

## EFFECTS OF RODENTS ON SURVIVAL OF TREE SEEDS AND SEEDLINGS INVADING OLD FIELDS

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**Abstract.** Tree invasion of old fields is an important process affecting landscape heterogeneity and species diversity, as well as the quality of wildlife habitat, in eastern North America. We examined the effects of tree seed and seedling predation by small mammals on the rate, spatial pattern, and species composition of tree invasion in old fields. We performed field experiments inside U-shaped enclosures built at forest–field edges, within which we manipulated the density of meadow voles (*Microtus pennsylvanicus*), which are major seedling predators. Although we did not directly manipulate density of white-footed mice (*Peromyscus leucopus*), which are major seed predators, mouse density was high wherever vole density was low. We introduced cohorts of seeds and seedlings of red maple (*Acer rubrum*) or sugar maple (*Acer saccharum*) [as specified in the *Methods* for each trial], white ash (*Fraxinus americana*), white pine (*Pinus strobus*), and tree-of-heaven (*Ailanthus altissima*), all common early invaders of old fields in our study area. Rates of seedling predation were higher in enclosures with higher density of voles, and voles showed distinct preferences for red maple, white ash, and *Ailanthus* over white pine. Predation rates on small seedlings were higher than on larger seedlings. Seedlings near the forest edge were killed at a lower rate than those >5 m into the field. Predation rates on seeds were higher in low-vole-density treatments, where mice were more abundant. Mice showed distinct preferences for white pine, avoided *Ailanthus*, and consumed sugar maple and white ash at intermediate rates. Predation rates on seeds were higher in shrub-dominated than in herbaceous old fields. Overall density of mice increased dramatically between 1994 and 1995, and seed predation rates increased concomitantly. In 1994, seed predation was most intense 5 m and 10 m into the field, and less intense at the forest–field edge and 20 m into the field; although a similar pattern was observed in 1995, the variation was not statistically significant. We conclude that both of these common small mammal species can have profound effects on survival of tree propagules near forest–field edges, but that their effects are strongly dependent on density. Voles had a strong, negative direct effect on seedling survival, but a positive indirect effect on seed survival by inhibiting seed predation by mice. Voles and mice: (1) showed distinctly different food preferences; (2) had their strongest effects at different positions with respect to the forest–field edge; and (3) had their strongest effects in different old-field types (herbaceous fields for voles, shrub-dominated fields for mice). These two species are not functionally redundant in their effects on old-field succession.

**Key words:** animal–plant interactions; functional redundancy; granivory; herbivory; meadow voles; *Microtus pennsylvanicus*; New York State, southeastern; old-field succession; *Peromyscus leucopus*; seed predation; seedling predation; white-footed mice.

### INTRODUCTION

Abandonment of agriculture in eastern North America has occurred in several major episodes in the past two centuries (Glitzenstein et al. 1990), resulting in landscapes consisting of patches of old fields embedded in a matrix of forests. These old fields represent a major component of the biological and habitat diversity of eastern landscapes (Marks 1983). Old fields often undergo succession from dominance by small herbaceous plants to dominance by larger woody plants (Bormann 1953, Buell et al. 1971, Pickett 1982). As trees from

the surrounding forest matrix gradually invade, old fields undergo profound changes in species composition (McDonnell and Stiles 1983, Myster and Pickett 1992), patch-type diversity (Kolasa and Pickett 1991), and wildlife habitat suitability (Fox 1990, Anderson et al. 1980, Risser 1995). Tree invasion typically occurs via dispersal of seeds, but because seed-dispersal distances of the dominant trees are severely limited ( $\approx 1$ –100 m from the parent tree canopy; Houle 1992, Ribbens et al. 1994, Greene and Johnson 1996), the most rapid changes in species composition generally occur at forest–field edges.

In herbaceous habitats of eastern North America, the meadow vole (*Microtus pennsylvanicus*) is the over-

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whelmingly dominant small-mammal species, in both numbers of individuals and biomass (Rose and Birney 1985, Ostfeld and Manson (1996). Meadow voles are largely restricted to herbaceous habitats, and use forests only as dispersal corridors (Tamarin et al. 1984). The white-footed mouse (*Peromyscus leucopus*) is the dominant small mammal in eastern forests (Baker 1968, Dueser and Porter 1986, Morris 1991, Wolff 1985), although they are known to use large gaps, clearcuts, forest edges, and open fields (Buckner and Shure 1985, M'Closkey and LaJoie 1975, Drickamer 1976, Kirkland 1990). Use of open habitat types by white-footed mice appears to be inhibited by the presence of meadow voles (Grant 1972, Bowker and Pearson 1975, M'Closkey and Fieldwick 1975, Kaufman and Kaufman 1989). As a result, use of old fields by white-footed mice tends to be concentrated in shrub-dominated patches, which are avoided by voles. Although the mechanisms by which these two species compete is not well understood, the generally larger voles ( $\approx 40$  g) appear to dominate and displace the smaller mice ( $\approx 20$  g) in areas of co-occurrence (Grant 1972). Thus, a combination of interspecific variation in habitat selection and competitive interactions between the dominant small-mammal species produces a discontinuity in the small-mammal community that parallels the pronounced discontinuity in the plant community along the forest-field edge.

Mammals are known to affect woody-plant invasion of temperate and tropical old fields both positively via dispersal and caching of seeds (Vander Wall 1990, 1994) and negatively via herbivory on seedlings and granivory (Schupp 1988, Myster and McCarthy 1989, Brown and Heske 1990, DeSteven 1991a, b, Gill and Marks 1991, Houle 1992, Bowers 1993, Vander Wall 1994). Meadow voles are major predators of tree seedlings in old fields (De Steven 1991b, Gill and Marks 1991, Ostfeld and Canham 1993). Ostfeld and Canham (1993) showed that seedling predation by meadow voles varied with vole density, resulting in near elimination of seedling cohorts when vole density was high. The effects of voles on seedling survival are likely to vary among old-field habitat types and among years because vole density varies considerably both spatially and temporally (e.g., Batzli 1992, Ostfeld 1992, Ostfeld et al. 1993, Diffendorfer et al. 1995). Predation by voles varied significantly among tree species that commonly invade old fields (Ostfeld and Canham 1993), and thus may have a substantial effect on both the rate and direction of old-field succession.

Mice in the genus *Peromyscus* are important seed predators in both forests and old fields (Kantak 1983, Mittelbach and Gross 1984, Sork 1984, Willson and Whelan 1990, De Steven 1991a, Gill and Marks 1991, Adams-Manson 1994, Ostfeld et al. 1994). Forest populations of mice are capable of strongly reducing tree seed survival (Ostfeld et al. 1994), and show distinct preferences among common tree species (Kantak 1983,

Wolff et al. 1985). However, *P. leucopus* populations inhabiting old fields have not been well studied, and neither their variability in density nor their food preferences in these habitats is well understood. Moreover, the effects of variation in population density of voles on density and seed predation by mice in old fields are unknown.

If voles and mice have different effects on invading tree propagules, then whether a vole or mouse population dominates a particular old field may be profoundly important to the species composition and spatial pattern of tree invasion. Our purpose in this study was to integrate the effects of voles on tree seedlings and mice on tree seeds in determining the rate, spatial patterns, and species composition of tree invasion in old fields and along forest-field edges. We tested three primary hypotheses: (1) high density of meadow voles results in higher predation rates on seedlings but, by reducing density of white-footed mice, causes lower predation rates on seeds; (2) due to specific habitat preferences of voles and mice, predation rates on seedlings are lowest near the forest edge and highest in the old-field interior, while the converse is true for seeds; and (3) preference rankings among the different tree species are different for voles and mice; that is, voles and mice are not functionally redundant in their effects on tree invasion. We carried out our experiments in old fields representing a gradient of shrub cover in order to understand whether the net effects of rodents varied with old-field community structure.

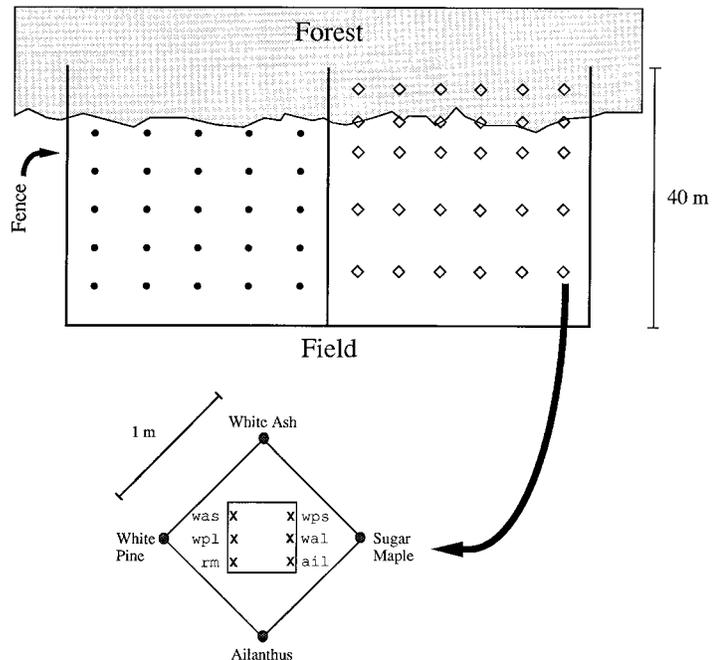
## MATERIALS AND METHODS

### *Sites, enclosures, and trapping*

All experiments were performed at or near the Institute of Ecosystem Studies (IES) in Dutchess County, southeastern New York (41°50' N, 73°45' W). We selected six old fields varying from sites dominated by herbaceous vegetation and lacking shrubs to sites dominated by shrubs. Herbaceous sites contained high coverage of the grasses *Schizachyrium scoparium*, *Bromus inermis*, and *Phleum pratense*, the forbs *Galium tinctorum*, *Solidago juncea*, *S. rugosa*, *Vicia cracca*, and *Centuria maculosa*, and two species of sedges (*Carex* spp.). Mixed herbaceous/shrubby sites contained honeysuckle (*Lonicera morrowii*), gray dogwood (*Cornus racemosa*), and multiflora rose (*Rosa multiflora*), and shrub-dominated sites contained large clones of gray dogwood.

At each of the six sites we built pairs of partial enclosures to facilitate the maintenance of vole populations at experimental levels. Enclosures were 40 × 40 m, and were made of 0.9 m wide galvanized hardware cloth (1.2 cm mesh), buried 0.4 m belowground. We riveted 10 cm wide strips of aluminum flashing to the tops of the fences to prevent movement by rodents. The pairs of enclosures shared a common wall (Fig. 1). Enclosures were erected at forest-field edges and ex-

FIG. 1. Schematic diagram of the design of paired experimental enclosures in a southeastern New York old field, and seed/seedling stations placed within those enclosures. The  $5 \times 5$  array of solid circles indicates positions of trap stations, and the  $5 \times 6$  array of open diamonds indicates positions of seed/seedling stations. Note that each enclosure within a pair had both trap stations and seedling stations. At bottom is an expanded diagram of the arrangement of seeds (outer array, solid circles) and seedlings (inner array, X symbols). For seedlings, was = white ash small; wps = white pine small; wpl = white pine large; wal = white ash large; rm = red maple; and ail = *Ailanthus*.



tended 5 m into the forest and 35 m into the adjacent old field. The forest edge of the enclosures was not fenced in order to allow rodents to travel freely across the forest–field edge. We expected that white-footed mice would enter and exit the enclosures freely, whereas voles would perceive the edge as a barrier and maintain populations largely within the enclosed old fields (Tamarin et al. 1984). Rare captures of marked voles in adjacent enclosures confirmed that forests were perceived as barriers to movement.

Within each enclosure we established a live-trapping grid consisting of a 5 by 5 array of permanent trap stations with 7.5 m between stations (Fig. 1). In the first year of the study (1994) we placed one folding Sherman live trap at each station; in 1995 we placed either a single Sherman trap or a single Longworth trap at alternating stations. Trapping was conducted every other week from early August 1994 until mid November 1995, but was suspended due to cold weather and snow during midwinter of 1994–1995. All small mammals except shrews were given a numbered metal ear-tag at first capture to allow individual identification. For each animal captured we recorded species, tag number, gender, reproductive condition, body mass, enclosure number, and trap station. Due to high capture probability, we estimated population density of rodents as the minimum number known to be alive.

We designated one enclosure of each pair as a high-vole-density treatment and the other as a low-vole-density treatment, using a coin toss. This manipulation allowed us to examine the direct effects of vole density on survival of tree seedlings as well as the indirect effects of voles on seed survival via their effects on

white-footed mice. To maintain differences between the two vole-density treatments, we removed selected numbers of voles from low-density enclosures and introduced them to high-density enclosures. To minimize the homing response of transplanted voles (Ostfeld and Manson (1996), we never moved voles between adjacent enclosures. These manipulations were performed during our biweekly trapping sessions. Our goal was to maintain substantial differences between the two treatments within each site, and to maintain relatively constant levels of each density treatment across sites. Due to variability among sites in habitat quality for voles, and to the lack of a fence on the forest edge, this latter goal was only partially met (see *Results: Rodent density*). We also expected that, due to inhibition of white-footed mice by voles and the ability of mice to enter and leave enclosures freely, the high-vole-density treatments would have low density of mice, and vice versa.

#### *Seed and seedling experiments*

Because predation by rodents on tree seeds and seedlings often occurs within a few days following dispersal and establishment (Ostfeld and Canham 1993), it was not feasible to monitor the fate of naturally occurring propagules. Therefore, our strategy was to introduce seeds and seedlings of native (and one non-native) species, all of which are common early invaders of old fields in our region. In September 1994 seed/seedling stations were established in all 12 enclosures. In each enclosure 6 replicate stations were placed at each of five distances from the forest edge, including 5 m into the forest (–5), the edge (0), and 5, 10, and 20 m into

the old field (Fig. 1). Stations were placed  $>3$  m from the fences and  $>1$  m from the trails we created while checking traps. Apart from these general spacing rules, specific coordinates for seed/seedling stations at each distance were then selected using a random number table. Stations consisted of a  $1\text{-m}^2$  outer array for seeds, within which was a  $0.25\text{-m}^2$  inner array for seedlings (Fig. 1). Species-specific seed and seedling locations in arrays were held constant with respect to the forest edge.

Seedlings (1–3 yr old) of red maple (*Acer rubrum*), white ash (*Fraxinus americana*), white pine (*Pinus strobus*), and the non-native tree-of-heaven (*Ailanthus altissima*) were collected on the grounds of IES and held in plastic tubes containing potting mix for 3–4 wk before being planted in the experimental plots. Only healthy seedlings showing no signs of disease or desiccation were used in experiments. All species were represented by small size classes (0.5–1.5 mm stem diameter at 1.0 cm above ground level), and white pine and white ash also were represented by a large size class (2.0–5.0 mm stem diameter). Seedlings were planted along the perimeter of the inner array of seedling stations in holes dug by trowels and watered liberally immediately after planting. Every effort was made to avoid disturbing the surrounding vegetation. Wooden coffee stirrers were placed  $\approx 2$  cm from seedlings to facilitate their relocation during censuses. To avoid scent contamination, latex or cotton gloves were worn while handling and checking all seedlings.

Seedlings were introduced in October 1994 and censused at  $\approx 2$ -wk intervals until December 1994, then censused again in March and May of 1995. During the last census all remaining seedlings were removed and examined to confirm survival status. Seedlings were introduced into only five of the six pairs of enclosures due to limited availability of materials on site. During each census seedlings were classified as being alive, alive with major debarking, alive with minor debarking, dead but not from herbivory, clipped at the top, clipped at the base, or missing. Past studies (Ostfeld and Canham 1993) demonstrated that voles clip seedlings at or near ground level, leaving a characteristic sharp angle in the remaining stem. Based on the presence of vole runways, diggings, and feces in the vicinity of missing seedlings, we felt confident that missing seedlings had been removed by voles (see also Ostfeld and Canham 1993). Therefore, we lumped clipped at the base and missing seedlings into the category “depredated” for further analyses. All other census classifications were lumped into the category “not depredated” (see *Methods: Statistical analyses*). Non-rodent herbivores, such as eastern cottontails (*Sylvilagus floridanus*) and slugs, may have been responsible for clipping at the top and debarking, but these types of herbivory rarely caused mortality of seedlings (Ostfeld, Manson, and Canham, *unpublished data*; see also Hulme 1996). With the exception of one site, we found

no evidence for frost-heaving causing seedling mortality (see also Gill and Marks 1991, Ostfeld and Canham 1993). Seedlings killed by frost-heaving, disease, or desiccation were excluded from analyses.

We used seeds of white ash (45 mg), white pine (17 mg), tree of heaven (31 mg), and sugar maple (*Acer saccharum*) (65 mg) for the seed predation experiments. All seeds were from regional seed sources and were purchased from F. W. Schumacher Company, Sandwich, Massachusetts, except tree of heaven, which was collected on IES property. Four plastic petri dishes 4 cm in diameter with drain holes, each containing five seeds of a single species, were placed 1 m apart at the outer array of seed/seedling stations (Fig. 1). Seeds were introduced in early November 1994 and late October 1995, during which natural dispersal of these seed types occurs, and were censused at  $\approx 2$ -wk intervals until March 1995 (1994 cohort) or December 1995 (1995 cohort). At each census the number of intact seeds was recorded. Latex gloves were worn during all censuses. The vast majority of damaged seeds showed gnawing marks on the seed coat, which is a characteristic sign of depredation by small mammals. Fecal pellets in dishes, runways, and other disturbances near the dishes provided further evidence that virtually all seed predation observed was due to small mammals.

#### Statistical analyses

Our dependent variables were categorical rather than continuous; therefore we analyzed patterns of predation on both seedlings and seeds using a categorical modeling approach (PROC CATMOD of SAS Institute 1990). Because of the large number of zero values in our data set, our approach was to fit linear models to functions of response frequencies using maximum likelihood estimation of parameters for the analysis of generalized logits. Statistical significance was determined by chi-square tests of the information matrix from the maximum likelihood calculations. We considered seed/seedling stations to be relatively independent units of replication. Due to small home ranges of the consumers (Ostfeld and Canham 1995), individual rodents were unlikely to have regularly visited  $>1$  station within an enclosure. Thus, the predation rates at individual stations largely reflected the activity of different animals. In addition, due to the inherent spatial variation in the vegetation, each seed/seedling station within an enclosure represented a unique combination of microhabitat characteristics, which may have affected the probability of predation. Therefore, we believe that analysis at the station level represents the most appropriate spatial scale from the perspective of predation risk for tree propagules during old-field invasion.

Because of considerable natural variation in background levels of seed and seedling density within our enclosures, which may have influenced rodent foraging patterns, we chose not to focus on calculating food preferences *sensu stricto*, which requires knowledge of

relative abundances of all available foods in an array. Instead, we were primarily interested in the cumulative effects of rodent consumers on the different seed/seedling species and size classes. Therefore, we focused on total cumulative predation rates as affected by the independent variables we manipulated. We use the term "preference" below to reflect differential predation on seeds or seedlings of different species or size classes.

For predation rates on seeds and seedlings, the independent variables of interest were: site (six levels for seed experiments, five for seedlings), tree species (four levels), vole density (two levels), and distance from the forest edge (five levels). All independent variables were fully crossed. For our initial analysis of seedling predation we eliminated the large size class of seedlings (white ash and white pine) to examine the effect of all other independent variables on seedling mortality. We then analyzed predation on white ash and white pine separately, using both small and large size classes. Two fates (depredated or live) were possible in the seedling experiments, whereas for the seed-predation experiments, six categories of the response variable were possible (zero to five seeds depredated). Degrees of freedom were calculated as  $(c - 1)(r - 1)$ , where  $c$  = the number of levels in the independent variable, and  $r$  = the number of possible categories of the response variable.

## RESULTS

### Rodent density

Our manipulation of vole density was successful in producing two discrete density levels by early autumn 1994; differences between high-density and low-density enclosures were sustained throughout the remain-

der of the study (Fig. 2). In the case of each pair of enclosures, the designated high-density enclosure maintained consistently higher vole density than the low-density grid. On average, vole density was roughly similar between years (Fig. 2). However, due to differences among sites in overall habitat quality, it was difficult to keep across-site variation lower than within-site variation in vole density. Therefore, we examined the effects of vole density both as a categorical variable (low or high, six replicates of each) and as a continuous variable (average density in each enclosure during the seedling or seed census period), to reflect the range of variation observed among all 12 enclosures.

Density of white-footed mice was extremely low during 1994 but increased substantially in 1995, reflecting the patterns observed in forest grid trapping near our experimental enclosures (Ostfeld et al. 1996; R. S. Ostfeld, *unpublished data*). Mouse density was consistently higher in low-vole-density than in high-vole-density enclosures (Fig. 2). Using each enclosure as an independent unit, the average density of white-footed mice during 2 yr of trapping was strongly and negatively affected by average density of meadow voles ( $r^2 = 0.637$ ,  $df = 11$ ,  $P = 0.002$ ; Fig. 3). In the low-vole-density enclosures in 1995, mouse density in the old fields averaged 4 mice per enclosure, or  $\approx 25$  mice/ha, which is approximately one-half the density observed in nearby forests at the same time (R. S. Ostfeld, *unpublished data*).

### Seedling predation

The rate of seedling predation was significantly higher in high- than in low-vole-density enclosures. Averaging across all tree species, predation rates were

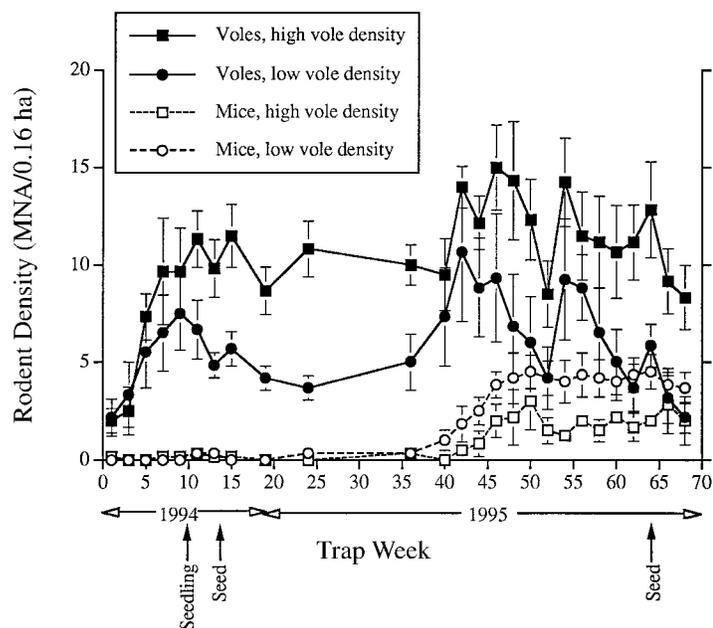


FIG. 2. Population sizes (minimum number alive per 0.16-ha enclosure) of meadow voles and white-footed mice for each trapping week. Squares represent means of the six replicates of the high-vole-density treatment, and circles represent means of the six replicates of the low-vole-density treatment. Solid and open symbols show vole and mouse density, respectively. Vertical lines show  $\pm 1$  SE around each mean. Vertical arrows with "seedling" and "seed" (below time scale) indicate the initiation of seedling- and seed-predation experiments.

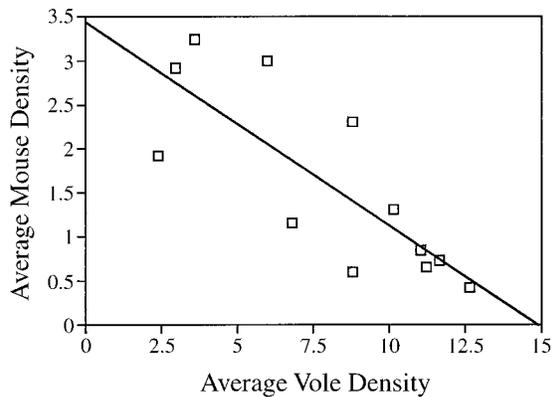


FIG. 3. Density of white-footed mice (minimum number alive per 0.16-ha enclosure) as a function of density of meadow voles (minimum number alive). Symbols represent means for each enclosure over the entire trapping period.

21.5% and 16.0% in high- and low-vole-density treatments, respectively (Table 1A). Using each enclosure as an independent unit, we observed a significant positive association between vole density and percent of seedlings killed ( $r^2 = 0.44$ ,  $df = 9$ ,  $P = 0.037$ ). Variation in seedling predation among sites was marginally significant (Table 1A). The two sites with the highest seedling predation were characterized by high percent cover of herbaceous plants and low cover of shrubs, and the lowest seedling predation rate was observed in the site with the highest coverage of shrubs. The one herb-dominated site with low seedling predation also supported low vole density in 1994.

Species of seedling had a significant effect on the probability of predation (Table 1A). White pine seedlings were avoided (12.8% consumed), whereas seedlings of white ash, red maple, and *Ailanthus* were killed

at approximately equal frequencies (21.7, 21.6, and 19.3%, respectively). The size of seedlings had a highly significant effect on predation rate (Table 1B). For the two species (white ash and white pine) in which we varied size of seedlings, smaller seedlings were more likely to be killed. However, as indicated by a significant species  $\times$  size interaction term (Table 1B), the effect was more pronounced for white ash, for which small seedlings were  $\approx 3.5$  times more likely to be killed (22.1% vs. 6.3%), than for white pine, for which small seedlings were about twice as likely to be killed (12.8% vs. 7.3%).

Seedlings placed 5 m, 10 m, and 20 m into the old fields were significantly more likely to be killed (22.5%, 29.6%, and 27.5%, respectively) than were seedlings at the forest edge (7.5%) or 5 m into the forest (6.7%) (Table 1A, Fig. 4A). The effect of distance from the forest edge was significantly more pronounced in high-vole-density than in low-vole-density treatments (density-treatment  $\times$  distance interaction term, Table 1A). In addition, the effect of distance from the forest edge was considerably higher at the three sites generally supporting higher vole density than at the two sites at which vole density was lower overall (site  $\times$  distance interaction term, Table 1A). The effect of distance from forest edge was restricted to seedlings in the small size classes. Both small and large seedlings were largely ignored ( $<10\%$  killed) at  $-5$  m and at the edge. At 5 m, 10 m, and 20 m into the field only a slight increase in predation rate occurred for large seedlings, whereas small seedlings experienced a five-fold increase in predation (Table 1B; Fig. 4B).

#### Seed predation

Overall rates of seed predation were nearly twice as high in 1995 (84.9%), when density of white-footed

TABLE 1. Results of the categorical modeling analysis of the seedling predation experiment in old fields in southeastern New York. (A) One analysis of all independent variables except Size, in which only small seedlings were included. (B) Second analysis on white ash and white pine only, with the independent variable Size as a main effect.

Variable	No. levels	df	Chi-square	P
(A) Site	5	4	8.26	0.082
Density treatment (Denstrt)	2	1	5.31	0.021
Site $\times$ Dnstrt		4	12.62	0.013
Distance from edge	5	4	49.09	$\ll 0.001$
Site $\times$ Distance		16	40.96	0.001
Denstrt $\times$ Distance		4	12.24	0.016
Species	4	3	11.63	0.009
Site $\times$ Species		12	18.49	0.102
Denstrt $\times$ Species		3	6.08	0.108
Distance $\times$ Species		12	14.00	0.301
(B) Size	2	1	16.12	$\ll 0.001$
Site $\times$ Size		4	3.52	0.475
Distance $\times$ Size		4	11.04	0.026
Denstrt $\times$ Size		1	1.00	0.318
Species $\times$ Size		1	4.10	0.043

Notes: Individual seedlings were categorized as depredated or alive; seedlings dying of causes other than predation were excluded from analysis. See *Methods: Statistical analyses* for descriptions of independent variables. Density treatment (Denstrt) refers to vole density.

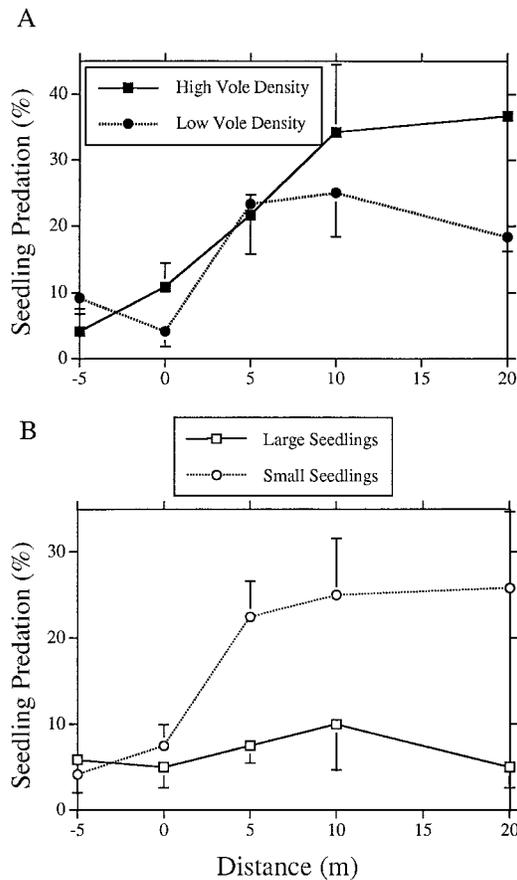


FIG. 4. Seedling predation rates as a function of distance from the forest-field edge, where -5 represents 5 m into the forest, 0 represents the edge, and 5–20 represent distances (m) into the old field. (A) Average seedling predation (small seedlings only) in the two vole-density treatments. (B) Seedling predation averaged across both vole-density treatments for small and large seedlings of white pine and white ash only. Vertical bars represent 1 SE above or below the mean.

mice was high, as in 1994, when mouse density was low (47.7%; Figs. 2, 5). As we had predicted, average rate of seed predation in 1994 was significantly higher in low-vole-density treatments (51.9%) than in high-vole-density treatments (43.6%; Table 2). However, the effect of vole density on seed predation disappeared in 1995 (Table 2), presumably because high density of mice in the surrounding forests caused these seed predators to use old-field habitats intensely even where vole density was high. Averaging across the two years, we observed a significant curvilinear relationship between seed predation rate in each enclosure and average mouse density during the period when experimental seeds were available ( $y = 67.3x^{0.22}$ ,  $r^2 = 0.71$ ,  $df = 23$ ,  $P < 0.001$ , Fig. 5).

Predation rates varied substantially among seed species during both years (Table 2, Fig. 6A). In 1994, 88.7% of white pine seeds were depredated, whereas only 25.7% of *Ailanthus* seeds were killed. Predation

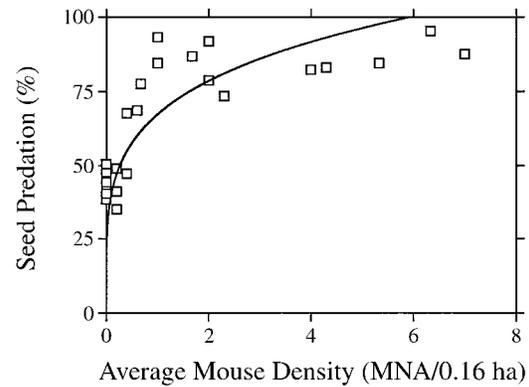


FIG. 5. Seed predation rates as function of grid-specific mouse density averaged over the duration of the experiment (1994–1995).

on sugar maple and white ash was intermediate, at 36.6% and 40.2%, respectively. In 1995, predation again was highest on white pine (98.1%) and lowest on *Ailanthus* (53.7%), but sugar maple (94.9%) and white ash (93.0%) seeds were killed at nearly the same high rate as white pine (Fig. 6A). Although in 1995 we observed no significant effect of vole density on total seed predation rates, a significant interaction between vole density and seed species existed (Table 2). No obvious differences existed between high- and low-vole-density treatments in predation rates on sugar maple, white ash, or white pine; however, predation rates on *Ailanthus* were substantially higher in high-vole-density enclosures (60.1%) than in low-vole-density enclosures (47.3%), suggesting that white-footed mice were behaving opportunistically in consuming this low-ranking species where vole density was high (Ebersole and Wilson 1980; Fig. 6B).

Predation rates on seeds varied with distance from the forest edge in 1994 but not in 1995 (Table 2, Fig. 7). However, contrary to our expectation of high predation rates in the forest interior and at the edge, seed predation in 1994 was higher at 5 m (52.7%) and 10 m (54.6%) than within the forest (-5 m; 43.0%), at the edge (0 m; 42.3%), or at 20 m into the field (46.0%). A qualitatively similar pattern was observed in 1995, but with high predation rates also occurring at -5 m (Fig. 7). In both years, seed predation varied significantly among sites (Table 2). In 1994, predation rates were higher at the three sites with highest percent cover of shrubs than at the three more herbaceous sites, but this pattern was less clear in 1995. In 1994, when vole density had a significantly negative effect on seed predation, the suppressive effect of vole density was most pronounced in the two most shrub-dominated sites (site  $\times$  vole-density interaction, Table 2).

#### DISCUSSION

Our results demonstrate that asymmetric interactions between populations of rodent herbivores and grani-

TABLE 2. Results of the categorical modeling analysis of the seed predation experiments in 1994 (A) and 1995 (B) examining behavior of *Peromyscus leucopus* and *Microtus pennsylvanicus* in old fields in southeastern New York.

Variable	No. levels	df	Chi-square	P
(A) 1994				
Site	6	25	422.36	≤0.001
Density treatment (Denstrt)	2	5	26.79	≤0.001
Site × Dnstrt		25	38.92	0.038
Distance from edge	5	20	38.53	0.008
Site × Distance		100	106.41	0.312
Denstrt × Distance		20	24.69	0.213
Species	4	15	652.76	≤0.001
Denstrt × Species		15	21.32	0.127
Distance × Species		60	76.50	0.074
(B) 1995				
Site	6	25	448.91	≤0.001
Density treatment (Denstrt)	2	5	4.12	0.533
Site × Dnstrt		25	25.01	0.462
Distance from edge	5	20	10.98	0.947
Site × Distance		100	73.87	0.977
Denstrt × Distance		20	22.37	0.321
Species	4	15	28.73	0.017
Site × Species		75	55.03	0.960
Denstrt × Species		15	26.32	0.035
Distance × Species		60	36.84	0.992

Notes: Chi-square tests were performed on the information matrix from maximum likelihood estimation of response parameters. For each dish containing five seeds, six predation outcomes were possible (zero to five seeds depredated); thus df are calculated as  $5 \times (\text{no. levels} - 1)$ . See *Methods: Statistical analyses* for descriptions of treatments (independent variables). Density treatment (Denstrt) refers to vole density.

vores strongly influenced the patterns of mortality in tree propagules along ecotones between forests and old fields. In our system, the dominant herbivore was the meadow vole, which had a direct negative effect on survival of young tree seedlings, but an indirect positive effect on survival of seeds, by suppressing density or activity levels of the dominant granivore, the white-footed mouse. However, we observed considerable variation between years and across sites in patterns of seed and seedling mortality, which we attribute to variation in rodent population density and habitat selection. We believe these results help clarify conflicting and confusing results of prior studies on seed predation in old fields.

#### Seedling predation

As predicted, predation rates on tree seedlings were higher where vole density was higher. However, even at "high" vole density, only 21.5% of seedlings overall were killed. This percentage, which is considerably lower than that observed by Ostfeld and Canham (1993), was probably a result of low density levels of voles in the present study relative to those observed by Ostfeld and Canham (1993) at their more mesic and fertile sites. The nearly complete elimination of entire cohorts of tree seedlings observed by Ostfeld and Canham occurred when vole density exceeded  $\approx 400$  voles/ha, which represents peak density in some cyclic populations (Batzli 1992). At moderate densities of  $\approx 100$ –300 voles/ha, 50–90% of experimentally introduced tree seedlings were killed by voles (Ostfeld and Can-

ham 1993). But at the densities observed in the present study ( $\approx 20$ –90 voles/ha), which represent densities observed in a cyclic low phase (Taitt and Krebs 1985, Batzli 1992), only  $\approx 15$ –20% of seedlings were killed by voles. Thus, we suggest that the probability of survival for tree seedlings in old fields depends strongly on the phase of the vole density cycle. In addition, we expect that seedlings invading habitat types in which food or cover was insufficient to support cycling populations of voles may never experience high predation rates.

Seedlings invading during a low phase in a vole cycle have a relatively high probability of surviving vole predation. Those that do survive appear to have a high likelihood of surviving the next peak in vole numbers via an escape in size. For both white ash and white pine, <7% of seedlings in the large size class, representing seedlings  $\approx 2$ –3 yr old, were killed by voles, in contrast to >20% predation on small ( $\approx 1$  yr old) white ash seedlings. Even among small size classes, certain species of seedling, particularly white pine (see *Results: Seedling predation*, above) and eastern hemlock (Ostfeld and Canham 1993) were avoided by voles. Thus, habitat types that support dense populations of meadow voles appear to act as a filter (Pickett and Cadenasso 1995) facilitating invasion by particular coniferous tree species over a set of commonly invading deciduous species, such as red maple, white ash, and *Ailanthus*.

Even under conditions when predation rates on seedlings were expected to be high, i.e., when vole density

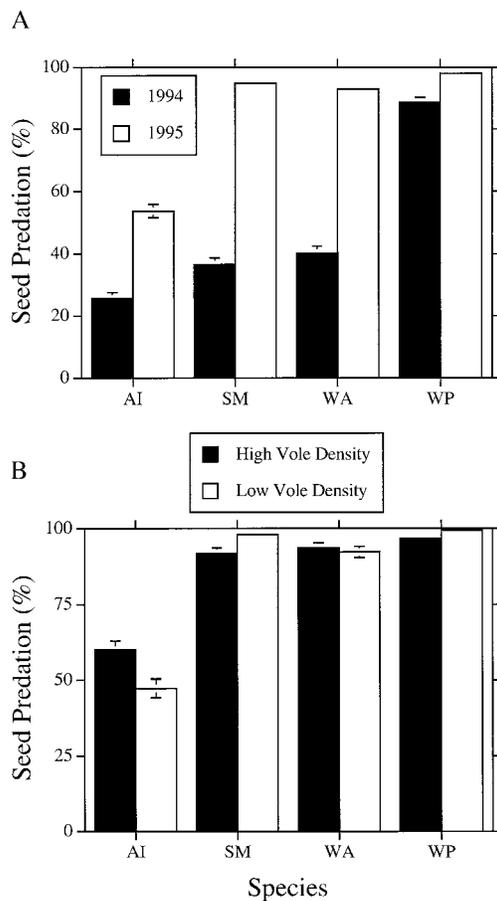


FIG. 6. Predation rates on four species of seed, where AI = *Ailanthus*, SM = sugar maple, WA = white ash, and WP = white pine. (A) Comparison of rates for 1994 and 1995. (B) Comparison of low-vole-density and high-vole-density treatments in 1995. Data show means  $\pm 1$  SE.

was relatively high and seedlings were small, predation rates were very low ( $\approx 5\%$ ) at the forest-field edge and 5 m into the forest (Fig. 4). Heavier seedling predation rates in old fields compared to adjacent forests also have been observed by Myster and McCarthy (1989), Myster and Pickett (1992), and Rankin and Pickett (1989). However, in the present study, predation rates increased rapidly from the edge to 5 m into the field, suggesting that seedling predation helps maintain the position of the forest edge, preventing or at least slowing the rate of encroachment.

#### Seed predation

In a recent paper, Hulme (1993) reviewed 36 studies of post-dispersal seed predation by rodents in a variety of habitat types, including both temperate and tropical forests, grasslands, and deserts. The majority of studies cited revealed significant variation in predation rates as a function of habitat type, seed species, and time. However, few general patterns emerge from these studies. For instance, predation rates may be heavier in

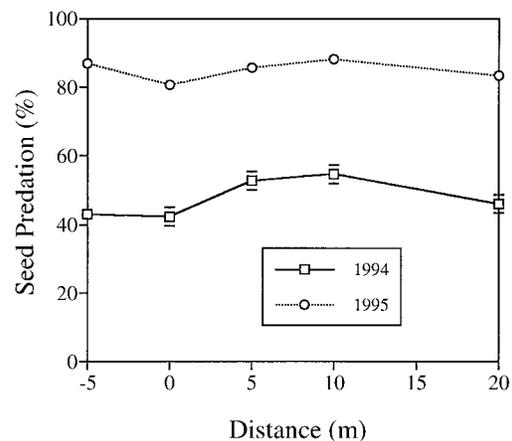


FIG. 7. Seed predation in 1994 and 1995 as a function of distance from the forest edge (see Fig. 4 legend for explanation of x-axis scale).

forests than in adjacent old fields or gaps (Webb and Willson 1985, Schupp 1988, Whelan et al. 1991, Myster and Pickett 1993), or the reverse (Willson and Whelan 1990, Whelan et al. 1991). Preference rankings of seed predators for various seed species may differ among old fields of different ages (Myster and Pickett 1993). Predation rates may be higher under woody or tall herbaceous vegetation (Bowers and Dooley 1993, Myster and Pickett 1993) or in open gaps (Whelan et al. 1991). Within temperate old fields and forests, post-dispersal predation on tree seeds is due predominantly to small mammals, as opposed to birds or insects (Webb and Willson 1985, Whelan et al. 1991, Ostfeld et al. 1994). We suspect that the spatial and temporal variation observed in various studies of seed predation is due to variation in the density, species composition, and habitat selection of small-mammal seed predators. These variables have seldom been quantified adequately in conjunction with seed predation studies in old fields.

One clear source of variation in seed predation rates within our enclosures was density of herbivorous meadow voles. In both years of our study, high-density populations of meadow voles discouraged use of the old-field sites by white-footed mice (Figs. 2, 3), as was also found by Grant (1972). In 1994, when mouse density was generally low, high density of voles was sufficient to significantly reduce seed predation rates by mice. However, in 1995, when mouse density was generally high, the inhibition of mice by high densities of voles was insufficient to reduce seed predation rates (see also Bowers and Dooley 1993). Rather than reducing overall predation rates by mice, high densities of voles appeared to change the foraging strategies of mice, causing them to opportunistically consume higher numbers of the least preferred species, *Ailanthus* (Fig. 6B). We suggest that unmeasured variation in density of voles in old fields may have been responsible

for some of the conflicting results obtained in prior studies of seed predation (Hulme 1993).

Variation in mouse density had two clear effects on patterns of seed predation. First, when density of mice was high (1995), predation rates on the most highly preferred species, white pine, did not change substantially, but those on the least preferred and intermediate species increased dramatically (Fig. 6A). Predation on sugar maple and white ash seeds, which were of intermediate ranking when mouse density was low (1994), was nearly equivalent to that on white pine when mouse density was high (1995). Predation rates on *Ailanthus* remained lowest even when mouse density was high, but more than doubled from 1994 to 1995. We suspect that, when population density is high, per capita food availability for mice declines (Wolff 1985, Wolff et al. 1985), and that mice expand their diet to include nonpreferred species (Ebersole and Wilson 1980). Second, when mouse density was low, seed-predation rates clearly were higher at 5 m and 10 m into the old field than at the forest-field edge, or farther into the interior of the forest or field. No significant effect of distance from edge occurred under conditions of high mouse density (Fig. 7). These results did not coincide with our prediction that seed predation rates would be higher within the forest and at the edge than within the field. However, the effect of heavy seed predation within 10 m of the forest edge reinforced patterns we observed with seedling predation, in maintaining current positions of forest-field edges.

#### *Integrating seedling and seed predation*

As old fields undergo succession from herbaceous to woody plant communities, their quality for different species of small-mammal consumers also changes. In earlier seral stages when old fields tend to be dominated by grasses and forbs, habitat quality for voles is generally high (Getz 1985, Rose and Birney 1985), and herbivory by voles may strongly inhibit tree invasion, particularly by palatable species such as maples, white ash, and *Ailanthus*. However, vole populations fluctuate dramatically even in high quality habitats (Batzli 1992, Ostfeld 1992), and we expect seedling predation to be relaxed during low phases. Invasion by unpalatable species such as pines and hemlock may occur even in the presence of dense populations of voles. Once shrubs and trees begin to invade old fields, habitat quality for voles deteriorates, but for mice it tends to increase (Kaufman and Kaufman 1989). In intermediate stages, when a heterogeneous mixture of grasses, forbs, and shrubs coexists, voles and mice also are likely to coexist (Bowers and Dooley 1993). In sites or years when voles dominate, recruitment by the primary deciduous invaders is expected to be low or nonexistent, particularly at distances  $\geq 5$  m from the forest edge. However, in years or sites when mice dominate, recruitment by pines is expected to fail, and deciduous invaders, particularly *Ailanthus*, will be favored. Predation on seeds

is relaxed only at the forest-field edge and  $\geq 20$  m into the field. Thus, in terms of their effects on tree invasion, mice and voles clearly are not functionally redundant. In conclusion, the composition of the small-mammal community in old fields appears likely to profoundly affect: (1) the rate of tree invasion, (2) the species composition of invaders, (3) the size (age) structure of invading trees, (4) the distance from the edge at which survival is most likely, and (5) the spatial pattern of invading trees.

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