Seed Dynamics of Eastern Redcedar in the Mixed-Grass Prairie

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ABSTRACT—We sampled the soil seed bank underneath and surrounding eastern redcedar (*Juniperus virginiana* L.) trees at two mixed-grass prairie sites in Nebraska. Our objectives were to investigate the seed bank for seed number and seed viability in various directions and distances from individual trees. Additionally, we planted seeds to determine seed longevity and viability in the soil seed bank. Six female trees were selected at each site. At each tree, 16 soil samples were collected using a 10 x 10 cm quadrat at four distances (inside the canopy and 0.5, 2, and 5 m from the canopy) in each of the cardinal directions. Seeds were counted and viability tested using 1% 2,3,5-triphenyltetrazolium chloride. We found that most seeds were recovered inside the canopy, and seed numbers rapidly declined as distance from the canopy increased. Seed recovery and viability over time decreased, with an average of only 3% of the potential seeds recovered. Our results indicate that eastern redcedar recruitment does not rely on long-term accumulation of seeds in the soil seed bank.

Key Words: eastern redcedar, Great Plains, *Juniperus virginiana*, soil seed bank

Introduction

Eastern redcedar (*Juniperus virginiana* L.) is a native, early successional, non-resprouting evergreen that occurs from the Great Plains to the East Coast and is found in every state east of the 100th meridian (Fowells 1965; Van Haverbeke and Read 1976). It is a prolific seed producer, with seeds ripening in the first season of seed development (Fowells 1965). Seeds of eastern redcedar are primarily avian dispersed, which may contribute to its rapid expansion into grasslands (Holthuijzen and Sharik 1985).

Eastern redcedar has expanded its range from fire-protected areas to adjacent grasslands (Fowells 1965; Owensby et al. 1973). In old fields and pastures of the eastern US, eastern redcedar will establish in the absence of disturbance and eventually be replaced by late-successional hardwoods (Oosting 1942; Fowells 1965). The absence of disturbance (i.e., fire and grazing) in the Great Plains also can lead to the establishment and expansion of eastern redcedar (Arend 1950; Bragg and Hulbert 1976; Bragg 1995; Seig et al. 1999). However, without disturbance in these grasslands, eastern redcedar essentially halts succession and develops an eastern redcedar forest (Owensby et al. 1973). For example, eastern redcedar canopy cover increased 2.3% per year in portions of the Kansas Flint Hills, resulting in a closed cedar canopy in only 40 years (Briggs et al. 2002).

The negative ecological implications of increased eastern redcedar densities on grasslands include reduced aboveground herbaceous biomass production (Engle et al. 1987; Smith and Stubbendieck 1990; Gehring and Bragg 1992), decreased plant diversity (Hoch and Briggs 1999), reduced understory plant canopy cover (Gehring and Bragg 1992), and an altered herbaceous plant community shifting from warm-season (C_4) to cool-season (C_3) plants (Gehring and Bragg 1992). A potential benefit of increased eastern redcedar is carbon storage (Norris et al. 2001). However, this may not outweigh the negative ecological implications of increased eastern redcedar.

Because eastern redcedar has become a serious ecological problem in the Great Plains, understanding its seed dynamics and establishment from the seed bank can help manage recruitment and eventually reduce expansion. Many grasses, forbs, and woody plants rely on their seed to accumulate in the soil seed bank until environmental conditions are optimal for germination and establishment (Thompson and Grime 1979; Thompson 1987). Although eastern redcedar is a prolific seed producer in the eastern US, seeds did not accumulate in the soil seed bank (Holthuijzen and Sharik 1984). The difference in successional patterns from the eastern US, where hardwoods replace eastern redcedar, to the Great Plains, where eastern redcedar can become the dominant woody plant, led us to investigate eastern redcedar seed dynamics in the Great Plains. It has been observed that eastern redcedar predominantly establishes on north-facing slopes (Ortmann 1995), which may influence the seed bank. We investigated the soil seed bank dynamics under and around eastern redcedar trees to determine if viable seeds accumulate in the seed bank. Understanding the viability and longevity of seeds in the soil seed bank will help explain its successional response in the center of the Great

Figure 1. Eastern redcedar in loess hills at the research site south of North Platte, Lincoln County, Nebraska. Photo by James Stubbendieck.

Plains and the western edge of eastern redcedar distribution. Specifically, we investigated the number of seeds in the seed bank and the viability of those seeds in various directions and distances from individual trees. Additionally, we planted seeds to determine the longevity and viability of seeds in the seed bank.

Methods

Study Areas

We conducted two studies at two sites in the mixed-grass prairie. The first site was located in Thomas County, southwest of Halsey, NE (41°N, 100°W). Soils at this site are mixed, mesic Typic Ustipsamments (Sherfey et al. 1965; Bowman et al. 1978). The second study site was in Lincoln County, southwest of North Platte, NE (40°N, 100°W) (Fig. 1). Predominant soils at this site are fine-silty, mixed (calcareous), mesic Typic Ustorthent (Bowman et al. 1978). Long-term average annual precipitation for both sites is about 500 mm, with most precipitation occurring during the growing season from

April to October (Sherfey et al. 1965; Bowman et al. 1978; NOAA 1990). The frost-free period for both sites is 152 days (Bowman et al. 1978). The vegetation is similar at both sites and consists of typical Sandhills vegetation. The dominant grasses are prairie sandreed [*Calamovilfa longifolia* (Hook.) Scribn.], sand bluestem (*Andropogon hallii* Hack.), sand lovegrass (*Eragrostis trichodes* Nutt.), little bluestem [*Schizachyrium scoparium* (Michx.) Nash], hairy grama (*Bouteloua hirsuta* Lag.), and needleandthread [*Hesperostipa comata* (Trin. & Rupr.) Barkw.]. Other dominant plants are western ragweed (*Ambrosia psilostachya* DC.), plains sunflower (*Helianthus petiolaris* Nutt.), soapweed (*Yucca glauca* Nutt.), and prairie rose (*Rosa arkansana* Porter) (Weaver and Albertson 1956).

Experiment I

We randomly selected six female trees bearing cones to determine the number of eastern redcedar seeds in the seed bank at each site. Transects were established from the base of each tree in the four cardinal directions. Four quadrats (10 x 10 cm) were placed along each transect at four distances (under the canopy halfway between the trunk and canopy edge, and 0.5, 2, and 5 m from the canopy edge) to sample the soil seed bank. Quadrats were randomly placed at each sample point either right or left of the transect and placed either 30 or 60 cm from the transect. Soil was excavated to a depth of 5 cm within each quadrat in May 1989, November 1989, May 1990, and November 1990. Soil and organic material was removed from the seeds using a series of four screens. Seeds were placed in an air column to remove any remaining soil particles and were stored for no longer than 21 days at 5°C. Viability was tested on 25 randomly selected seeds from each excavated quadrat. Seeds were soaked in distilled water for 18 to 24 hours to soften the seed coat. Each seed was cut beside the embryo and stained using 1% 2,3,5-triphenyltetrazolium chloride to determine seed viability (Ulvinen 1973).

Experiment II

We conducted a seed recovery experiment to determine the longer-term (more than one growing season) viability of eastern redcedar seeds in the soil seed bank. Seeds were hand-collected from trees at a site located halfway between Halsey and North Platte, NE. To facilitate germination, seeds were stratified using a cold-moist stratification method (Schopmeyer 1974) be-

fore being planted at each site. Three 1.0 x 1.5 m plots were located on areas devoid of eastern redcedar on each of three aspects, (1) north-facing slopes, (2) south-facing slopes, and (3) flat or no measurable slope. Plots were enclosed with woven-wire fence to restrict movement of small mammal and avian predators in areas not grazed by livestock. Seeds were planted in 1.5-m-long rows spaced 10 cm apart. Four stratified seeds were planted at each sample point on two dates, May 1989 and May 1990. One row from each plot on each of the three aspects was randomly selected in July and October 1989 and seeds excavated from the 15 sample points, with 60 seeds potentially recovered. In 1990 and 1991, one row from each plot of seeds planted in 1989 and 1990 on each of the three aspects was randomly selected in May, July, September, and November. Eastern redcedar seeds were cleaned of soil and organic matter and tested for viability using the techniques described in Experiment I.

Data Analyses

Both experiments were designed as randomized block designs with site being the blocking factor. There were no site differences, so data were combined. The variables measured in Experiment I were the number of seeds in the seed bank and seed viability, which were analyzed by distance from the canopy in the four cardinal directions over time. In Experiment II, the variables measured were the number of seeds recovered and the viability of those seeds on three aspects over time. Variables for both experiments were analyzed using analysis of variance and the means were separated using least significant difference (Littell et al. 1996). All significant interactions or main factors are reported at $P \leq 0.05$.

Results and Discussion

Eastern redcedar seeds did not appear to accumulate in the soil outside the canopy, and seeds did not remain highly viable in the seed bank for an extended time. These results are similar to eastern redcedar seed dynamics in the eastern US (Holthuijzen and Sharik 1984; Holthuijzen and Sharik 1985). Although eastern redcedar produces large quantities of seed (Holthuijzen and Sharik 1985), most of the seed falls inside the canopy, with seed viability being low and variable (Holthuijzen and Sharik 1984). Even with low seed viability, if the seeds were to remain inside the canopy, seedlings would compete for resources. These data dispel two commonly held notions in the

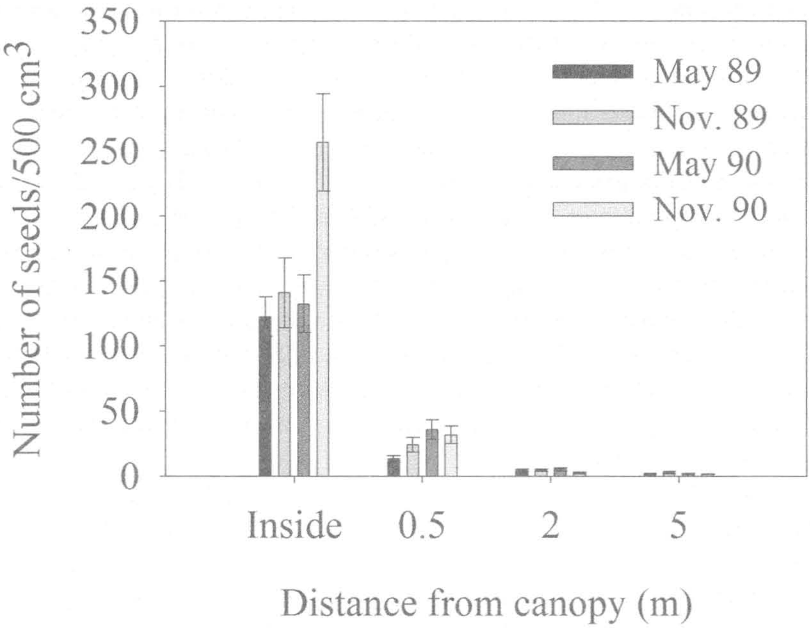

Figure 2. Number of eastern redcedar seeds in the seed bank by date (May 1989, November 1989, May 1990, and November 1990) as distance from the canopy increases.

Great Plains. The first is that following removal from the landscape, eastern redcedar reestablishment beneath old canopies relies on the accumulation of multiple seed crops in the seed bank. The second is that multiple seed crops are dispersed across the landscape and wait for appropriate environmental conditions to establish. Our data indicate that most seedling recruitment depends on seeds from the current year's seed crop. Seed viability was variable, but the overall trend was that of decreasing viability over time. Consequently, we expect that seeds in the soil are not significantly contributing to eastern redcedar expansion because viable seeds did not accumulate beyond the canopy.

Experiment I

There was no date x distance x direction interaction for the number of eastern redcedar seeds excavated from the soil seed bank. However, there

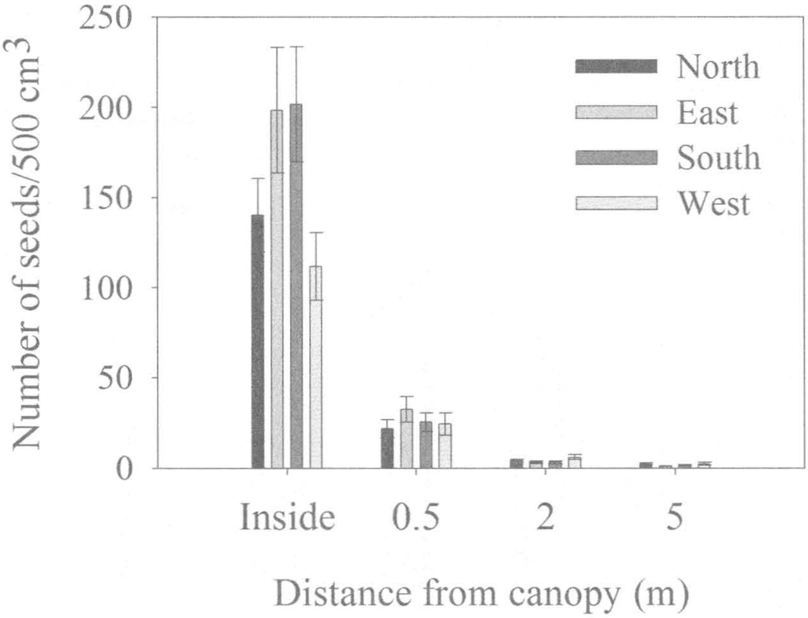

Figure 3. Number of eastern redcedar seeds in the seed bank by direction (north, east, south, and west) as distance from the canopy increases.

were date x distance and direction x distance interactions for the number of seeds recovered in the seed bank (Fig. 2). The greatest number of seeds recovered was found inside the canopy, and the number of seeds in the seed bank declined as distance from the canopy increased. The sample date with the most seeds recovered inside the canopy was November 1990. Inside the canopy, the directions that had the greatest numbers of seeds were east and south (Fig. 3). The annual prevailing wind at North Platte, NE, is from the northwest (NOAA 1998) and may explain why the most seed was found on the east and south sides of the trees. Although eastern redcedar does not rely on wind for long-distance seed dispersal based on seed morphology, wind can affect seed deposition near the canopy.

No interaction between date x distance x direction was detected for eastern redcedar seed viability in the seed bank. There was a date x direction interaction, but seed viability did not appear to depend on the direction the seed was deposited from the tree or time of year the seed was recovered

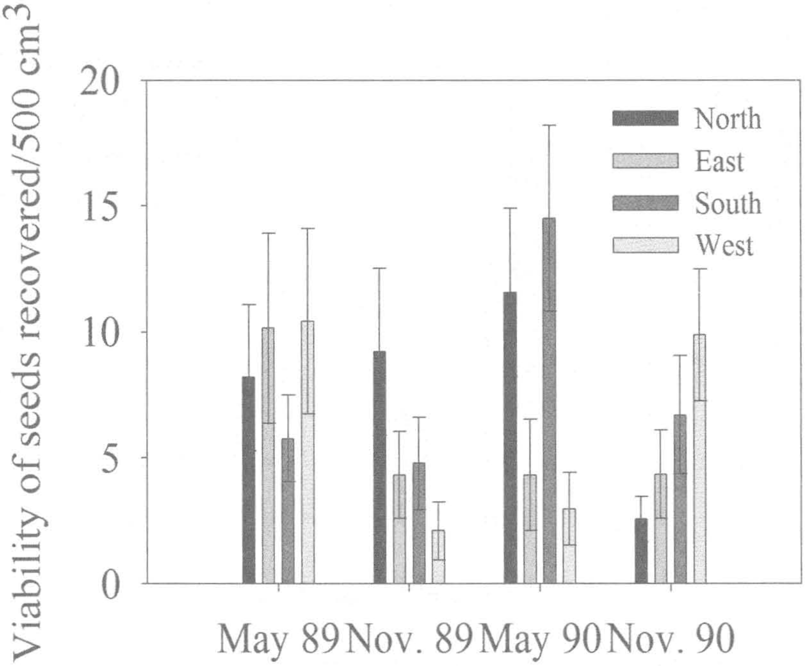

Figure 4. Seed viability (%) of eastern redcedar seeds by direction (north, east, south, and west) for May 1989, November 1989, May 1990, and November 1990.

(Fig. 4). This indicates that seed viability may not be sensitive to certain microclimate environments. The main factor of distance was significant for seed viability. Seed viability was greatest 0.5 m from the canopy edge (Fig. 5).

The greatest numbers of seeds were found inside the canopy. As distance from the tree increased, the number of seeds in the seed bank decreased. Similarly, in the eastern US, as distance from the eastern redcedar canopy increased, the number of seeds in the seed bank decreased, with few seeds recovered greater than 6 m from the seed source (Holthuijzen et al. 1987). Seed distribution beyond the canopy relies primarily on avian dispersal in the eastern US (Holthuijzen et al. 1987; Joy and Young 2002). Therefore, dispersal of seed from the source would reduce seed accumulation near the canopy.

Precipitation is an important component in determining the amount of annual seed production. However, *Juniperus* species can intercept from 25%

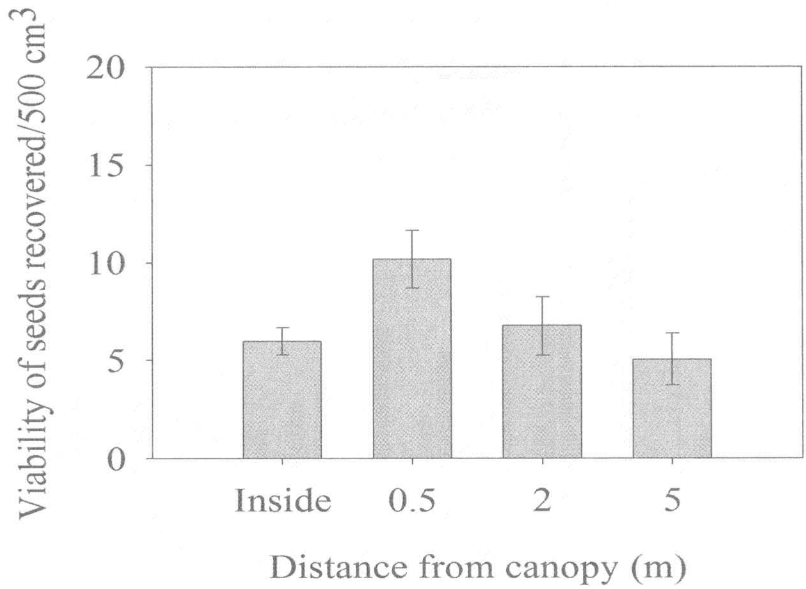

Figure 5. Seed viability for eastern redcedar seeds averaged over direction and date for inside the canopy and 0.5, 2, and 5 m from the canopy edge.

to 40% of the precipitation in their canopies (Skau 1960; Thurow and Hester 1997). The most seed recovered inside the canopy occurred in November 1990. Above-average precipitation during a portion of the growing season may explain the increased seed recovered inside the canopy at that sample date. We suspect that at 0.5 m from the canopy, moisture would be adequate for seedling establishment, as compared to inside the canopy, where precipitation is intercepted, and greater than 2 m from the canopy, where the lack of protection would lead to desiccation of the seeds. The few seeds found beyond the canopy would be subjected to microclimatic variations that could possibly influence seed accumulation or lack thereof in the seed bank.

Experiment II

The aspect (north-facing, south-facing, or no discernible slope) on which seeds were planted had no influence on the number of seeds recovered or viability of those seeds. Therefore, the number and viability of seeds recovered were averaged over the three aspects. Less than 10% of the seeds

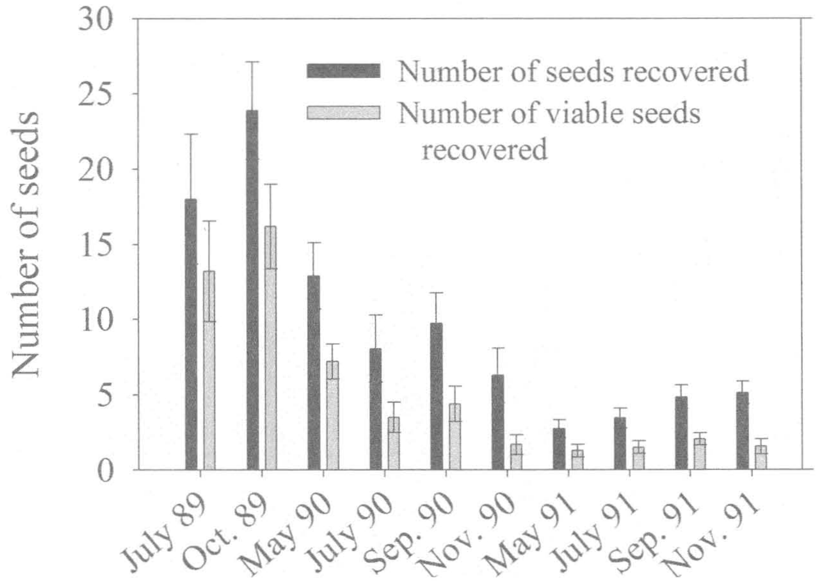

Figure 6. Eastern redcedar seeds recovered and number of viable seeds recovered from seeds planted in May 1989.

planted in 1989 were recovered 28 months later (Fig. 6). The number of viable seeds recovered also decreased over time, with less than half of the seeds recovered being viable at the conclusion of the study. The number of seeds recovered decreased from 18 in July 1989, to five in November 1991, and the number of viable seeds recovered decreased from 13 in July 1989 to two in November 1991. Consequently, only 3% of the seeds planted in 1989 were capable of germinating 28 months after planting.

Of the 60 seeds planted in each row in 1990, only four seeds were recovered in July 1990 and two seeds in November 1991. The mean number of viable seeds recovered was two in July 1990 and one in November 1991 (Fig. 7). The position on the landscape did not influence eastern redcedar seed recovery or seed viability. Instead, time appeared to be the greatest factor influencing seed dynamics.

Eastern redcedar seeds recovered from different aspects (north-facing, south-facing, or no discernible slope) did not differ in viability. Away from eastern redcedar canopies, there appeared to be no advantage for seeds to occupy certain landscape positions. One constant among planted seeds in

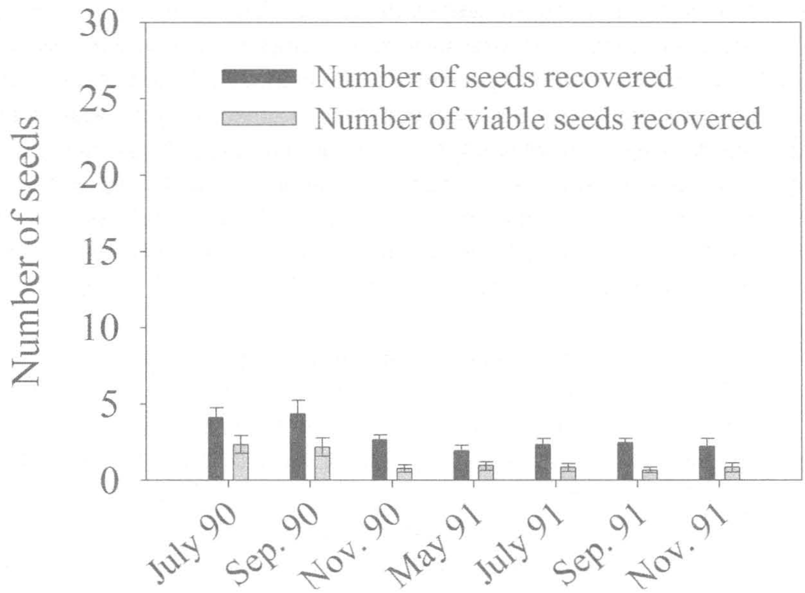

Figure 7. Eastern redcedar seeds recovered and number of viable seeds recovered from seeds planted in May 1990.

both years of the study was a low recovery rate. Even though seeds were protected from predation, only 3% of the potential number of seeds was recovered after 18 months. Birds and small mammals were excluded from the plots, but there may have been seed loss through insect herbivory or seed decomposition. Therefore, accumulation in the seed bank does not appear to be a reliable recruitment mechanism for eastern redcedar in the mixed-grass prairie. Similar results were found in the eastern US, where it was determined that eastern redcedar does not accumulate in the seed bank (Holthuijzen et al. 1987). Even though eastern redcedar occurs in different ecosystems from the East Coast to the Great Plains, seed dynamics appear to be similar.

Conclusions

Fragmentation of the landscape and removal of disturbance contribute to the expansion of eastern redcedar into grasslands (Owensby et al. 1973; Coppedge et al. 2001; Briggs et al. 2002). Eastern redcedar has become a

problem with both economic and ecological consequences (Briggs et al. 2002). Planting eastern redcedar in windbreaks as a conservation practice has also contributed to this expansion (Briggs et al. 2002). To reduce future eastern redcedar seedling recruitment, it becomes necessary to remove female cone-bearing trees when implementing eastern redcedar management. Annual seedling recruitment of eastern redcedar appears to be dependent on the current year's seed production and avian dispersal, not on the seed bank. Theoretically, eastern redcedar population expansion should cease after the seed source has been removed.

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