Effects of Meadow Vole Population Density on Tree Seedling Survival in Old Fields

Richard S. Ostfeld; Charles D. Canham

EFFECTS OF MEADOW VOLE POPULATION DENSITY ON TREE SEEDLING SURVIVAL IN OLD FIELDS[1]

RICHARD S. OSTFELD AND CHARLES D. CANHAM

*Institute of Ecosystem Studies, The New York Botanical Garden, Mary Flagler Cary Arboretum,
Box AB, Millbrook, New York 12545 USA*

Abstract. Voles (Mammalia: Arvicolidae) are reported to be key consumers of tree seedlings in some habitats, but their importance in old-field succession is not known. Natural populations of voles fluctuate widely in density, and we sought to determine the effects of vole density on seedling predation. We used a randomized block design, with meadow voles maintained at three density levels (low, medium, high; three replicates of each) in field enclosures for 17 mo. We introduced young seedlings of five tree species into the enclosures. Three cohorts of seedlings were planted under intact vegetation, and one was planted in small areas from which we had cleared all vegetation. Overall predation rates were high for all cohorts planted under intact vegetation. There was a significant effect of vole density on seedling predation rates for two of these three cohorts; nearly all seedlings were destroyed in enclosures with high vole density. Predation rates by voles were highest for white ash and red maple, intermediate for white pine, and lowest for eastern hemlock and red oak. For the cohort planted in small clearings, mean predation rates were low and there was no density effect. Spatial variation in seedling predation rates was higher in enclosures with low and medium densities of voles than in high-density enclosures. In three of the cohorts there was a significant block effect, with the same block consistently having the highest predation rates. Evidence suggests that the block effect was caused by genetic differences among voles. Seedling predation by voles can: (1) delay old-field succession by reducing the number of tree invaders; (2) create patchiness by concentrating surviving seedlings in certain microsites; and (3) alter relative abundances of invading species via differences in palatability or apparency. We suggest that the population dynamics of voles be viewed as a *keystone process* in old-field succession.

Key words: density dependence; herbivory; keystone process; Microtus pennsylvanicus; old-field succession; tree invasion; tree seedlings; voles.

INTRODUCTION

In many terrestrial habitats of eastern North America dominance by herbaceous vegetation occurs only in early stages of succession after natural disturbance or release from farming or other human management (Marks 1983). Seedlings of trees and shrubs often persist under the herbaceous canopy for several years, but eventually saplings emerge and begin to shade plants of smaller stature, giving rise to rapid and profound changes in community structure and composition (e.g., Pickett 1982). Eventually, most communities develop into forests or shrub thickets. Factors affecting the survival of tree seedlings within herbaceous communities are fundamental to this process of old-field succession.

Invasion of herbaceous communities by tree seedlings can be affected by small mammals (Myster and McCarthy 1989, De Steven 1991), especially voles (family Arvicolidae) (Gill and Marks 1991). Although the diet of voles consists primarily of grasses, sedges, and forbs (Batzli 1985, Ostfeld 1985), these rodents are known to gnaw tree seedlings and saplings, and are sometimes an important agent of tree mortality (Byers

1985, Rousi et al. 1990). Voles are capable of killing tree seedlings by severing the main stem near ground level or uprooting the entire seedling.

The impact of voles on tree seedlings and saplings, and thus their importance in successional processes, varies tremendously in space and time (Gill and Marks 1991), but the causes of this variation are unknown. Population density of many vole species is known to fluctuate an order of magnitude or more, often with fairly regular peaks every 3–5 yr (e.g., Hansson and Henttonen 1990). In some forest plantations, damage by voles coincides with outbreak years and is minimal or absent otherwise (Rousi 1988). Therefore, it is possible that gnawing on trees is a response by voles to nutritional and other stresses associated with peak densities. Alternatively, some tree herbivory may occur at all densities, but cumulative damage may be noticeable only at vole peaks.

Voles show distinct food preferences for certain species of herbaceous plants, and their foraging behavior can rapidly change the composition of plant communities, especially at high vole densities (e.g., Batzli and Pitelka 1971, Cockburn and Lidicker 1983, Batzli 1985). Preferences by voles for particular tree species (Bucyanayandi et al. 1990) may cause differential mortality

among seedlings and strongly influence the likelihood that these species will successfully invade old fields. In addition, because voles rely on vegetative cover for protection from predation (Birney et al. 1976), the location of a tree seedling (under cover or in the open) is likely to have a strong effect on its probability of being killed by a vole.

In this report we describe an experimental approach to understanding the importance of meadow vole (*Microtus pennsylvanicus*) density to tree seedling survival within herbaceous communities. Our general goals are to understand: (1) the effects of vole population dynamics on the rate and direction of old-field succession; and (2) the factors affecting the likelihood that individual seedlings will escape from vole predation. To this end we tested whether vole density affects predation on tree seedlings, and if so whether the effect varies with species of tree seedling. In addition, we tested for differences in the effects of vole density when tree seedlings were placed in small clearings vs. under intact vegetation.

MATERIALS AND METHODS

Study site and experimental design

We performed a series of experiments in a 2-ha old field on the property of the Mary Flagler Cary Arboretum of the Institute of Ecosystem Studies in Dutchess County, southeastern New York. The field had been mown every 1–2 yr since abandonment from corn cultivation in the early 1970s. Dominant plants in the field included the grasses *Bromus inermis, Poa pratensis, Arrhenatherum elatius,* and *Phleum pratense* and the forbs *Galium mollugo, Solanum carolinense, Glecoma hederacea, Oxalis repens, Potentilla* spp., *Hieracium pratense,* and *Solidago* spp.

We employed a randomized block design to study the effects of vole density on tree seedling survival. In May and June 1990 we constructed nine 40 × 40 m fenced enclosures (Fig. 1). Fences were made of 1.3 m wide galvanized hardware cloth (1.3 cm mesh), with 0.5 m belowground and 0.8 m aboveground. The nine enclosures were divided into three blocks. Blocks 1 and 2 were contiguous, and were separated from block 3 by a hedgerow (Fig. 1). The plant species composition of blocks 1 and 2 was similar, whereas block 3 was more mesic and had a higher percent cover of sedges (*Carex* spp.) and goldenrods (*Solidago* spp). The three enclosures within each block were assigned randomly to either a low, medium, or high vole density treatment giving us three replicates of each density level.

Manipulation of vole density

Live-trapping grids were established in June 1990 within each enclosure. Each grid consisted of 25 trap stations 7.5 m apart, with 5 m between the outermost trap stations and the fence. Initially, one Longworth live trap was placed at each station; when vole density
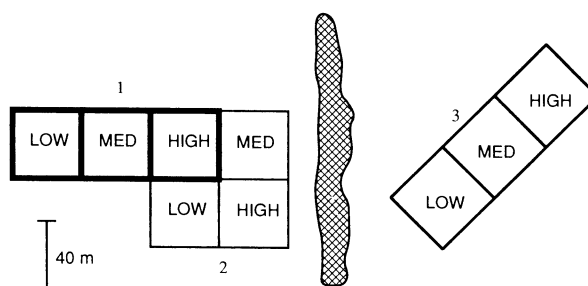

FIG. 1. Diagram of the study site, consisting of nine 0.16-ha enclosures divided into three blocks, as represented by different line thicknesses. Blocks 1 and 2 were separated from block 3 by a hedgerow, indicated by cross hatching. Within each enclosure was a trapping grid. Enclosures were assigned randomly to either low, medium, or high vole density treatments.

grew such that ≥80% of traps contained voles on any single trapping day, a second trap was placed at each station within that enclosure. Thus, high density enclosures typically had two traps per station. Traps were supplied with crimped oats for bait and cotton batting for insulation, and were covered with a board for protection from rain and snow. Traps were set for two consecutive nights every 2nd wk from June 1990 to November 1991. All small mammals captured (except shrews) were given individually numbered metal ear tags on first capture, and on all captures were checked for tag number, body mass, sex, reproductive condition, and trap station. All small mammals were then released at the point of capture. Traps were locked open between trap sessions. In addition to meadow voles, low numbers of shrews (*Blarina brevicauda* and *Sorex cinereus*), white-footed mice (*Peromyscus leucopus*), meadow jumping mice (*Zapus hudsonius*), and eastern chipmunks (*Tamias striatus*) were captured. None of these other species is herbivorous.

In late June 1990, vole density in all enclosures was reduced to two breeding pairs by removing adults and independent young. Vole density was subsequently managed at three different levels. Density of voles was estimated using the minimum number alive method (Krebs 1966). Designated high density enclosures were allowed to grow freely throughout the experiment. In low and medium density enclosures, vole numbers were regulated by removing subadults (20–30 g) during the regular trapping sessions. We avoided removing adults in order to minimize the impact on social organization, which is dominated by interactions among adults (Ostfeld 1985, Wolff 1985). For the medium density enclosures, if >15 adult + subadult voles were caught on day 1, the excess were removed on day 2. For the low density enclosures, voles were removed in excess of 5 adults + subadults. For both densities, fewer voles were removed if removing the excess would (1) require removing an entire litter, or (2) seriously alter the sex ratio. Voles removed from the enclosures were released several kilometers away. Due to high population growth

rates, during some seasons we trapped on selected low and medium density enclosures each week in order to maintain targeted densities. We felt it unnecessary to have a "no voles" control because we were able to ascribe virtually all seedling mortality (see below) to either vole predation or other causes.

In order to remove medium-sized herbivorous mammals common in the area, such as woodchucks (*Marmota monax*) and eastern cottontails (*Sylvilagus floridanus*), we set six Tomahawk live traps for five consecutive days in each of the enclosures during July 1990. One woodchuck was captured and removed; no further evidence of the presence of woodchucks or rabbits was detected. Feces and other sign of white-tailed deer (*Odocoileus virginianus*) were seen inside the enclosures occasionally in June–August 1990, but not thereafter.

Introduction and monitoring of seedlings

Tree seedlings were introduced to the enclosures in four distinct cohorts. Cohort 1 was introduced in September 1990. At a distance of 1–2 m from each of five randomly chosen trap stations within each enclosure, 10 16-mo-old red maple (*Acer rubrum* [Aceraceae]) seedlings and 5 16-mo-old white ash (*Fraxinus americana* [Oleaceae]) seedlings were planted. Seedlings were arranged in three parallel rows of five seedlings each, with 40 cm between seedlings and rows. The row of white ash seedlings was placed between the two rows of red maple seedlings. For this and all other cohorts, seedlings were planted in holes made with the sharp end of a pickaxe or a trowel, and were watered immediately after planting but not thereafter. Latex or cotton gloves were worn during planting.

Cohort 2, planted in November 1990, consisted of two parallel rows of five 30-mo-old red maple seedings, placed 40 cm apart, at each of two randomly chosen trap stations per enclosure.

For cohort 3, 6-wk-old seedlings of red oak (*Quercus rubra* [Fagaceae]), red maple, white pine (*Pinus strobus* [Pinaceae]), and eastern hemlock (*Tsuga canadensis* [Pinaceae]) were planted in June 1991 at each of three randomly chosen stations per enclosure. At each station, the seedlings were planted into an array of four rows, with 30 cm between seedlings and rows. Each row consisted of 10 seedlings of a given species, and the row position of each species was randomized. Cohorts 1–3 were planted under intact vegetation.

For cohort 4, all aboveground and overhanging vegetation was clipped from three randomly located 60 × 330 cm quadrats per enclosure. Resprouting vegetation was treated with the herbicide Roundup (glyphosate) to create patches of bare soil. In July 1991, 10 8-wk-old red oak seedlings were planted 30 cm apart in a single row in the middle of each cleared quadrat. Thus the seedlings were 30 cm from the edge of the intact vegetation.

Seedlings from all species were germinated from commercially obtained seed and grown in a lath house (two growing seasons for cohort 1, three growing seasons for cohort 2) or a greenhouse (6–8 wk for cohorts 3 and 4). The only exception was for red maple seedlings in cohort 3, which were collected as naturally occurring, newly germinated seedlings from a local forest. Seedlings for cohorts 1 and 2 had no leaves and were winter-hardened at the time they were planted.

Seedlings were monitored approximately on a monthly basis from the time of planting to the end of the study. The fate of each seedling was categorized as: Live (no sign of predation); Damaged Live (gnawed leaves, stem, or terminal bud but still alive); Damaged Dead (evidence of gnawing and dead); Dead (intact dead seedling with no sign of predation); Missing (seedling not found despite locating site); and Unknown (planting site not located; this applied to only three seedlings in cohort 3). For our analysis, Missing seedlings were considered Damaged Dead. We are confident that this was correct in almost all cases because: (1) Seedlings were planted in precisely designated locations, and the chances that an existing seedling was missed were extremely small; therefore, Missing seedlings were truly gone. (2) Often there were signs of vole activity, e.g., diggings, runways, or feces, within a few centimeters of the Missing seedlings. (3) There were no other mammalian herbivores present in the enclosures. Two other potential causes of disappearance, i.e., snail and slug herbivory and frost heaving, were deemed unlikely. Most seedlings were large and woody enough that snails and slugs were incapable of removing them completely (cohort 3 is one possible exception). Moreover, no molluscs were active at the time of planting cohort 2 (November 1990; R. S. Ostfeld and C. D. Canham, *personal observations*), which experienced the most immediate and severe predation (see *Results: Seedling predation*). No evidence of frost heaving was found; frost heaving was a rare cause of seedling mortality within intact vegetation in an old field in south-central New York (Gill and Marks 1991).

Statistical analyses

We used analysis of variance of the randomized block design to examine the effects of tree species, vole density, and block on seedling predation rate (SAS 1987). Predation rates were transformed with an angular transformation ($\arcsin(\sqrt{x})$) before the analyses. We have presented only the results of the final census taken for each cohort because (1) in almost all cases, treatment effects, if they appeared at all, were present in all census periods, and (2) differences in the cumulative predation rates at the end of the experiment are more relevant to the demography of tree invasion in these communities than any transient differences in seedling predation rate on interim dates. We have also used data on predation rates at the three to five individual
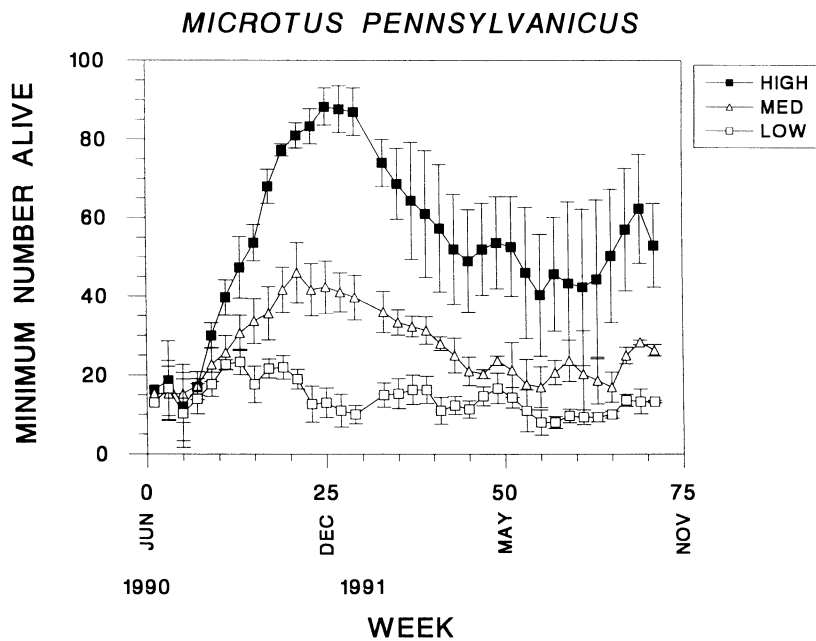
MICROTUS PENNSYLVANICUS

FIG. 2. Population density (minimum number alive) of meadow voles in the three density treatments through time. Values are means (± 1 SE) of the three replicates of each density level.

stations used within each enclosure for cohorts 1 (red maple only) and 3 to examine vole density effects on variability in predation rates within enclosures. For this analysis, the standard deviation (rather than the mean) of the untransformed predation rates for the stations within each enclosure was used as the dependent variable in an ANOVA. All of these analyses treated individual enclosures as the unit of replication (i.e., $n = 3$ for each density level). Thus, the two to five stations within each enclosure were pooled for estimates of predation rate. Although the enclosure is clearly the most appropriate level of replication for our experimental design, it reduces the power of the analyses to detect significant effects of the density treatments. Whereas the two to five individual stations within each enclosure represent pseudoreplicates (sensu Hurlbert 1984) in that they are all located within the same 40 × 40 m enclosure, our data on vole movement (R. S. Ostfeld and C. D. Canham, *unpublished data*) show that voles were rarely caught at traps adjacent to more than one of the individual stations. Thus, the predation rates at individual stations reflected the activity of different animals. It can also be argued that the station-level analysis is at a more appropriate spatial scale from the point of view of tree invasion in old fields than the larger, enclosure-level analysis. For these reasons, we have also done ANOVAs on mean predation rates using individual stations as the unit of replication in cases where the results of the more conservative enclosure-level analyses were not significant. Pairwise comparisons among treatment means were done using the REGWF test in PROC GLM in SAS to control for the experimentwise error rate (SAS 1987).

RESULTS

Vole density

By late August 1990, the densities of meadow voles (adults, subadults, and juveniles) in the low, medium, and high density treatments were distinctly different, and remained different throughout the remainder of the study (Fig. 2). Density on one of the high density enclosures declined during midsummer of 1991 to approximately the same level as the medium density enclosure from that block (block 3). By late summer, however, recruitment had restored population size on that enclosure to a higher level. Averaged over the whole study period, vole densities under the three different treatments were equivalent to ≈75, 180, and 380 voles/ha, for low, medium, and high density, respectively. All these densities fall within the range of naturally occurring densities for this species (Boonstra and Rodd 1983, Taitt and Krebs 1985). However, typical low densities for unenclosed populations of this species are on the order of 10–50 voles/ha (Taitt and Krebs 1985). Such low densities could not be maintained in the enclosures due to the risks of extinction in low density enclosures.

Seedling predation

Cohort 1.—More than 80% of red maple and white ash seedlings had been killed by voles on high vole density treatments within 1 mo after planting. After 1 yr, cumulative predation reached 96.0% for each species (Fig. 3). Red maple seedlings on medium density treatments experienced mortality similar to high density treatments (Fig. 3A), and both maple and white
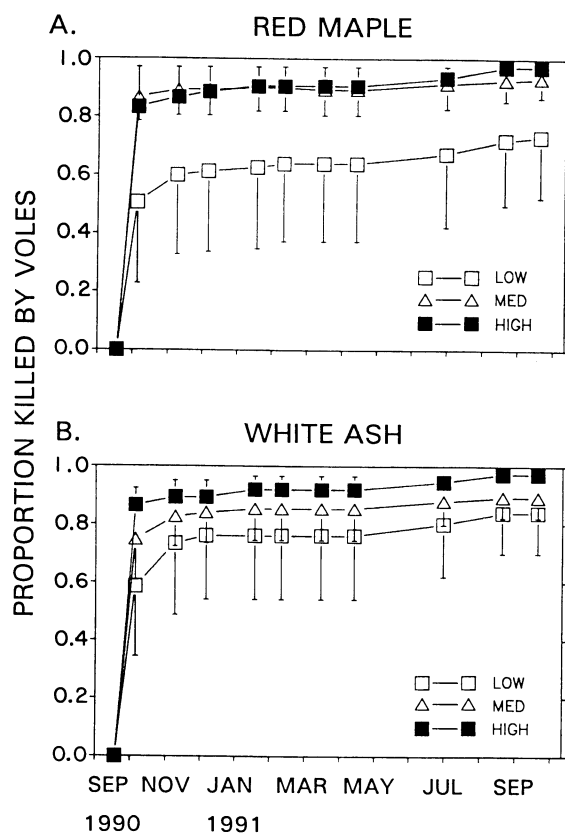
A. RED MAPLE

B. WHITE ASH

FIG. 3. Cumulative proportion of cohort 1 tree seedlings killed by voles in the three density treatments. Values are means (± 1 SE) of the three replicates of each density level.

ash seedlings reached an apparent asymptote of 93.3 and 89.3% cumulative predation, respectively, after 1 yr on medium density treatments. On low density treatments, predation was substantially less intense only for red maple, reaching 50.7% after 1 mo and 73.3% after 1 yr. For white ash, predation even on low density treatments reached 84.0% after 1 yr (Fig. 3B). Given the high degree of between-enclosure variability in predation, particularly in low density treatments (Fig. 3), the enclosure-level ANOVA showed no significant effect of vole density on seedling predation for either red maple or white ash. The ANOVA did reveal a block effect ($F_{2, 12} = 12.17$, $P = .0013$), with block 1 having the highest predation rate. An analysis at a smaller spatial scale, using individual stations as replicates, showed a highly significant effect of vole density on seedling predation, with no difference between red maple and white ash (density: $F_{2, 84} = 8.61$, $P < .001$; species: $F_{1, 84} = 0.80$, $P = .38$).

Cohort 2. — Within 10 d after planting, 91.1% of red maple seedlings in high density treatments had been killed by voles. After 1 mo, predation reached 95.6%, and gradually climbed to 97.8 $\pm$ 1.1% (mean $\pm$ 1 SE) after 11 mo. On the low and medium density treatments, predation after 10 d was 60.0 and 62.2%, respectively. Over the following 10 mo cumulative pre-

dation climbed gradually to 76.7 $\pm$ 16.7% and 75.5 $\pm$ 21.2%, respectively.

Given the high variability in predation among low and medium density grids, neither the enclosure-level nor station-level ANOVAs showed statistically significant effects of vole density on seedling predation. A block effect was not detected for this cohort.

Cohort 3. — For all four species, predation occurred soon after planting and increased only modestly over the following 4 mo. ANOVA at even the conservative enclosure level showed significant effects of vole density, tree species, and block (density: $F_{2, 28} = 5.35$, $P = .011$; species: $F_{3, 28} = 2.98$, $P = .048$; block: $F_{2, 28} = 3.79$, $P = .035$). Predation was consistently lowest on low density treatments (Fig. 4). The ranking of predation among tree species was red maple > white pine > eastern hemlock > red oak, although only red maple and red oak were significantly different in pairwise comparisons. Block 1 again had a significantly higher predation than the other two blocks.

Cohort 4. — Predation on red oak seedlings planted in small clearings was much lower than observed for any of the cohorts of seedlings planted under intact vegetation. Predation was not significantly different among the density treatments, ranging from 26.7 $\pm$ 25.0% (mean $\pm$ 1 SE) for low density, 18.8 $\pm$ 17.2% for medium density, to 20.0 $\pm$ 20% for high density enclosures after 4 mo. Virtually all predation occurred in block 1, resulting in a significant block effect (block: $F_{2, 4} = 93.62$, $P < .001$).

Within-grid variability. — In addition to the substantial degree of variability at the between-enclosure level (as measured by the standard errors in Figs. 3 and 4 and the block effects), predation also varied among stations within enclosures. Cohorts 2 and 4 were not examined for within-enclosure variability due to the low number of stations used in cohort 2, and the low predation in cohort 4. Similarly, white ash in cohort 1 was not analyzed because of the low number of seedlings planted at individual stations. For cohort 1, within-enclosure variability was highest for the medium density treatments (standard deviations of cumulative proportion of seedlings killed by predators [$n = 5$ stations per enclosure]: low = 0.059; medium = 0.123; high = 0.041). Block 1, with the highest average predation, had the lowest variability in predation within enclosures (SD = 0.030 vs. 0.123 for block 2 and 0.070 for block 3); however, the differences among density treatments and blocks for cohort 1 were not significant. For three of the four species in cohort 3, low and medium density treatments had the highest within-enclosure variation in seedling predation (Fig. 5). Although the effect was strongest during intermediate census periods, vole density still had a marginally significant effect on variability in predation at the final census ($F_{2, 33} = 2.74$, $P = .08$) (Fig. 5). Enclosure-level ANOVA revealed no species or block effect on within-enclosure variability in predation for cohort 3. Our results
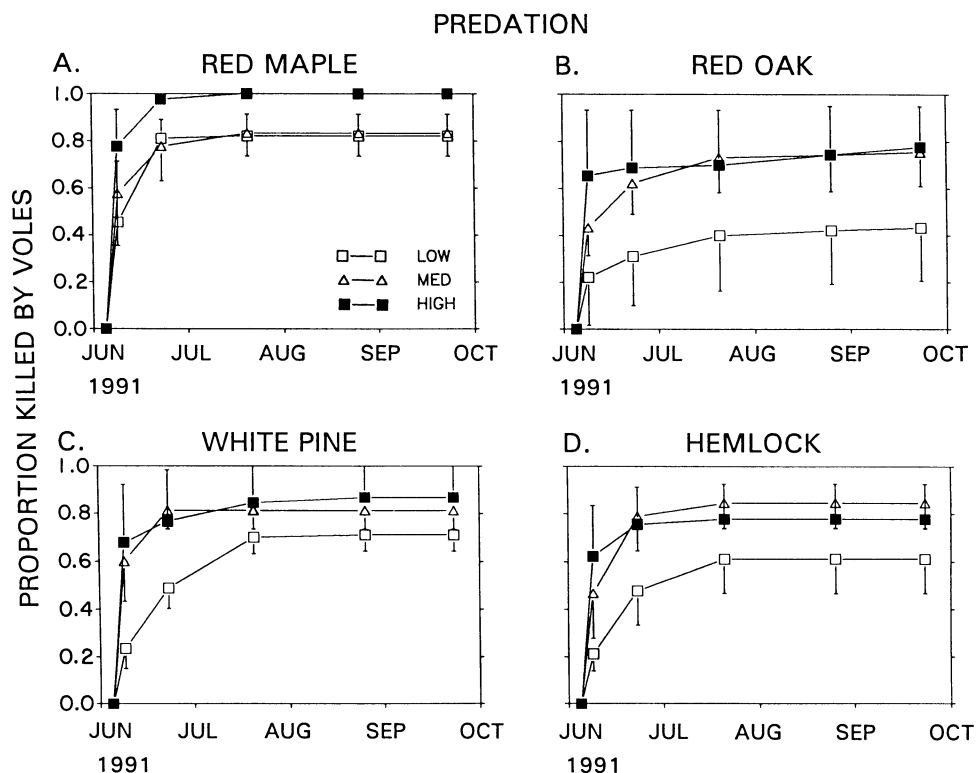
PREDATION

FIG. 4. Cumulative proportion of cohort 3 tree seedlings killed by voles in the three density treatments. Values are means (± 1 SE) of the three replicates of each density level.

suggest that high vole densities will result in fairly uniformly high seedling predation; however, low and even medium vole densities can give rise to highly variable seedling predation within areas the size of our 0.16-ha enclosures.

DISCUSSION

Our experiments confirm recent conclusions that meadow voles are voracious predators of tree seedlings in old fields (Gill and Marks 1991), and that seedling predation by mammals (including voles, gophers, woodchucks, rabbits, and deer) can play an important role in affecting the rate and direction of old-field succession (Huntly and Inouye 1988, Myster and McCarthy 1989, Rankin and Pickett 1989, De Steven 1991, Gill and Marks 1991). Although previous studies have documented high levels of herbivory by mammals, there has been little effort to identify the species of herbivore responsible for seedling predation or the effects of herbivore population dynamics on patterns and rates of herbivory. Our results show that even when larger mammalian herbivores are excluded, meadow voles alone can have a profound effect on tree seedling survival, and that the intensity and spatial pattern of herbivory depend on vole density.

For all three cohorts of seedlings planted under intact vegetation, predation exceeded 40% (averaged across replicates) within 1–2 mo, irrespective of vole density

or species of seedling. Predation leveled off rapidly, reaching asymptotic levels varying from $\approx 50\%$ (red oak under low vole density; Fig. 4) to near 100% (red maple under high vole density; Fig. 3). There was a clear effect of vole density on predation for two of these three cohorts, and mean predation always was highest in high vole density treatments. Predation in medium density treatments was sometimes nearly equivalent to that in high density treatments (cohort 1; Fig. 3), and sometimes similar to that in low density treatments (cohort 2), indicating that the effects of vole density may incorporate thresholds rather than varying continuously. In contrast to seedlings planted beneath intact vegetation (cohorts 1–3), seedlings planted in small clearings (cohort 4) were much less likely to be killed by voles, as also shown by Gill and Marks (1991), and there was no effect of vole density on predation.

Small mammals are important predators of tree seedlings and saplings in Fennoscandia (Kanervo and Myllymäki 1970, Larsson 1975), England (Pigott 1985), Canada (Bucyanayandi et al. 1990), the United States (Huntly and Inouye 1988, Myster and McCarthy 1989, De Steven 1991, Gill and Marks 1991) and Chile (Murua and Rodriguez 1989). Despite anecdotal observations of damage coinciding with outbreaks of small mammals (Myllymäki 1977, Rousi 1988), our study is the first to show experimentally a relationship between small mammal density and seedling predation.
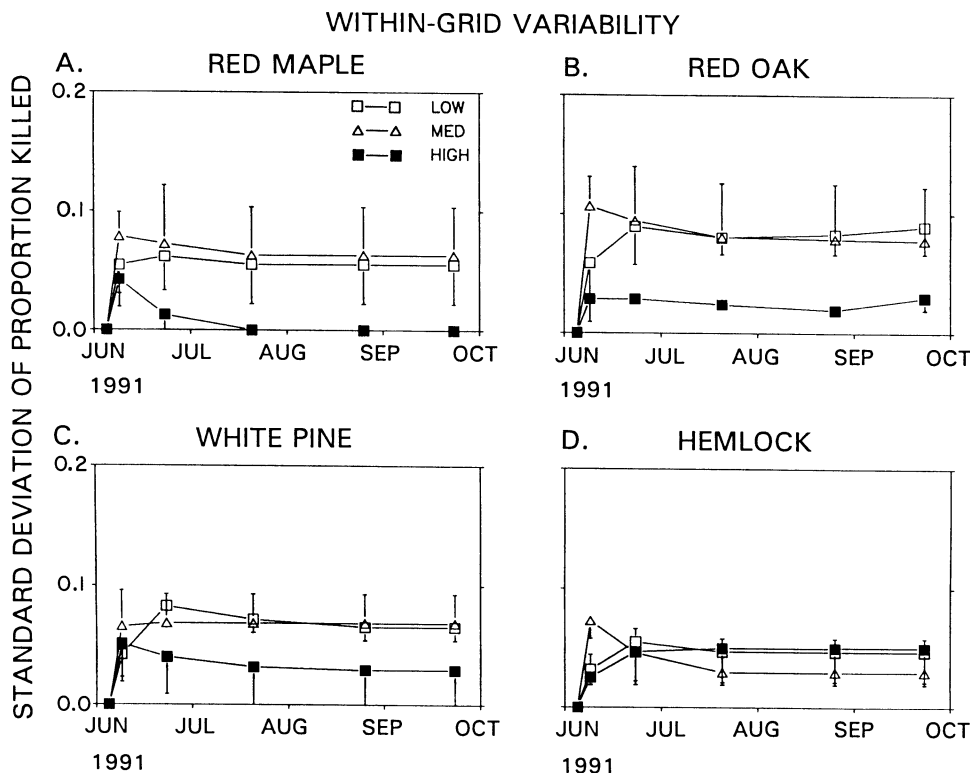
WITHIN-GRID VARIABILITY

FIG. 5. Degree of variability among stations (within each grid) in predation rates for cohort 3 seedlings. Values are means (±1 SE) of the standard deviations of the three replicates within each density level.

Populations of many species of voles, including *M. pennsylvanicus*, fluctuate cyclically with 3–4 yr between peaks (e.g., Taitt and Krebs 1985, Hansson and Henttonen 1990). The densities at which we maintained vole populations were representative of the natural range of density variation in this species, with the possible exception of the very low phase of the natural cycle. Because seedling predation was substantial even where vole density was low, we expect that under natural conditions voles will have a consistently strong negative impact on tree seedling survival in old fields. However, since extreme levels of predation occurred primarily in high vole density treatments, we expect that virtually complete elimination of cohorts of tree seedlings is episodic.

Lower predation under low vole density may be a result of a smaller proportion of space being used intensively by voles. At low population density, vole home ranges tend to be more widely spaced, and interstitial areas exist where little activity occurs (Ostfeld et al. 1985, Wolff 1985, Zwicker 1989). As density increases, the degree of overlap of home ranges of adjacent individuals increases, and interstitial areas tend to disappear (Gaines and Johnson 1982, Ostfeld et al. 1985). On a broader spatial scale, the degree of homogeneity of habitat use increases with density in many vole species (Ostfeld 1992). Thus we hypothesize that refugia for seedlings from vole predation are more

common or more extensive at low than high vole density, giving rise to higher predation at higher vole density. This hypothesis is supported by the higher degree of within-enclosure (station-to-station) variation in seedling predation in low and medium density enclosures than in high density enclosures (Fig. 5).

Most seedling predation occurred quickly after seedlings were introduced, and there was relatively little predation after 1–2 mo. A similar pattern was observed by Myster and McCarthy (1989) and Gill and Marks (1991). It is possible that by planting seedlings we artificially attracted voles to their vicinity and inflated their likelihood of being killed. We doubt this is true, since our use of gloves avoided scent contamination, and we were careful to restore surrounding vegetation to its predisturbance conditions. Individual small-mammal herbivores tend to use ≈20%–50% of their entire home ranges each day (meadow voles and California voles (*M. californicus*): R. S. Ostfeld, *unpublished data*; cotton rats: Spencer et al. 1990). Thus, any individual vole is likely to visit its entire home range within a few days, which is likely to lead to a rapid response of voles to newly appearing seedlings.

We suspect that seedling predation has at best a minor functional role in the nutritional biology of meadow voles. The tree seedlings we planted cannot be an important component of the voles' diet because of their insignificant biomass, poor nutritional quality (Batzli

1985, Bergeron and Jodoin 1987), and potential toxicity (particularly the conifers: Roy and Bergeron 1990a). Seedlings for cohorts 1 and 2 had no leaves at the time they were planted (September and November, respectively). Moreover, many of the damaged seedlings were severed at or near ground level and left in place, indicating that they were rejected as food (but see Roy and Bergeron 1990b). Predation levels were approximately the same for cohort 3, planted in summer when food availability is high, as for cohorts 1 and 2, planted in autumn, when alternative foods are less abundant. We hypothesize that voles killed seedlings largely in the process of sampling (tasting) plants. If in the process of sampling potential food items, voles learn that seedlings are relatively unpalatable, then this would explain the observed rapid response to seedlings after introduction.

Our results show clear differences in levels of predation among tree species, with the following overall ranking: white ash > red maple > white pine > eastern hemlock > red oak. These differences were not simply due to differences in size or "woodiness." Although red maple tends to be the most "herbaceous," and red oak was the largest of the 6-wk-old seedlings in cohort 3, the 2-yr-old red maples from cohort 2, which were quickly decimated, were larger than the red oaks from cohort 3, which suffered the lowest predation. Species differences in predation probably represent differences in palatability or apparency. Differences in palatability among different provenances or species of tree seedlings have been shown for meadow voles in Quebec (Bucyanayandi et al. 1990, Roy and Bergeron 1990a) and field voles (*M. agrestis*) in Finland (Rousi 1988, Rousi et al. 1990).

For all cohorts block 1 had the highest predation, and for three of the four cohorts there was a highly significant block effect on seedling predation. However, this block effect was not a result of any habitat differences we could detect (cf. Bergeron and Jodoin 1989). Block 1 was contiguous with and similar to block 2, and these two blocks were much more similar to each other in community composition than either was to block 3. Overall, block 1 tended to have slightly lower vole density than the other two blocks. Thus we hypothesize that the voles in block 1 were intrinsically more likely to kill seedlings than were voles in the other blocks. These behavioral differences persisted from September 1990 (introduction of cohort 1) to June 1991 (introduction of cohort 4), during which there was >80% turnover of individuals in the vole population. Because there is little or no evidence for cultural learning in voles that could explain the persistence of their behavior across several generations (Wolff 1985), we hypothesize that this behavior has a genetic basis. Geographic variation in bark consumption that appears to be genetically based has been shown in bank voles (*Clethrionomys glareolus*) (Hansson 1986). Persistent differences among individual voles in their aggressiveness towards tree seedlings, whether or not they are heritable, may be critical in giving rise to spatial variation in seedling survival and old-field succession. Individual differences among animals are increasingly being viewed as essential to population dynamics (Łomnicki 1988, Pulliam 1989), and we suggest they may be important to community level interactions as well.

Variation in seedling predation as a result of fluctuating populations of small mammals is likely to be a major factor regulating the invasion of old fields by trees, and hence is critical to old-field succession. While some tree seedlings may become established immediately following abandonment of land from cultivation (e.g., Rankin and Pickett 1989), and before vole densities may have built up, successful tree invasion (i.e., emergence above the herbaceous or shrub canopy) often requires periods of >50 yr in the Hudson Valley (C. D. Canham, *personal observations*). During much of this period, old fields, particularly on mesic sites, have a dense herbaceous cover that provides suitable habitat for meadow voles. Moreover, many fields in the region are abandoned not from cultivation but from hayfields or pastures with an existing, dense herbaceous community.

Because the highest predation occurred at densities corresponding to a cyclic peak, and predation was relaxed somewhat at lower densities, we predict that seedlings invading in a nonpeak year will be more likely to escape from vole predation. Escape from predation will be particularly likely if seedlings grow to a size at which they are substantially less palatable before the next vole peak. However, this "escape in size" may require several years of growth. Therefore, we predict that both the timing and the magnitude of multiannual fluctuations in vole density will be critical to the process of tree invasion of old fields.

High spatial variation in predation at low and medium densities (Fig. 5) may offer some seedlings a high probability of escape simply by virtue of their location. Relaxed predation may occur in the interstices between vole home ranges, or in certain microsites that are less likely to be used by voles. Small disturbances clearly offer seedlings protection from vole predation.

We have not attempted to address the effects of seedling density on predation. Natural seed rain and germination patterns result in a continuum of local population sizes and distribution patterns of seedlings. In our experiments, seedlings consistently were planted with 30–40 cm spacing, but a wider or narrower spacing may affect predation. Individual seedlings that are within a local group may be more detectable, and therefore at higher risk of predation by foraging voles. Conversely, seedlings with many neighbors may be individually less likely to be killed by a vole than those that are more isolated.

We suggest that the population dynamics of voles be viewed as a keystone process in old-field succession.

This view differs from the keystone species concept (Paine 1969) in that the dynamical properties of the animal population, rather than simply its presence or absence, are emphasized (see also Hunter 1992). Seedling predation by voles can: (1) delay succession by reducing the number of tree invaders; (2) create patchiness by concentrating surviving seedlings in certain microsites; and (3) alter relative abundances of invading species via differences in palatability or apparency. Vole populations with different dynamical patterns, particularly their degree of "cyclicity" (Henttonen et al. 1985, Ostfeld 1988) may exert profoundly different effects on the rate and direction of succession.

LITERATURE CITED

Batzli, G. O. 1985. Nutrition. Pages 779–811 *in* R. H. Tamarin, editor. Biology of New World *Microtus*. American Society of Mammalogists Special Publication Number 8.

Batzli, G. O., and F. A. Pitelka. 1971. Condition and diet of cycling populations of the California vole, *Microtus californicus*. Journal of Mammalogy 60:740–750.

Bergeron, J. M., and L. Jodoin. 1987. Defining "high quality" food resources of herbivores: the case for meadow voles (*Microtus pennsylvanicus*). Oecologia (Berlin) 71:510–517.

Bergeron, J. M., and L. Jodoin. 1989. Plant composition in relation to vole damage in coniferous plantations. Forestry Chronicle 65:206–209.

Birney, E. C., W. E. Grant, and D. D. Baird. 1976. Importance of vegetative cover to cycles of *Microtus* populations. Ecology 57:1043–1051.

Boonstra, R., and F. H. Rodd. 1983. Regulation of breeding density in *Microtus pennsylvanicus*. Journal of Animal Ecology 52:757–780.

Bucyanayandi, J., J. Bergeron, and J. Menard. 1990. Preference of meadow voles (*Microtus pennsylvanicus*) for conifer seedlings: chemical components and nutritional quality of bark of damaged and undamaged trees. Journal of Chemical Ecology 16:2569–2579.

Byers, R. E. 1985. Management and control. Pages 621–646 *in* R. H. Tamarin, editor. Biology of New World *Microtus*. American Society of Mammalogists Special Publication Number 8.

Cockburn, A., and W. Z. Lidicker, Jr. 1983. Microhabitat heterogeneity and population ecology of an herbivorous rodent, *Microtus californicus*. Oecologia (Berlin) 59:167–177.

De Steven, D. 1991. Experiments on mechanisms of tree establishment in old-field succession: seedling survival and growth. Ecology 72:1076–1088.

Gaines, M. S., and M. L. Johnson. 1982. Home range size and population dynamics in the prairie vole, *Microtus ochrogaster*. Oikos 39:63–70.

Gill, D. S., and P. L. Marks. 1991. Tree and shrub seedling colonization of old fields in central New York. Ecological Monographs 61:183–206.

Hansson, L. 1986. Geographic, inherent variation in feeding behavior of a vole and its implications in pest control. Journal of Mammalogy 67:587–589.

Hansson, L., and H. Henttonen. 1988. Rodent dynamics as community processes. Trends in Ecology and Evolution 3:195–200.

Henttonen, H., A. D. McGuire, and L. Hansson. 1985. Comparisons of amplitudes and frequencies (spectral analyses) of density variations in long-term data sets of *Clethrionomys* species. Annales Zoologici Fennici 22:221–227.

Hunter, M. D. 1992. Interactions within herbivore communities mediated by the host plant: the keystone herbivore concept. Pages 288–326 *in* M. D. Hunter, T. Ohgushi, and P. W. Price, editors. Effects of resource distribution on animal–plant interactions. Academic Press, New York, New York, USA.

Huntly, N., and R. Inouye. 1988. Pocket gophers in ecosystems: patterns and mechanisms. BioScience 38:786–793.

Hurlbert, S. H. 1984. Pseudoreplication and the design of field experiments. Ecological Monographs 54:187–211.

Kanervo, V., and A. Myllymäki. 1970. Problems caused by field vole, *Microtus agrestis*, in Scandinavia. EPPO Bulletin 5:11–26.

Krebs, C. J. 1966. Demographic changes in fluctuating populations of *Microtus californicus*. Ecological Monographs 36:239–273.

Larsson, T. 1975. Damage caused by small rodents in Sweden. Ecological Bulletin (Stockholm) 19:47–56.

Łomnicki, A. 1988. Population ecology of individuals. Princeton University Press, Princeton, New Jersey, USA.

Marks, P. L. 1983. On the origin of the field plants of the northeastern United States. American Naturalist 122:210–228.

Murua, R., and J. Rodriguez. 1989. An integrated control system for rodents in pine plantations in central Chile. Journal of Applied Ecology 26:81–88.

Myllymäki, A. 1977. Outbreaks and damage by the field vole, *Microtus agrestis* (L.), since World War II in Europe. EPPO Bulletin 7:177–208.

Myster, R. W., and B. C. McCarthy. 1989. Effects of herbivory and competition on survival of *Carya tomentosa* (Juglandaceae) seedlings. Oikos 56:145–148.

Ostfeld, R. S. 1985. Limiting resources and territoriality in microtine rodents. American Naturalist 126:1–15.

———. 1988. Fluctuations and constancy in populations of small rodents. American Naturalist 131:445–452.

———. 1992. Small-mammal herbivores in a patchy environment: individual strategies and population responses. Pages 65–116 *in* M. D. Hunter, T. Ohgushi, and P. W. Price, editors. Effects of resource distribution on animal–plant interactions. Academic Press, New York, New York, USA.

Ostfeld, R. S., W. Z. Lidicker, Jr., and E. J. Heske. 1985. The relationship between habitat heterogeneity, space use, and demography in a population of California voles. Oikos 45:433–442.

Paine, R. T. 1969. A note on trophic complexity and community stability. American Naturalist 103:91–93.

Pickett, S. T. A. 1982. Population patterns through twenty years of old field succession. Vegetatio 49:45–59.

Pigott, C. D. 1985. Selective damage to tree-seedlings by bank voles (*Clethrionomys glareolus*). Oecologia (Berlin) 67:367–371.

Pulliam, H. R. 1989. Individual behavior and the procurement of essential resources. Pages 25–38 *in* J. Roughgarden, R. M. May, and S. A. Levin, editors. Perspectives in ecological theory. Princeton University Press, Princeton, New Jersey, USA.

Rankin, W. T., and S. T. A. Pickett. 1989. Time of establishment of red maple (*Acer rubrum*) in early oldfield succession. Bulletin of the Torrey Botanical Club **116**:182–186.

Rousi, M. 1988. Resistance breeding against voles in birch: possibilities for increasing resistance by provenance transfers. EPPO Bulletin **18**:257–263.

Rousi, M., H. Henttonen, and A. Kaikusalo. 1990. Resistance of birch (*Betula pendula* and *B. platyphylla*) seedlots to vole (*Microtus agrestis*) damage. Scandinavian Journal of Forest Research **5**:427–436.

Roy, J., and J. Bergeron. 1990a. Role of phenolics of coniferous trees as deterrents against debarking behavior of meadow roles (*Microtus pennsylvanicus*). Journal of Chemical Ecology **16**:801–808.

Roy, J., and J. Bergeron. 1990b. Branch-cutting behavior by the vole (*Microtus pennyslvanicus*): a mechanism to decrease toxicity of secondary metabolites in conifers. Journal of Chemical Ecology **16**:735–741.

SAS. 1987. SAS/STAT guide for personal computers. Version 6 edition. SAS Institute, Cary, North Carolina, USA.

Spencer, S. R., G. N. Cameron, and R. K. Swihart. 1990. Operationally defining home range: temporal dependence exhibited by hispid cotton rats. Ecology **71**:1817–1822.

Taitt, M. J., and C. J. Krebs. 1985. Population dynamics and cycles. Pages 567–620 *in* R. H. Tamarin, editor. Biology of New World *Microtus.* American Society of Mammalogists Special Publication Number **8**.

Wolff, J. O. 1985. Behavior. Pages 340–372 *in* R. H. Tamarin, editor. Biology of New World *Microtus.* American Society of Mammalogists Special Publication Number 8.

Zwicker, K. 1989. Home range and spatial organization of the beach vole, *Microtus breweri.* Behavioral Ecology and Sociobiology **25**:161–170.