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Effects of litter, distance, density and vegetation patch type on postdispersal tree seed predation in old fields

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Because the fate of seed rain is critical to understanding the invasion of old fields by trees, we investigated spatial and temporal variation and difference among six tree species in seed predation. Very few *Juniperus virginiana* seeds were lost to predation but predation for all other test species was reduced by additions of *Quercus* litter and *Solidago* litter. *Carya tomentosa* seed predation was also reduced by increasing distance from the forest edge. In addition to litter and distance effects, differing starting densities of *Acer rubrum* seeds significantly affected predation rates but *Fraxinus americana* rates were not affected. Also, predation was greater under patches of woody vegetation compared to herbaceous patches. All results show spatial variation. Temporal variation was implied when, with increasing age of old field (from 7 to 17 years since abandonment), seed predation increased and the order of decreasing seed preference changed from *Acer, Cornus florida, Carya, Quercus rubra, Fraxinus* and *Juniperus* to *Quercus, Acer, Fraxinus* and *Carya*. Overall, for tree seeds in old fields, litter, distance to forest edge and starting density affect predation rates, there is less predation in herbaceous patches compared to woody patches and the amount of predation increases and the order of seed preference changes with increasing old field structure.

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Because woody plants are the compositional and structural dominants during most of old field succession in the eastern United States (Oosting 1942, Bard 1952) and are functionally significant throughout (e.g. as perches, see McDonnell and Stiles 1983), the dynamics of their invasion and establishment is critical to an understanding of old field succession. Seeds of common tree species in New Jersey old fields have short viability (Schopmeyer 1974) and do not contribute to a persistent old field seed bank (Oosting and Humphreys 1940, Livingston and Allessio 1968). This implies that establishment comes from dispersed seed and the fate of seed rain is critical in determining invasion dynamics, rate of succession and growth, and spatial distribution of trees.

Post-dispersal seed predation is an important mechanism determining seed survival in a variety of communities (e.g. tropics, deserts, steppes, grasslands; Janzen 1971, O'Dowd and Gill 1984, Schupp 1988a, b) and is critical for regeneration in eastern deciduous forests and invasion of old fields (Mittelbach and Gross 1984, Gill and Marks 1991). Past studies have shown that seed predation differs between species (Mittelbach and Gross 1984), decreases with distance from seed source (Janzen 1970, Clark and Clark 1984, Howe et al. 1985, Coates-Estrada and Estrada 1988, Schupp 1988a, Sork et al. 1988) and increases with increasing structure and greater composition of vegetation (Thompson 1982, Casper 1987). Seed predators prefer certain microhabitats over others and therefore seed predation is often spatially heterogeneous (Thompson 1982, Sork 1983, Mittelbach and Gross 1984, Louda and Zedler 1985, Webb and Willson 1985, Casper 1987, Schupp

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1988a, b). In addition, predation may be seed density-independent (Mittelbach and Gross 1984, Webb and Willson 1985) or seed density-dependent (Casper 1987, Sork et al. 1988) depending on the foraging behavior of the seed predators (Reichman and Oberstein 1977).

Seed predation is also influenced by changes in the type and density of litter (Price and Jenkins 1986, Schupp 1988b). Litter is one of the dominant features of the microhabitat of tree seeds in old fields after dispersal, and interactions between litter and old field plants (Monk and Gabrielson 1985) are potentially complex and contrasting (Facelli and Pickett 1989). Litter may decrease seed survival by increasing fungal growth (Shaw 1968) or by increasing seed predation (Abbott and Quink 1970, Price and Jenkins 1986, Schupp 1988b). Alternatively, litter may increase seed survival by facilitating dispersal (Jarvis 1964, Shaw 1968, Barnett 1977) and increasing germination of large seeds (Barrett 1931, Schopmeyer 1974, Sork 1983). Litter changes seed detectability because rodents rely on olfaction to locate seeds and litter may affect odor diffusion (Price and Jenkins 1986). Also, tree seeds differ in the intensity of odors released and predator species differ in their olfactory capabilities (Schupp 1988a).

Here we continue experiments on tree invasion and establishment in old fields at the study site (McDonnell and Stiles 1983, Myster and McCarthy 1989) and focus on the spatial variation, temporal variation and the difference among species in tree seed predation. We ask these questions: 1) How does the rate of seed predation differ among tree species? 2) How is the rate of seed predation influenced by a microhabitat of differing types of litter?, by increasing distance from forest into the old field?, by vegetation patch type and structure of old field? 3) Is the variation of these results explained by differences in seed characteristics such as mass or dispersal mechanism? Or, 4) Do the results correlate better with known diet and habitat preferences of the mammalian seed predators?

Study site, species, and methods

The study site was the Hutcheson Memorial Forest Center (HMF) located approximately 10 km E of New Brunswick, Middlesex County, New Jersey, USA (40°30′N, 74°34′W). HMF has a *Quercus-Carya* canopy and a *Cornus florida* understory (Bard 1952). The two old fields used in the experiment are adjacent to the forest and were abandoned from agriculture 7 and 17 years ago. The younger field is dominated by herbaceous perennials (e.g., *Erigeron annuus* and *Solidago* spp.) with a few scattered tree saplings. The older field is dominated by patches of *Juniperus virginiana, Rosa multiflora, Cornus florida* and *Solidago* spp.

Six species of tree seeds were used in three experiments. Wind-dispersed species were *Acer rubrum* and *Fraxinus americana*, bird-dispersed species were *Juniperus virginiana* and *Cornus florida*, and mammal-dispersed species were *Quercus rubra* and *Carya tomentosa* (source Gleason and Cronquist 1963). These are among the most abundant tree species during the first 32 years of old field succession at HMF (Buell et al. 1971, Pickett 1982, Myster and Pickett 1992) and include dominant species in the old-growth forest. Seeds of *Acer*, *Juniperus* and *Cornus* were collected at HMF. *Fraxinus*, *Quercus* and *Carya* seeds were purchased from Sheffield Seed Co., Locke, New York. Seeds with visible insect damage were rejected and not used in the experiments. All species except *Acer* are dispersed in the autumn, but *Acer* seeds were present on the ground in the old fields at the start of the experiments. *Acer* seeds were stored when dispersed in the spring using Forest Service guidelines (Schopmeyer 1974). Seeds of *Juniperus* and *Cornus* had fruit or fleshy seed coats removed mechanically.

At the beginning of the experiments potential seed predators, gray squirrels (*Sciurus carolinensis*, Barrett 1931) and white-footed mice (*Peromyscus leucopus*, Whitaker 1966), were the only species caught using wire cages for medium-sized mammals and Sherman live traps for small mammals. We placed cages and live traps in the 7-yr old field and the 17-yr old field during the entire first week of September and the entire first week of October. The cages and live traps were checked every day during the week of sampling. In 20 wire cages in each field, we found 4 squirrels in the 7-yr and 9 squirrels in the 17-yr old field during the 7 trap days in September and 2 squirrels in the 7-yr field and 5 squirrels in the 17-yr field during the 7 trap days in October. During these trap days in the 10 live traps in each field, we found 10 mice in the 7-yr field and 8 mice in the 17-yr field in September and 7 mice in the 7-yr field and 7 mice in the 17-yr field in October. *Peromyscus* is the most abundant small mammal in HMF old fields (Pearson 1959) and *Sciurus* is abundant in old fields and forest as well. The rest of the observed HMF seed predator guild (Martin et al. 1961) consists of white-tailed deer (*Odocileus virginianus*) and raccoon (*Procyon lotor*).

Litter and distance to forest edge

We tested the effect of mammal exclosures, litter, and distance to forest edge on seed survival in the 7-yr field using four treatments: (1) cages of 1 cm^2 mesh hardware cloth (0.25 m × 0.25 m × 0.10 m) anchored to the ground to exclude mammalian seed predators, (2) locally collected *Quercus* spp. litter placed at a naturally occurring density of 100 g m^{-2} (J. Facelli, pers. comm.), (3) locally collected *Solidago* spp. litter placed at a naturally occurring density of 100 g m^{-2} (J. Facelli, pers. comm.) and (4) a control without any of the other

Table 1. Summary of significant logistic regression analysis results ($p < 0.05$) for number of seeds remaining per plot in the distance × litter microhabitat experiment in the 7 year old field. All tests had 3 degrees of freedom. There were 18 interactions tested that were not significant.

Species	Source of variation	Standard error	χ^2	p
Acer rubrum	*Quercus* litter	0.4174	22.14	0.0001
Acer rubrum	*Solidago* litter	0.4340	23.31	0.0001
Fraxinus americana	*Quercus* litter	0.3473	25.30	0.0001
Fraxinus americana	*Solidago* litter	0.3371	21.86	0.0001
Cornus florida	*Quercus* litter	0.4805	26.85	0.0001
Cornus florida	*Solidago* litter	0.3600	16.64	0.0001
Quercus rubra	*Quercus* litter	0.3926	21.77	0.0001
Quercus rubra	*Solidago* litter	0.5133	27.14	0.0001
Carya tomentosa	*Quercus* litter	0.4909	16.43	0.0001
Carya tomentosa	*Solidago* litter	0.4904	14.97	0.0001
Carya tomentosa	Distance	0.5221	29.44	0.0001

treatments. For each of the four treatments, five seeds of each of the six tree species were placed on separate waterproof fine-grained 13 cm × 13 cm sandpaper squares to reduce seed losses due to wind and rain. All squares for all experiments were ordered randomly and anchored to the ground. For those treatments with litter, litter was placed on top of seeds. Therefore, the experimental unit consisted of 24 squares containing five seeds apiece and each 0.2 m from the nearest square. The order of the six species and the four treatments for each species was completely random. We placed 20 replicates of the experimental unit next to the forest edge which translated into each replicate being 10 m from the next. We also placed 20 replicates 15 m away from the forest edge, again 10 m apart, to test for the effect of distance to forest on seed survival.

Density

We tested the effect of initial seed density on seed survival in the 7-yr field for two of the species: *Acer rubrum* and *Fraxinus americana*. Seeds were placed at densities of 5, 25 and 125 seeds on randomly located separate sandpaper squares. The six squares together were 0.5 m apart and defined the experimental unit. Five replicates of the experimental unit, 20 m from each other, were established next to the forest edge.

Patch type

Lastly, we tested the effect of vegetation patch type on seed survival in the 17-yr field. The experimental unit consisted of *Acer rubrum*, *Fraxinus americana*, *Quercus rubra* and *Carya tomentosa* seeds placed on separate sandpaper squares at a density of 5 per square with squares 0.2 m apart. Five patches each of *Juniperus virginiana*, *Rosa multiflora* and *Solidago* spp. were chosen randomly in the field and an experimental unit placed under each patch. *Juniperus* is a coniferous tree, *Rosa* is a rambling shrub and *Solidago* is a herbaceous plant with extensive asexual reproduction. The patches ranged in size from 1–5 m^2 and were between 5 and 20 m apart. Thus, the treatments were replicated 5 times each for a total of 15 patches. The distance to the forest edge from each patch was measured and used in a linear regression analysis to investigate the relationship between distance to forest edge and predation rates. In addition, distance was used as a covariate in other analyses. We started the experiments on 9 September 1989 and recorded the number of seeds on all sandpaper squares weekly until 5 November 1989. Because discarded seed coats and mice fecal pellets were found near most of the sandpaper squares, seed losses are assumed to be and probably are due to seed predation (Schupp and Frost 1989). Therefore, results will be presented in terms of seed loss but treated as seed predation in the discussion section.

We investigated treatment effects using logistic regression analysis (a categorical data model; SAS 1985) and indicating the range of response values (Gaines and Rice 1990, Javier Cabrera, Rutgers Statistics Dept, pers. comm.). We could not use analysis of variance because the range of values for seed number remaining (0 to 5) was too narrow to approximate a continuous function, because too many squares had no seeds remaining and because the distributions were not normal (Peter Morin, Rutgers Ecology Dept, pers. comm.). For all experiments data was gathered when the first square was emptied of seeds, three weeks after the start of the experiment. This was done so as not to confound treatment effects with time in the same field. Therefore, significant differences in total number of seeds lost are also significant differences in rate of seed loss. We also computed the coefficient of concordance (Greig-Smith 1983) to investigate differences between orders of seed loss between the two fields.

Table 2. Logistic regression results for density experiment in 7 year old field based on percentage of seeds remaining. Both tests had 2 degrees of freedom.

Species	Standard error	χ^2	p
Acer rubrum	0.2223	0.32	0.5693
Fraxinus americana	0.3911	20.05	0.0111

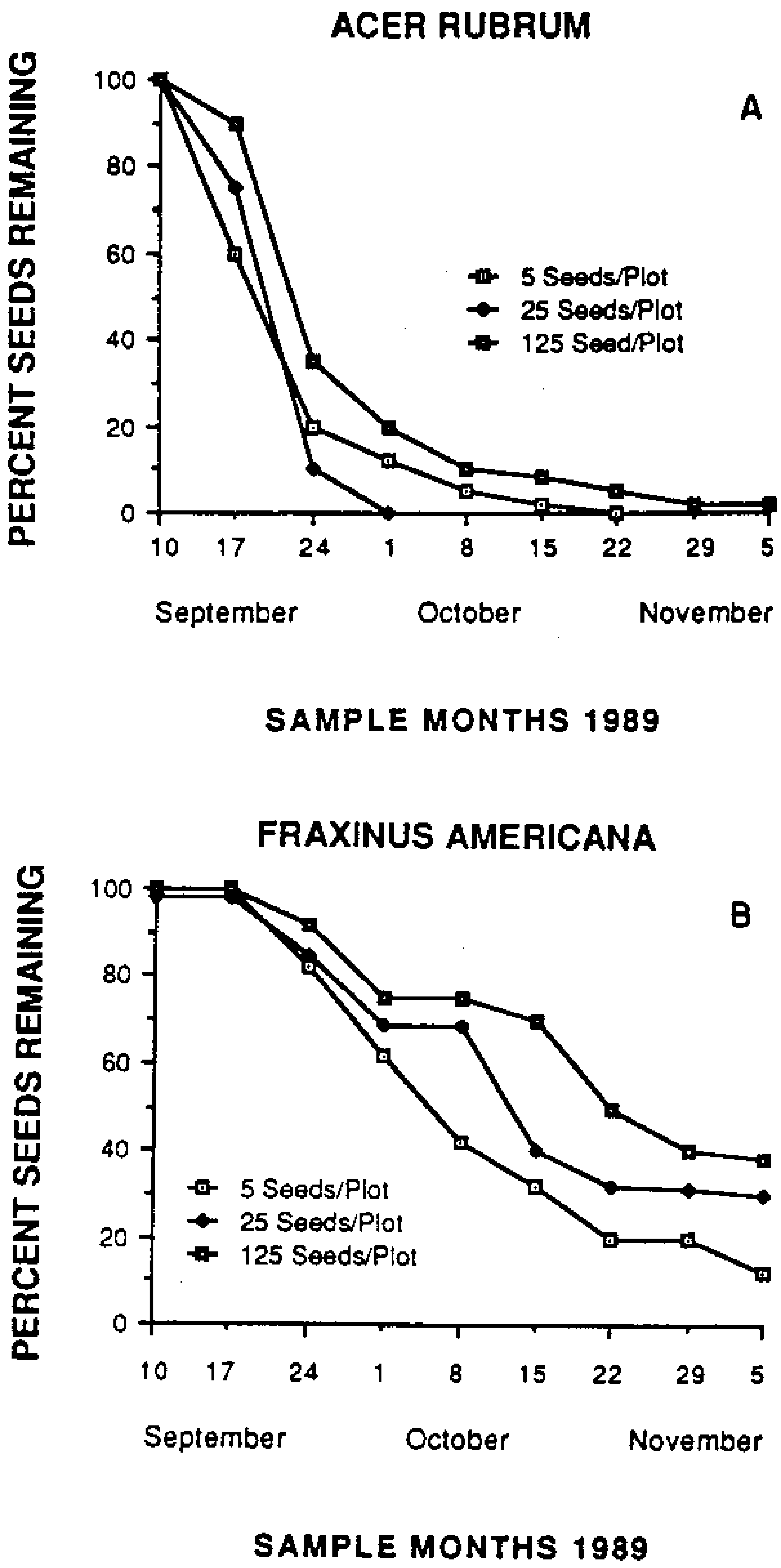

Fig. 1. A) Percent of *Acer rubrum* seeds remaining over time pooled from all five squares for the three density treatments in the 7 year old field. B) Percent of *Fraxinus americana* seeds remaining over time pooled from all five squares for the three density treatments in the 7 year old field.

Results

Litter and distance to forest edge

Cages significantly reduced seed loss ($\chi^2 = 25.22$, df = 3, p = 0.0001) for all species except *Juniperus* ($\chi^2 = 0.31$, df = 3, p = 0.93) which lost less than 5% of its seeds regardless of treatment. Species differed in the number of seeds lost (*Acer* 99%, *Fraxinus* 84%, *Cornus* 97%, *Quercus* 96%, *Carya* 44%) regardless of treatment ($\chi^2 = 19.11$, df = 5, p = 0.0001). Seed loss was reduced significantly by *Quercus* and *Solidago* litter for *Acer*, *Fraxinus*, *Cornus*, *Quercus*, and *Carya* (Table 1). In addition, seed loss was reduced significantly by increasing the distance from the forest edge for *Carya*. Interactions between distance and cage, distance and *Quercus* litter and distance and *Solidago* litter were not significant for any test species. The percent loss of seeds was between 1% and 5% of initial density per day (similar to Mittelbach and Gross 1984) with *Acer* having a higher rate than the other species.

Density

Acer and *Fraxinus* differed in the number of seeds lost (*Acer* 92%, *Fraxinus* 24%) regardless of initial density ($\chi^2 = 18.35$, df = 1, p = 0.001). Density significantly influenced loss of *Fraxinus* seeds but not *Acer* and both species had greater loss at low densities (Table 2; Gill and Marks 1991). Seed loss was more rapid for *Acer* than for *Fraxinus* at all densities and few *Acer* seeds remained at the end of the experiment compared to *Fraxinus* (Fig. 1a, b). As in the first experiment, the percent loss of seeds was between 1% and 5% of initial density per day with *Acer* having the highest rate.

Patch type

Species differed in the number of seeds lost (*Acer* 89%, *Fraxinus* 75%, *Quercus* 100%, *Carya* 88%) regardless of patch type ($\chi^2 = 21.88$, df = 3, p = 0.0001). *Quercus* showed total seed loss in all patch types. Loss of *Fraxinus and Carya* was significantly greater in the woody patches (see Willson and Whelan 1990) of *Juniperus virginiana* and *Rosa multiflora* compared to the herbaceous patches of *Solidago* spp. (Table 3). Because linear regressions of seeds remaining vs distance to forest were not significant for any of the four species (Table 4), seed losses were probably due to patch type and not because of any effect of distance to the forest edge. Futhermore, analyses using distance as a covariate were non-significant. The percent of seed loss was 1 to 7% per day with *Quercus* having a higher rate compared to other species.

All species except *Acer* suffered significantly greater losses in the older field (Table 5; $\chi^2 = 12.82$, df = 3,

Table 3. Mean ± standard error of seeds remaining for each species in each patch type and logistic regression analysis results for mean seeds remaining at end of the experiment in 17 year old field.

Species	Patch type			χ^2	p
	Solidago	*Rosa*	*Juniperus*		
Acer rubrum	1.0±0.1	0.4±0.1	0.0±0.0	1.01	0.351
Fraxinus americana	2.6±0.3	0.5±0.1	0.4±0.2	19.01	0.001
Quercus rubra	0.0±0.0	0.0±0.0	0.0±0.0	–	–
Carya tomentosa	1.4±0.3	0.4±0.1	0.2±0.1	22.21	0.001

$p = 0.02$). The losses were also faster in the older field compared to the younger field (Figs 2a, b, 3). In addition, the order of decreasing seed loss (*Quercus* > *Acer* > *Fraxinus* > *Carya* in the older field and *Acer* > *Cornus* > *Carya* > *Quercus* > *Fraxinus* > *Juniperus* in the younger field) was significantly different between the two fields ($p < 0.05$; Kendall's coefficient of concordance, Greig-Smith 1983).

Discussion

Although species can be compaired by dispersal mode and the accompaning seed characteristics (e.g. mass [order of seeds by fresh mass is *Carya* 4.4 g > *Quercus* 3.5 g > *Cornus* 0.08 g > *Fraxinus* 0.043 g > *Acer* 0.015 g > *Juniperus* 0.005 g] and morphology), they show individualistic responses to seed predation. For wind-dispersed species, initial density and vegetation patch effects were significant for *Fraxinus* but not for *Acer*. This may have been due to greater predation for *Acer* which has a larger predator guild (Martin et al. 1961) that may include both density-dependent and density-independent predators. This density-dependent predation on *Fraxinus* seeds also found in other studies (Casper 1987, Sork et al. 1988) implies that some predators do not eat all seeds in a patch once discovered and may be reluctant to remain exposed long enough to consume all seeds (Gill and Marks 1991). However, there is not convincing evidence in the number of *Fraxinus* seeds remaining at the end of the experiment or in the reduced predation at higher densities for both *Acer* and *Fraxinus* to suggest satiation of seed predators (Janzen 1971). Bird-dispersed and mammal-dispersed species also responsed individually. *Juniperus* seed predation was much less than *Cornus* suggesting that ants are probably not seed predators (Holthuijzen and Sharik 1984, Mittelbach and Gross 1984).

Early in old field succession at HMF, both seeds and seedlings of wind- and bird-dispersed tree species decrease in density exponentially with distance from the forest edge (McDonnell and Stiles 1983, Myster and Pickett 1992). Our results from the younger experimental field suggest that leaf litter, found only close to the forest edge, may help contribute to the increased seedling density found there by reducing predation. However for the control seeds without litter, the lack of a distance effect for five out of the six test species does not support the seed shadow hypothesis (Janzen 1970, Connell 1971) of reduced predation with distance from fruiting adult.

We cannot definitively answer questions concerning the relative importance of seed characteristics vs predator diet preferences and habits in determining our results. Indeed, plant and animal characteristics may influence each other and their effects may be difficult to separate completely (e.g. diet preferences and energy/nutrient content of seeds). Also, the plant variables we discuss (seed mass and dispersal mode) may not be the only important seed characteristics that can influence predation (e.g. chemical composition) and we do not manipulate animal predators directly or allow for differential access to seeds. Nevertheless, we can look for relationships between our results and plant/animal characteristics in order to construct hypotheses for future experimentation. Our results did not correlate well with plant seed characteristics. We found species-specific responses in predation rate across all three experiments and, therefore, any similarity in effect due to similar dispersal mode, seed mass or morphology did not show

Table 4. Results of regression analysis performed on seeds remaining in plots in patches vs distance to forest edge in 17 year old field.

Species	R^2	Y-intercept	Slope	p
Acer rubrum	0.20	−1.81	0.08	0.08
Fraxinus americana	0.04	−2.28	0.05	0.47
Quercus rubra	–	–	–	–
Carya tomentosa	0.13	−0.85	0.58	0.17

Table 5. Mean ± standard error of seeds remaining on squares without treatments in the 7 and 17 year old field.

Species	7 year old field	17 year old field
Acer rubrum	0.41±0.02	0.66±0.05
Fraxinus americana	2.70±0.08	1.20±0.41
Quercus rubra	0.86±0.12	0.00±0.00
Carya tomentosa	3.08±0.98	0.66±0.09

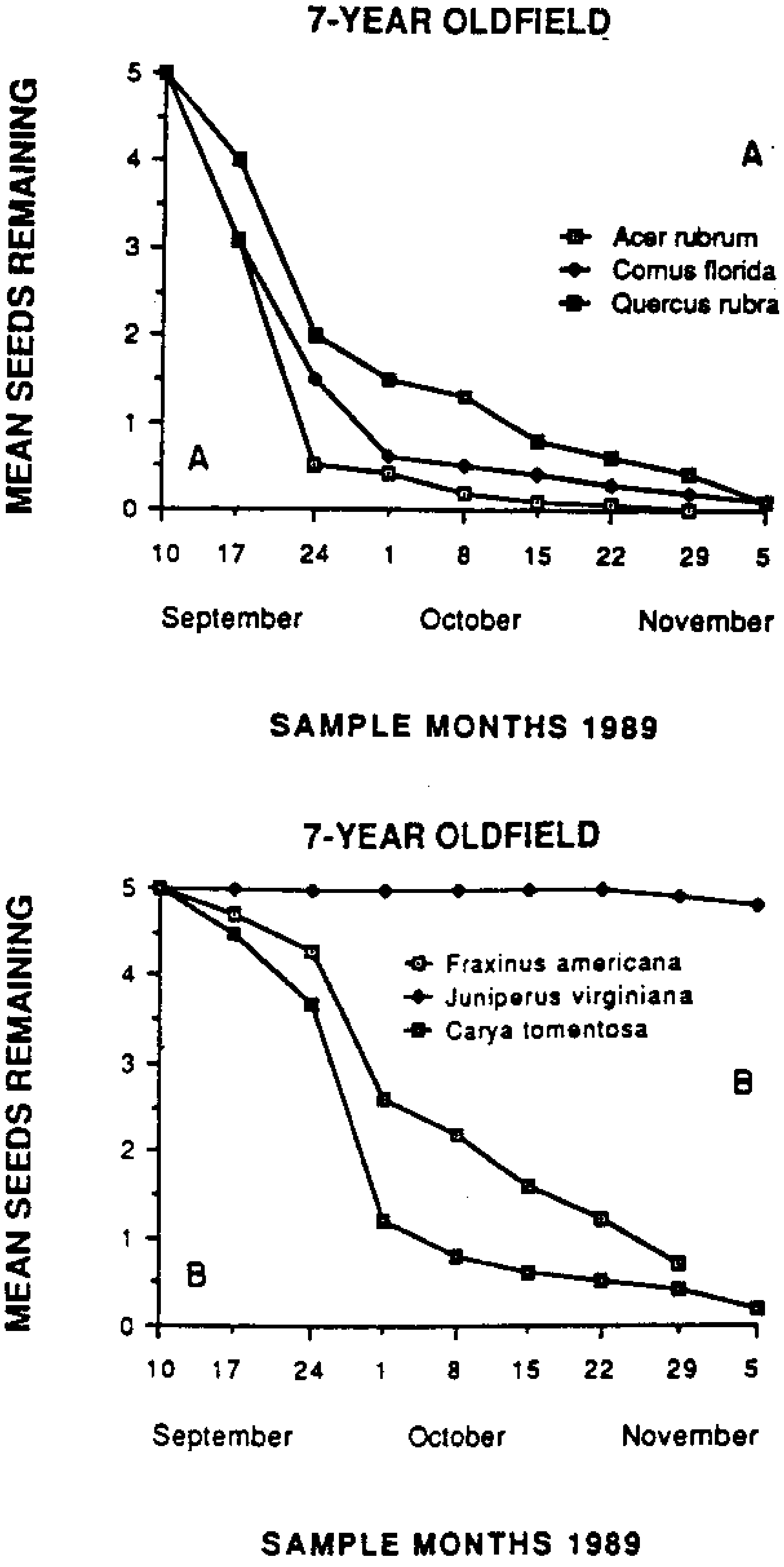

Fig. 2. A) Mean seeds remaining pooled from control squares of *Acer*, *Cornus*, and *Quercus* over time in the 7 year old field. B) Mean seeds remaining pooled from control squares of *Fraxinus*, *Juniperus*, and *Carya* over time in the 7 year old field.

up consistantly in our results. For example, the order of seeds by mass (*Carya* > *Quercus* > *Cornus* > *Fraxinus* > *Acer* > *Juniperus*) differs greatly from the order of seed loss in all experiments. The lack of correspondence was also found by Willson and Whelan (1990); however, our range of seed masses may be restricted compared to other habitats (e.g. those in the wet tropics; Louda and Zedler 1985, Uhl 1987) which have shown a closer relationship between seed mass and level of predation.

In general, our results are much more consistent with diet and habitat preferences of known seed predators at HMF. The distance effects, density effects, and increased predation under woody patches reflect the preference of seed predators for woody vegetation (Pearson 1959, Nixon et al. 1968, Pearson and Pearson 1977, Lotze and Anderson 1979, Webb and Willson 1985, Gill and Marks 1991). Greater predation and a change to the consumption of larger seeds in the older field, also found by DeSteven (1991), both support a shift to an increase in diversity, mass and abundance of predators with successional time (Pearson 1959, Mittelbach and Gross 1984). In addition, plant species that showed the most seed predation were generally the same species that are a greater part of the diet of HMF seed predators (Martin et al. 1961). Taken together, our results suggest that HMF seed predators are generalists (Martin et al. 1961) whose diet is mainly restricted by energy budget considerations and what they can find while avoiding open space. At the end of the experiment some of the seeds surviving in the older field do so beyond a 26 m distance from the forest edge, suggesting that a browse zone (Bartholomew 1970) of enhanced predation may still exist near the forest.

All our results document variation in the effect of tree seed predation in old fields (Schupp 1988a, Willson and Whelan 1990). Spatial variation was shown by distance effects and implied by litter, density, and vegetation patch effects because litter (Facelli and Carson 1991) and vegetation are spatially heterogeneous in old fields and seed density decreases with distance from the forest edge (McDonnell and Stiles 1983). Temporal variation was implied by differences between old fields of differing age and structure. In addition, tree species differed in seed predation rate in all three experiments. It is important to document this variation if we are to under-

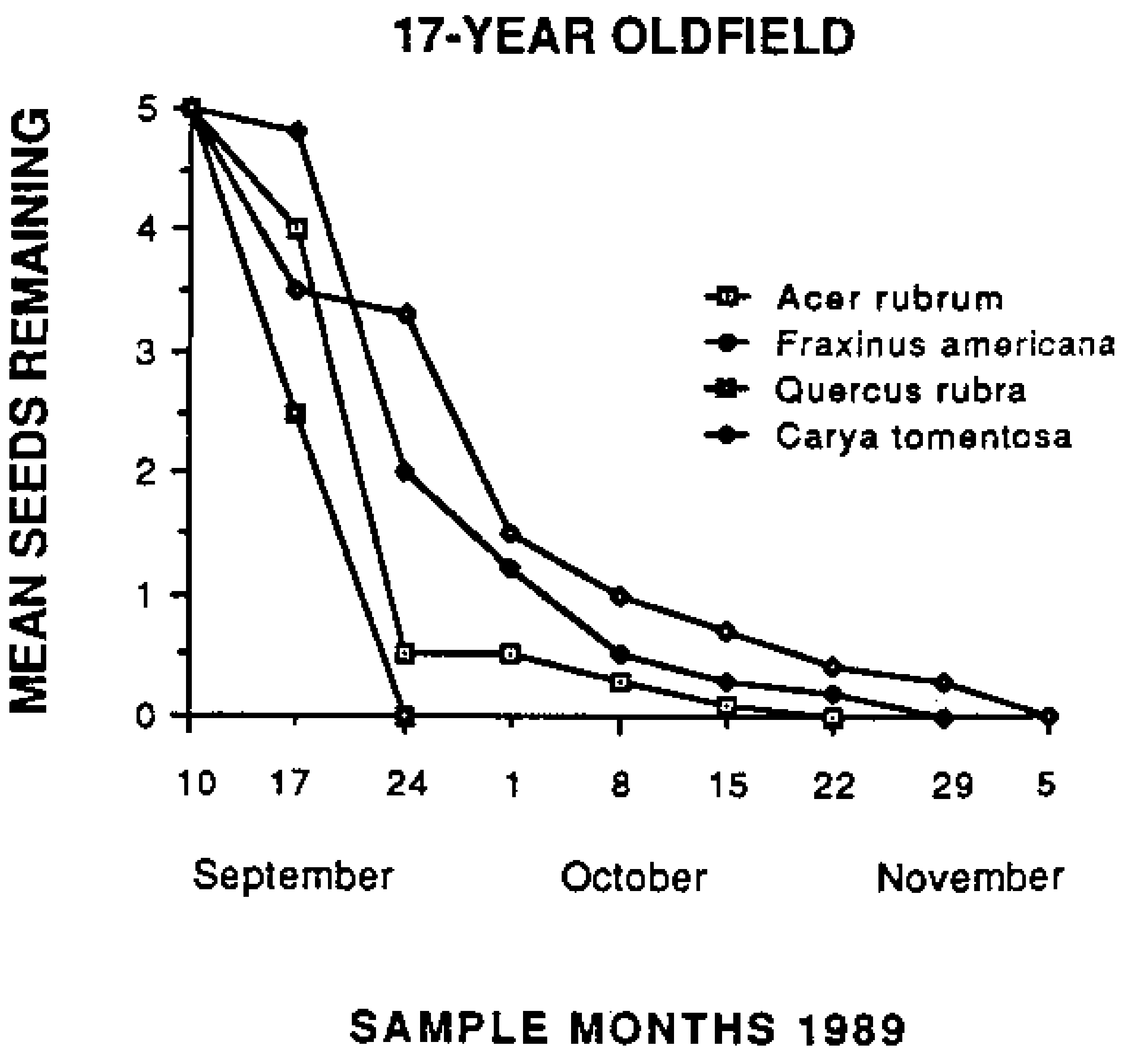

Fig. 3. Mean seeds remaining pooled from all treatment squares of tree species over time in the 17 year old field.

stand the mechanisms that control tree invasion in old fields (Buell et al. 1971) and the net effect of these mechanisms on tree seedling establishment (Louda 1982, Robertson et al. 1990). By documenting this variation we help to quantify probabilities for tree invasion windows in old fields (Gross 1980, Rankin and Pickett 1989). These windows conceptualize the role of seed predation in old field tree establishment.

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