was identified with plastic, numbered ear tags for permanent identification. Female junipers with berry production were selected as the target trees. Each tree was characterized by measuring trunk diameter at ground level, canopy width in 2 directions, tree height and growth habit in July 1989.

Juniper berry production was estimated using a modified reference unit method (Holthuijzen et al. 1987). Berries on a representative unit, the number of units per branch, and the number of branches per tree were counted. The product of these 3 factors provided an estimate of berry production. Estimated and actual production on a subsample of 15 branches were measured and a regression was calculated to correct for observer bias.

The soil seed bank was sampled using a 100-cm^2 plot (10 cm × 10 cm) placed at the base of the tree, mid-way between the bole and the canopy dripline, at the dripline, and at 1-m intervals for 5-m past the dripline in July 1989. The litter layer and the top 5 cm of the A horizon were collected by coring and bagged separately. The entire sampling procedure was repeated in each cardinal direction at each tree to minimize the effects of slope. All sampling depressions were refilled with soil to prevent confounding the seed rain experiment. The extraction technique for determining seed bank size was used because juniper seeds were large enough (5 to 7 mm diameter) to be separated from soil samples by dry sieving and sorting (Brown 1992). Subsamples of 200 seeds from both the litter layer and soil were scarified and tested for viability using the tetrazolium staining technique. Additional subsamples of 500 seeds from both the soil and litter were scarified with sandpaper, placed in a growth chamber (constant 30°C, 12 hour light) on wet blotter paper, and observed weekly for 70 days to determine germinability.

Seed rain was estimated by collecting all seeds on the soil surface at the same locations used for the soil seed bank study. Samples were collected in January 1990 after the majority of seeds had fallen from the trees. All seeds were counted and a subsample of 200 seeds per treatment was used to determine viability using the tetrazolium staining technique. An additional 800 seeds were scarified and tested for germinability using the same growth chamber conditions listed above.

The juvenile juniper population was sampled in 20 randomly located transects on each replication. The 2 motte sizes of 5 or fewer and 10 or more trees were not spatially isolated so we could not identify juvenile seedling density relative to those specific tree arrangements. Seedling density was collected in chained areas (motte arrangements) and bulldozed areas (single trees). Juniper trees were considered as juveniles if they were <1-m in height and showed no signs of reproduction. Height and number of all juvenile junipers within 30-X 2-meter transects were recorded.

The seed population was analyzed as a split-split plot analysis of variance. Replication and tree arrangement were included in the whole plot, distance from the bole of the tree as the first split, and seed location (seed rain, litter or soil) as the second split. Seed density data were log transformed (log(n+1)) prior to analysis to reduce the heteroscedacity of variances (Mead 1988); square root transformations were not sufficient to normalize the residuals. All tests were conducted at $p<0.05$. Mean separation was conducted using Duncan's multiple range test when appropriate. Viability and germinability percentages were analyzed using a one-way analysis of variance. The sole independent variable was tree spatial arrangement.

Results

Tree Characteristics

Mean canopy diameter was significantly greater for trees on the single tree and undisturbed areas (564 cm, SE=23) than for trees on the small and large motte areas (438 cm, SE=19). Mean tree height was not significantly different across the spatial arrangements (407 cm, SE=11). Mean seed production was 15,364 seeds per tree (SE=1,352) across all tree spatial arrangements.

Seed Bank Characteristics

The distribution of seeds around juniper trees was not affected by tree arrangement alone, but was affected by three 2-way interactions between tree arrangement, distance from the tree, and seed location in or on the soil. Seed density in either mineral soil, litter or as seed rain was significantly affected by distance from the bole of the tree (Fig. 1). The number of seeds actually incorporated into the soil was lowest at the bole of the tree and increased significantly at both the mid-canopy and dripline locations. Density then remained constant with increasing distance from the dripline of the tree to 5 m. Seed density in the litter layer was greatest at the bole of the tree (4,780 seeds m^{-2}) and

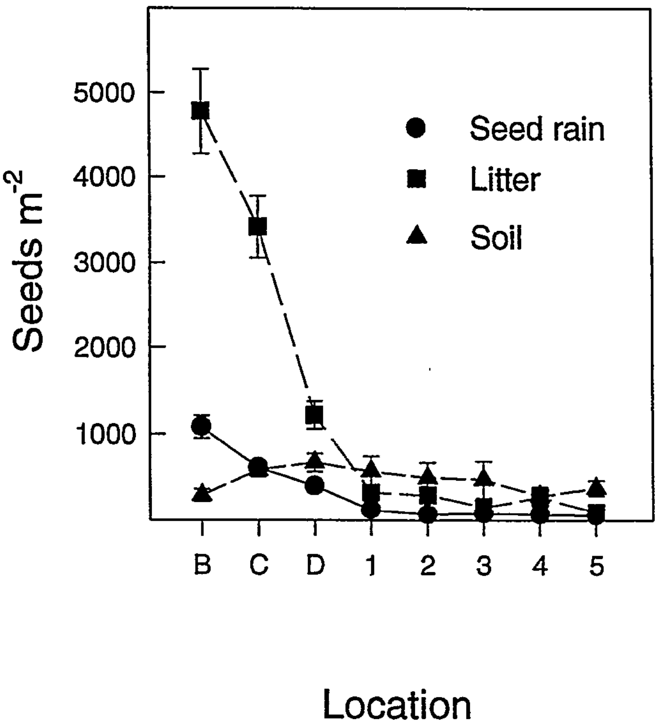

Fig. 1. Mean seed density m^{-2} on the soil surface, in the litter and in the soil at the bole (B), mid-canopy (C), dripline (D) and at 1-m intervals away from *Juniperus ashei* trees. Vertical bars represent ± 1 SE.

decreased rapidly to the dripline location (1,222 seeds m^{-2}). The litter-layer seed bank continued to decrease significantly with distance from the bole until only 97 seeds m^{-2} were found 5 m away from the tree (Fig. 1). Seed rain was concentrated under the canopy of the tree with the highest density (1,083 seeds m^{-2}) at the bole and only 123 seeds m^{-2} 1 m from the canopy edge. Seed rain decreased another 50% within 2 m of the canopy edge and remained low to a distance of 5 m.

Tree spatial arrangement and distance from the target tree also affected the distribution of seeds in the seed bank. Most seeds were located under the canopy of trees, with the greatest density at the bole and the lowest density at the dripline (Fig. 2). The interaction between tree arrangement and distance from the bole was apparent at locations not under tree canopies. Seed density was greater for the large and small mottes at the 1 to 3-m distances than for the other tree arrangements. Seed density at locations not under the tree canopy was always significantly lowest for the single trees.

Seed Viability and Germinability

Four percent of the soil seed bank (8 seeds from 200 tested) was viable. About 38% of the seeds were desiccated and decayed to the extent that they crumbled when handled. Of the 1,000 seeds tested for germinability, no seeds germinated during the 70-day observation period. There were no significant differences in viability or germinability for seeds in the litter layer or the mineral soil.

Almost half (48%) of the seeds present from the current year seed rain were viable according to the tetrazolium tests. After scarification, only 5% of the seeds germinated during the 70-day observation period. Viability and germinability were not significantly affected by any of the tree arrangements.

Juvenile Seedling Bank

There were no significant differences in the density of juvenile seedlings between replications. Mean density was 408 seedlings ha^{-1} (SE = 118) with a mean height of 23.5 cm (SE = 5). Density of juvenile plants was also not significantly affected by the type of mechanical clearing. Mean density in the one-way chained area was 556 ha^{-1} (SE = 234) and in bulldozed area was 317 ha^{-1} (SE = 96).

Invasion Potential

A simple model of potential invasion was developed using the residual seed bank, seed rain, viability and germinability data for each of the tree arrangements. The actual ground area of each concentric ring representing the distance from the bole of the tree was calculated based on average sized mature juniper trees. A density of 50 reproducing trees ha^{-1} in mature native communities was assumed for modelling purposes. At this assumed density, the small and large motte arrangements affected significantly less area than either single trees or native communities (Fig. 3). When 20 to 50 trees were left on the site, spatial arrangement of single trees yielded approximately 30% more land area affected by seed rain than the same number of trees in either small motte or large motte arrangements. When only 10 trees ha^{-1} were left on the site, there were no differences in land area affected between the 3 tree patterns.

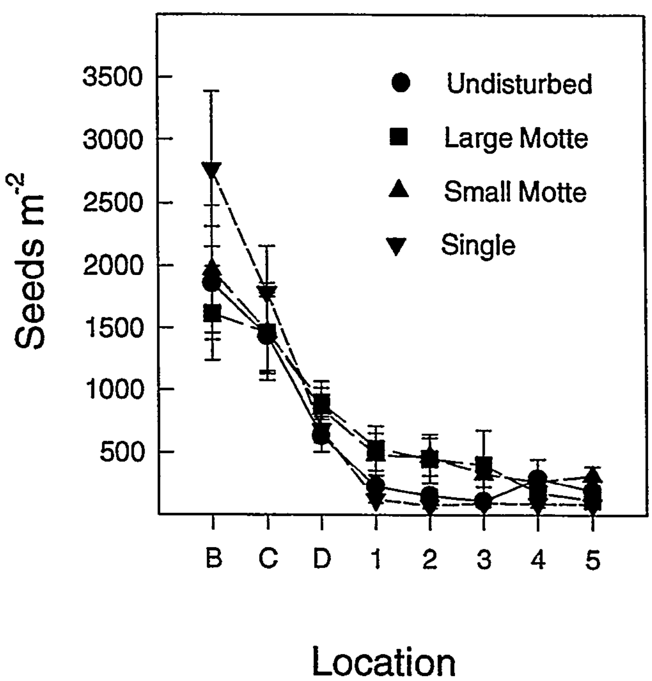

Fig. 2. Mean seed density m^{-2} around individual trees at the bole (B), mid-canopy (C), dripline (D) and at 1-m intervals away from *Juniperus ashei* trees. See the text for treatment descriptions. Vertical bars represent ± 1 SE.

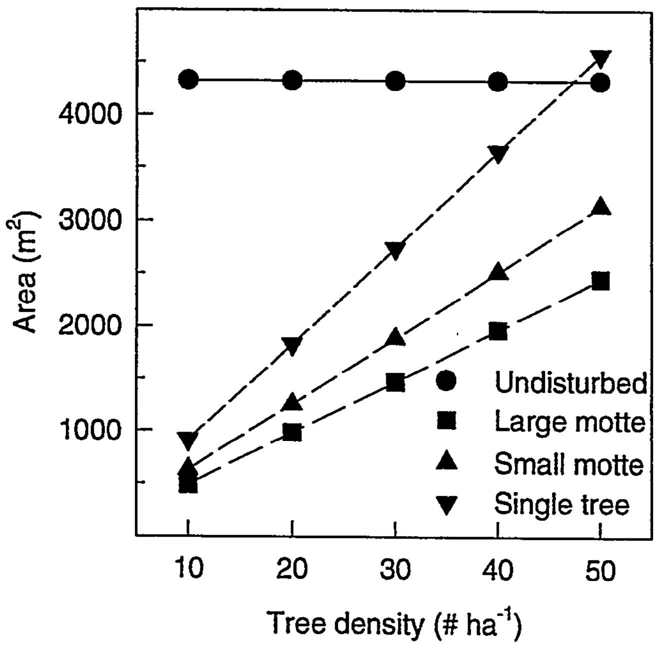

Fig. 3. Predicted area affected by seed input by increasing tree density from 4 different spatial arrangements of trees. See the text for a description of the spatial arrangements.

Table 1. Mean (S.E.) seed density of *Juniperus* seeds on the soil surface, in the litter and in mineral soil surrounding trees in 4 spatial arrangements.

	Tree arrangement							
	Undisturbed		Large Motte		Small Motte		Single Trees	
	(No. m^{-2})							
Surface	301	(54)	306	(43)	275	(40)	366	(74)
Litter	1221	(226)	1197	(204)	1437	(254)	1424	(302)
Soil	318	(65)	618	(141)	593	(92)	347	(40)

Discussion

Juniper seed is covered with a large fleshy fruit or berry typically associated with vertebrate dispersal (Howe and Smallwood 1982) and is a staple in the winter diet of frugivorous birds in both Europe (Jordano 1993) and in the United States (Holthuijzen et al. 1987, Chavez-Rameriz 1992). Robins (*Turdus migratorius*) and cedar waxwings (*Bombycilla cedrorum*) are the predominant avian consumers of ashe juniper berries and may account for substantial dispersal on a local scale (Chavez-Rameriz 1992). Although these birds were observed in our study area, they did not harvest seeds from any of our target trees. The total number of seeds estimated using the seed rain data and the land area affected around trees or mottes of trees accounted for nearly all the annual seed production estimated for individual trees. Furthermore, the fleshy berry was intact on all seeds found in the seed rain experiment, suggesting that vertebrate dispersal had not occurred. Since these birds feed on the seeds while still on the tree rather than after they fall on the ground (Chavez-Rameriz 1992), avian dispersal seems to affect only a small portion of the available seed crop. The decreased importance of avian dispersal would most likely result from either: 1) the recent increase in the density of ashe juniper on the Edwards Plateau and a satiation of the bird population; or 2) the highly variable density of avian predators between years (Taylor, pers.com.). Almost all of the annual seed crop was, therefore, dispersed close to the mature plant.

The reservoir of viable seeds in the litter and mineral soil was immense (Table 1). In every tree arrangement, there were more than 95,000 seeds in the seed bank yielding 3,767 viable seeds which could potentially replace the single mature tree. The density of germinable seeds was much less, however, since germinability under the test conditions was 0% in the litter and mineral soil. In our trials 0 seeds germinated from the 1,000 tested, but a germinability rate of even 1 in 10,000 would contribute substantially to a new juniper community. Blomquist (1990) reported a similar low viability and germination rate for ashe juniper seeds on the Sonora Experiment Station in Texas.

Density of germinable seeds on the soil surface ranged from 284 seeds in the small motte groups to 495 seeds around the single trees (Table 2). These seeds were not protected from avian predation by being incorporated into the litter and mineral soil, so post-dispersal predation could reduce the number of available seeds (Auld 1986, Keeley 1987).

Seeds in the seed bank were concentrated under the canopy of mature plants in all the manipulated tree arrangements. The treatment associated with single trees removed the litter layer, resulting in the removal of that portion of the seed bank, consequently most seeds (>80%) were found under the canopy of the mature, seed-producing trees and only 5% of the seed bank was found as far as 5 m from the edge of the canopy. Soil disturbance was less severe in the small and large motte arrangements so only 65% of the soil seed bank was under mature trees. In undisturbed communities, the seed population was distributed evenly under the

Table 2. Mean density of viable and germinable *Juniperus* seeds on the soil surface, in the litter layer and in mineral soil surrounding trees in 4 spatial patterns.

	Tree Arrangement							
	Undisturbed		Large Motte		Small Motte		Single Trees	
	Viable	Germinable	Viable	Germinable	Viable	Germinable	Viable	Germinable
	(seeds m^{-2})							
Surface	7,720	386	5,891	294	5,691	284	9,923	495
Litter	2,560	0	1,865	0	2,277	0	2,583	0
Soil	1,176	0	1,755	0	1,646	0	1,207	0

tree canopies and in the interspaces. Tree spacing in the untreated community was closer than 5m and this tree density was characterized by an increased density in the seed bank at the 4- and 5-m intervals. Seed density increased at these points because seeds could have come from more than 1 tree.

Spatial arrangement of trees can affect reinvasion rates of treated juniper communities. If residual density of trees is greater than 20 trees ha^{-1}, then leaving trees in groups of 5 or 10 to create islands of juniper mottes will result in a lower potential invasion rate than leaving the same number of trees as randomly distributed single trees. The single trees serve as satellite foci for the invasion process, which increases the rate of spread for the population (Moody and Mack 1988). Leaving trees in mottes reduces the distribution of seeds into the interspace regions so potential invasion is lower. Post-dispersal seed predation and movement were not investigated in this study so it is possible that an unknown number of seeds may be redistributed by either vertebrates or invertebrates. These seeds may be placed in microsites which favor establishment (Chavez-Rameriz 1992) or they may be placed in areas where establishment is impossible (Auld 1986).

The juvenile seedling bank represents a major potential source of juniper reinvasion of mechanically disturbed sites. The seedling bank consists of trees of unknown ages that have been suppressed under the canopy of mature juniper trees and as such are already established and only have to grow to regain dominance. Within the areas containing the small and large mottes, seedling density approached the density of mature trees in undisturbed communities. Smeins (1990) reported 766 trees ha^{-1} as the average density of ashe juniper trees in an undisturbed exclosure on the Edwards Plateau whereas the density on the one-way chained area was 555 trees ha^{-1}. The seedling bank on the areas containing the single trees was much smaller at 316 trees ha^{-1}, but still represents a major source of plants for the reinvasion process.

The seed bank of *Juniperus ashei* is immense but has a very low viability and germinability. Seed rain is concentrated under canopies of existing trees with only 5% of the seed being found 5m from the tree. The spatial arrangement of trees left on a site into single trees, small mottes or large mottes can significantly affect the invasion rates. Trees which are left in groups affect less total area per tree than the single trees. Lastly, the juvenile seedling bank contains a sufficient number of seedlings for ashe juniper to regain dominance in the community simply through growth of juvenile plants. Successful, long-term management of ashe juniper populations is unlikely without considering both the input of new seed and reduction of the seedling bank.

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