The effects of tree seed and seedling density on predation rates by rodents in old fields[1]

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Abstract: Seed and seedling predation by rodents along forest-field edges can influence the dynamics of tree invasion into old fields. As predicted by the Janzen-Connell escape hypothesis and the predator satiation hypothesis, the effects of rodents on tree propagules may be modified by variation in the distribution and abundance of tree propagules. We tested these hypotheses in old-fields using a series of U-shaped enclosures in southeastern New York State. We maintained two densities (high *versus* low) of meadow voles (*Microtus pennsylvanicus*), which are the principal seedling predators and dominant rodent competitors at our sites. High density of voles significantly reduced density of white-footed mice (*Peromyscus leucopus*), which are the primary seed predators. Within enclosures we manipulated the density and spacing of red maple (*Acer rubrum*) seeds and black birch (*Betula lenta*) seedlings. We used three densities of red maple seeds (1500, 750, and 150 seeds/2 m²) arranged to mimic natural leptokurtic declines in seed density with distance from a hypothetical seed source. The density of black birch seedlings was also manipulated at three levels (50, 20, and 10 seedlings/ 2 m²). Seed predation was uniformly high overall (approx. 99%) in three adjacent plots irrespective of seed density. However, predation was significantly lower in isolated, low-density plots. These results suggest that mice were not satiated by the range of seed densities typical for old fields and instead foraged in a distance-responsive manner consistent with predictions of the escape hypothesis. In contrast, seedlings in high density plots experienced significantly lower predation than those in medium- and low-density plots, suggesting that voles were satiated by plots of high seedling density. These patterns were clearest within enclosures having high vole density, highlighting the importance of competitive interactions in modifying the foraging decisions of rodents in old fields.
Keywords: tree invasion, seed predation, seedling predation, escape hypothesis, predator satiation, *Peromyscus leucopus*, *Microtus pennsylvanicus*, old field, seed density, seed distribution, seedling density, herbivory.

Résumé: La prédation exercée par les rongeurs sur les graines et les plantules le long des bordures entre les champs et les forêts peut influencer la dynamique d'invasion des champs abandonnés par les espèces arborescentes. Comme le prédisent l'hypothèse de la fuite formulée par Janzen et Connell ainsi que l'hypothèse de la satiation des prédateurs, l'effet des rongeurs sur les propagules d'espèces arborescentes peut être modifié par la répartition et l'abondance des propagules. Nous avons testé ces hypothèses dans des champs abandonnés en utilisant une série d'enclos en U, dans la section sud-est de l'état de New York. Nous avons maintenu deux densités (élevée et faible) de *Microtus pennsylvanicus*, le principal prédateur sur les plantules et le rongeur dominant, au point de vue compétitif, sur nos sites. Une densité élevée de *Microtus* réduit de façon significative la densité de *Peromyscus leucopus*, un granivore important. À l'intérieur des enclos, nous avons contrôlé la densité et l'espacement de graines d'érable rouge (*Acer rubrum*) et de plantules de bouleau noir (*Betula lenta*). Nous avons utilisé trois densités de graines d'érable rouge (1500, 750 et 150 graines/m²) de façon à imiter une réduction progressive de la densité de graines avec la distance depuis une source hypothétique. La densité de plantules de bouleau noir a également été contrôlée à trois niveaux (50, 20 et 10 plantules/m²). La prédation sur les graines était uniformément élevée (*ca* 99 %) à l'intérieur des parcelles qui étaient rapprochées les unes des autres et ce, indépendamment de la densité de graines. Cependant, la prédation était significativement réduite sur les parcelles isolées les unes des autres et ayant une densité de graines plus faible. Ces résultats suggèrent que *Peromyscus* n'était pas rassasié pour la gamme de densités de graines typiques des champs abandonnés, mais plutôt qu'il récoltait les graines en fonction de la distance depuis la source, ce qui est en accord avec les prédictions de l'hypothèse de la fuite. Par contre, les plantules dans les parcelles à haute densité ont subi moins de prédation que celles des parcelles à moyenne et à faible densités, ce qui suggère que *Microtus* était rassasié sur les parcelles de densité élevée. Ces patrons étaient particulièrement évidents à l'intérieur des enclos à haute densité de *Microtus*, soulignant l'importance des interactions compétitives pour les décisions de récolte des rongeurs dans les champs abandonnés.
Mots-clés: champ abandonné, densité de graines, densité de plantules, granivorie, herbivorie, hypothèse de la fuite, invasion par des espèces arborescentes, *Microtus pennsylvanicus*, *Peromyscus leucopus*, prédation exercée sur les graines, prédation exercée sur les plantules, répartition de graines, satiation du prédateur.

Introduction

Tree invasion into temperate old fields often induces profound changes in species composition, shifting dominance from small herbaceous species towards later succession woody species (Buell *et al.*, 1971; Pickett, 1982). In the northeastern United States, predation on seeds and seedlings by white-footed mice (*Peromyscus leucopus*) and meadow

voles (*Microtus pennsylvanicus*), respectively, may play an important role in regulating the invasion of old fields by trees (Mittelbach & Gross, 1984; Gill & Marks, 1991; Ostfeld & Canham, 1993; Ostfeld, Manson & Canham, 1997). The foraging of these small mammals can influence the rate, composition, and spatial pattern of tree invasion, however, the net effect of these animals appears to be mediated by changes in vegetation cover and competitive interactions between them (Ostfeld & Canham, 1993; Ostfeld, Manson & Canham, 1997).

Natural variation in the density and distribution of tree propagules in old fields can be considerable (McDonnell & Stiles, 1983; Johnson, 1988; Rankin & Pickett, 1988; Houle, 1994; Hill, Canham & Wood, 1995) and may influence the foraging of mice and voles and thus their effects on tree invasion dynamics. Although seed input into old fields is typically lower than in adjacent forests (Johnson, 1988), the response of mice to variation in seed abundance in these habitats may be limited because the number of mice in old fields appears contingent upon the amount of suitable cover (M'Closkey & LaJoie, 1975; Anderson, 1986) and the degree of competitive exclusion by meadow voles (Grant, 1972; Ostfeld, Manson & Canham, 1997). Similarly, meadow vole density in old fields can fluctuate dramatically (Taitt & Krebs, 1985; Batzli, 1992), which may result in changes in their ability to respond to variation in the abundance of tree seedlings. This study builds on previous research by examining how variation in the distribution and abundance of seeds and seedlings along forest edges may interact with variation in the abundance of small mammal consumers to determine the impact of rodents on tree invasion into old fields.

Predictions concerning the response of seed and seedling predators to variation in the distribution and abundance of tree propagules vary considerably. The escape hypothesis (Janzen, 1970; Clark & Clark, 1984; McCanny and Cavers, 1987; Houle, 1995) predicts that the probability of survival for tree propagules should increase with distance from the parent tree due to seed- and seedling-predators' tendency to concentrate their activity on high-density aggregations near parent trees (Janzen, 1970; Connell, 1971; but see Hubbell, 1980). Thus, in areas where this hypothesis is presumed to operate, animal consumers are predicted to exhibit a positive density-dependent response to tree propagule density. In contrast, the predator satiation hypothesis (Janzen, 1971; Silvertown, 1980; Crawley & Long, 1995) suggests that large numbers of prey items may overwhelm the consumptive capacity of resident predators, resulting in a negative density-dependent pattern of predation with the per capita probability of seed survival highest in dense aggregations of seeds (Sweeney & Vannote, 1982).

These apparently contradictory predictions may be explained by examining the ratio of the number tree propagules present in a given area relative to the abundance of potential consumers. As this ratio increases there may be a transition point at which the escape hypothesis becomes less important and predator satiation becomes more important in explaining the spatial patterns of seed and seedling recruitment (Boucher, 1981; Augspurger & Kitajima, 1992; Condit, Hubbell & Foster, 1992; Forget, 1992; Schupp, 1992; Burkey, 1994). If and when this transition occurs may depend largely on interactions between the level and extent of seed input, whether consumers are capable of responding to changes in seed or seedling density in a functional or a numerical manner, and their degree of dietary specialization (Janzen, 1970; 1971; Kelly, 1994). In developing the predictions of the escape hypothesis in tropical forests, Janzen (1970) focused primarily on host-specific seed predators, such as insects, which are capable of rapid reproduction in response to variation in seed density. However, generalist consumers such as rodents, which dominate temperate systems, may be capable of generating similar patterns (Janzen, 1970; Clark & Clark, 1984). Rodent seed predators can be facultatively host-specific, responding to seed density by forming search images for the most common type of prey (Begon & Mortimer, 1981; Greenwood, 1985), and this may result in the positive density-dependent predation patterns predicted by the escape hypothesis. Although such a transition point has been suggested for forests (Schupp, 1992), little is known about the utility of these hypotheses in explaining patterns of tree propagule survival in adjacent habitats where the patterns of seed input and the responses of the consumer community may differ substantially.

We used seed and seedling additions, designed to mimic natural densities and patterns of dispersion along old field-forest edges, to test the relative importance of the escape hypothesis *versus* predator satiation in predicting patterns of seed and seedling predation in old fields. Specifically, we tested: *i*) whether rates of seed and seedling predation by small mammals increased or decreased with increasing seed and seedling density, *ii*) whether predation rates varied with seed density *per se* or with distance from high density patches, and *iii*) how competitive interactions among meadow voles and white-footed mouse influenced their responses to variation in the distribution and abundance of tree propagules in old fields.

Material and methods

STUDY SITE

We conducted all experiments in five study sites located at or near the Institute of Ecosystem Studies (IES) in southeastern New York (41° 50' N, 73° 45' W). Study sites were located along the border of forests and adjacent old fields. Herbaceous cover in old fields included a mixture of grasses (*Schizachyrium scoparium*, *Bromus inermis*, and *Phleum pratense*), forbs (*Solidago juncea*, *S. rugosa*, *Galium tincturum*, and *Centuria maculosa*), as well as two species of sedges (*Carex spp.*). Sites where shrub cover was present contained various combinations of multiflora rose (*Rosa multiflora*), honeysuckle (*Lonicera morrowii*), and gray dogwood (*Cornus racemosa*).

ENCLOSURES AND TRAPPING

To examine how the abundance of small mammals in old fields may affect their response to variation in seed and seedling density, all experiments were performed in five pairs of 40 m × 40 m, U-shaped, animal enclosures. Enclosures were located along the forest-field edge of study sites and extended five meters into forests and 35 meters out into fields (Figure 1). Enclosures were constructed with 0.9 m tall, 1.2 cm mesh, galvanized hardware cloth buried to a depth of approximately 0.4 m. A 0.5 m buffer strip of vegetation was mowed on either side of fences and a 10 cm-wide strip of aluminum flashing was riveted to the top of each fence to further prevent escape.

We manipulated the density of meadow voles within enclosures to test whether responses of voles to seedling density varied with vole density. In addition, we tested for indirect effects of voles on the response of mice to the
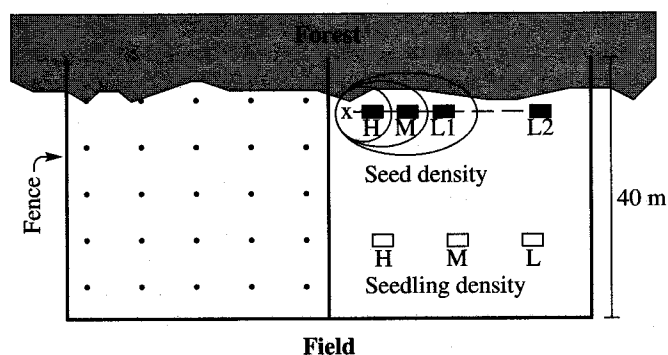
FIGURE 1. Schematic diagram of one of the five study sites. Seeds and seedling density plots were located at 5 and 20 m into the field, respectively. Density plots and grids of traps (solid dots) were replicated in every enclosure. Enclosures at a site were randomly assigned to either a high or low vole density treatment which was maintained throughout the duration of experiments. Concentric rings of declining seed density with distance from a hypothetical seed source (marked with an x) were represented by adjacent high (H), medium (M), and low density (L1) plots parallel to the forest edge. An additional low density plot (L2) represented the tail of the seed distribution where seed density may stay relatively constant with distance from a potential seed source.

density and distribution of seeds. Previous work has shown that overall mouse activity and seed predation intensity may be reduced in areas of high vole density (Ostfeld, Manson & Canham, 1997). We randomly assigned one enclosure in each pair to either a high or a low vole density treatment. The fence design allowed mice to move in and out of enclosures freely while escape by voles was inhibited due to their avoidance of forests (Tamarin, Reich & Moyer, 1984). To manipulate vole densities as well as monitor the distribution and abundance of other species of small mammals active at our study sites, we established 5 by 5 trapping grids, with 7.5 m spacing between traps within each enclosure (Figure 1). A standard mark-recapture program was carried out bi-weekly throughout the duration of experiments, using medium size Sherman traps (5.1 cm × 6.4 cm × 15.2 cm) and Longworth traps at alternating trap stations. Vole density treatments consisted of adding or removing juvenile/sub-adult voles to or from designated high- and low-vole density enclosures, respectively. Animals removed from low density treatments were never added to adjacent high density enclosures. Furthermore, we avoided moving adult voles to minimize the impact of the density manipulations on social interactions between residents. Trapping was conducted for two consecutive days with traps checked each morning. All captured animals, except shrews, were given a numbered metal eartag for future identification. Animals were identified to species, weighed, and checked for reproductive condition before either being released at the point of capture or removed to another site. We estimated the abundance of voles and mice at out study sites using minimum number known alive (MNA) due to the high capture probabilities of both species.

SEED AND SEEDLING DENSITY EXPERIMENTS

In order to test our predictions regarding the relative importance of the escape hypothesis *versus* predator satiation, we manipulated red maple (*Acer rubrum* L.) seed and
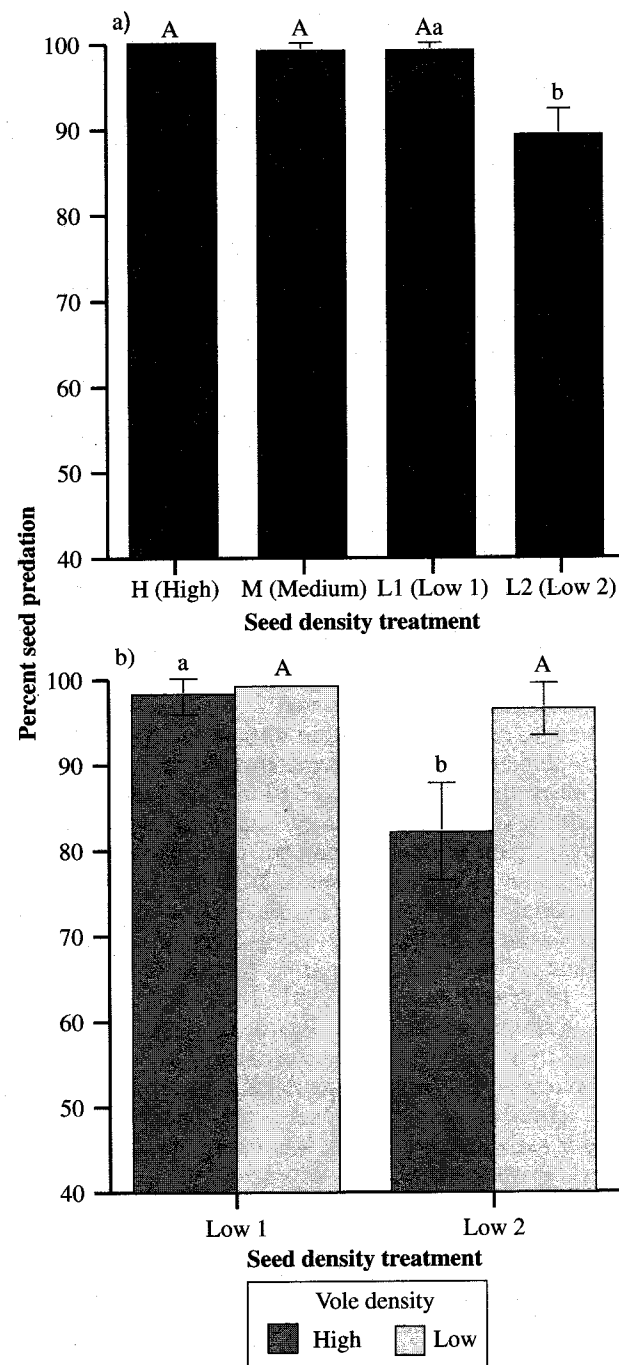

FIGURE 2. Proportion of seeds consumed by the termination of the six week experiment: a) means (± 1 SE) from combining all sites for each of the seed density manipulations (H, M, L1 and L2; see Figure 2);b) similar means (± 1 SE) in the two low density plots (L1 and L2) controlling for the effects of vole density. Means sharing the same letter were not significantly different from one another. Means demarcated by letters of similar case were analyzed in the same contingency table analysis. Means and standard errors were calculated after converting the survival data (yes/no) into 1/0 analogs.

black birch (*Betula lenta* L.) seedling densities in 1 m × 2 m plots located within each enclosure (Figure 1). These species are preferred intermediately by mice and voles, respectively (Hjalten & Palo, 1992; Ostfeld & Canham, 1993;

Ostfeld, Manson & Canham, 1997). As the rank of a particular tree species in mouse and vole preference hierarchies may effect the overall quantities of seeds/seedlings consumed by these animals, and thus their response to variation in tree propagule density, using red maple and black birch reduced potential biases introduced by strong preference/avoidance behavior. These tree species are common old field invaders in the region (Hill, Canham & Wood, 1995) but were rare or absent from the vicinity of our enclosures (R. H. Manson, pers. observ.). Additionally, we minimized the effects of natural variation in seed and seedling density on our experimental manipulations through the timing of our experiments in late spring and early summer. During this time, red maple is the only tree producing seeds, many of which germinate immediately, and the previous year's seed crop is at its most reduced state, following a fall, winter, and spring of exposure to predators.

Both microhabitat and distance from the forest edge were standardized for all plots as these factors are known to influence small mammal foraging (Mittelbach & Gross, 1984; Lima & Dill, 1990; Ostfeld & Canham, 1993; Ostfeld, Manson & Canham, 1997; Manson & Stiles, 1997). All plots were placed in grass-dominated areas with seed and seedling density plots located 2 m and 20 m from the forest edge, respectively. These distances corresponded to areas within enclosures that previous research has indicated experience the greatest depredation by mice and voles, respectively (Ostfeld, Manson & Canham, 1997) and thus, where variation in density may be most important to tree propagule survival. At distances ≥ 20 m from the forest edge, spatial variation in the density of tree seedlings may be influenced more by micro-topography or habitat structure than by proximity to parent plants (McDonnell & Stiles, 1983; Gill & Marks, 1991; Hill, Canham & Wood 1995). Creating an additional low-density plot at a greater distance from the high-density plot seemed to not mimic the distribution of seedlings in old fields typically observed at these distances, and we chose to test only whether the predator satiation hypothesis was operational, and not to address the escape hypothesis with seedlings.

Plots of red maple seed were positioned to mimic natural leptokurtic declines in seed density with distance from a seed source (Figure 1). Adjacent high (H), medium (M), and low density (L1) plots, each separated by a 1 m buffer zone devoid of introduced seeds, were placed parallel to the forest edge. An additional, isolated, low density (L2) plot was placed 10 m from other seed density plots to represent the tail end of a seed dispersal curve where seed density may remain relatively constant with increasing distances from the seed source (Ribbens, Silander & Pacala, 1994). High, medium, and low density plots contained 1500, 750, and 150 seeds/2 m², respectively, which is within the range of densities commonly observed for this species near forest edges (C. D. Canham, pers. observ.). All seeds (> 90% viability) were purchased from Sheffield's Seed Co., Inc., Locke, New York.

In late May 1995, seeds were distributed within plots by dropping them from a height of 1 m above treatment plots. Seed densities were approximate, based on the mean weight (0.86 ± 0.06 g) of 10 separate samples of 50 red maple seeds. To measure the proportion of seeds removed in each density treatment, two parallel transects of five petri dishes (2.5 cm diameter), each containing a single seed, were placed in the center of each plot. Transects were located 0.33 m from the edge of treatment plots with similar spacing between transects and for dishes within transects. Holes were drilled in the bottom of petri dishes for drainage. Seed survival in dishes (presence/absence) was monitored bi-weekly for six weeks. In most cases, seed predation by mice was indicated by a characteristic pattern of damage to the seed coat from which the embryo was excised as well as feces left in or near the petri dish. Missing seeds were also classified as depredated by small mammals because of the presence of clearly depredated seeds in the vicinity of petri dishes and prior evidence that small mammals are the overwhelmingly dominant seed predator in these sites (Ostfeld, Manson & Canham, 1997).

Black birch seeds were germinated at the IES greenhouse, transplanted into individual compartments of greenhouse flats upon reaching a height of 3 cm, and then allowed to acclimate for three weeks. Only healthy seedlings of approximately the same size (4-5 cm tall) were used in field experiments since previous work has shown voles to be sensitive to seedling size (Ostfeld, Manson & Canham, 1997). Seedling density plots were separated by 10 m and seedlings within plots were planted 10 cm apart in parallel, evenly spaced, rows of 10 in July 1995. Variation in plot-specific seedling density was established by planting 1, 2, or 5 rows of seedlings, thus creating low, medium and high density plots, of 10, 20, and 50 seedlings, respectively within the 1 m × 2 m treatment plots located in each enclosure (Figure 1). Seedlings were transplanted using small hand trowels with minimal disturbance to the surrounding vegetation and were watered liberally once at the time of planting. Flags marked the location of ten seedlings from a single row in each plot and their survival status was monitored bi-weekly for a period of six weeks. Seedlings were scored as being alive, dead but not due to herbivory, clipped at the base, or missing during each census period. Voles characteristically kill seedlings by clipping the stem near ground level leaving a noticeable diagonal edge. The clipped shoots of some seedlings are left in place, whereas others are removed and probably consumed (Ostfeld & Canham, 1993; Ostfeld, Manson & Canham, 1997). Other obvious signs of vole activity such as feces, runways, and digging in the vicinity of the marked locations of missing seedlings all suggested that they were removed by voles. Cotton gloves were worn whenever seeds and seedlings were handled in order to avoid scent contamination.

STATISTICAL ANALYSIS

The response variables (survival: yes/no) of both the seed and seedling density experiments were categorical and therefore we analyzed the experiments using a categorical modeling, contingency table approach (PROC CATMOD; SAS, 1990). We analyzed both dependent variables (proportion of seeds and seedlings depredated after six weeks) by fitting linear models to functions of response frequencies using maximum likelihood estimation of parameters for the analysis of generalized logits, allowing us to control for the

large proportion of zeros in our data set. Statistical tests of general association were calculated for three-way contingency tables using likelihood ratio Chi-squares (G^2), whereas tests for linear association between row and column variables were examined using Mantel-Haenszel Chi-squares (Q_{MH}).

The effects of seed and seedling density were examined by comparing predation in adjacent high, medium and low seed density plots. The effect of distance from neighborhoods of high seed density on seed survival was determined by testing for a difference between removal rates in the low seed density plot (L1) near the high and medium density plots and the isolated low density plot (L2; Figure 2). The categories of seedling survival "missing" and "clipped at the base" were lumped during the analysis into the survival category "no". Seedlings dying due to other causes during the experiment were excluded from analyses.

The effectiveness of the vole density treatment, the relationships between average mouse and vole density within enclosures and seed and seedling survival, respectively, as well as the effect of vole density on mouse abundance were analyzed using General Linear Models (GLM). All of these analyses used density estimates (MNA) generated from trap weeks corresponding to seed and seedling predation trials. Unless otherwise stated, all statistical tests were performed at an alpha level of 0.05.

Results

TRAP DATA

Over the course of 2500 trap-nights accumulated during seed and seedling density manipulations, we captured five species of small mammals. Meadow voles were by far the most abundant species, making up 62.5% of captures, followed by white-footed mice (15.5%), short-tailed shrews (*Blarina brevicauda*; 12.6%), eastern chipmunks (*Tamias striatus*; 8.7%), and meadow jumping mice (*Zapus hudsonius*; 0.55%). Feces and seed remains left around seed dishes suggested that white-footed mice were the major seed predator active at our study sites. Patterns of seedling clipping, as well as runways and digging around the seedling density plots indicated that voles were the primary seedling predator. Similar patterns were observed in separate experiments conducted at the same sites during the same year (Ostfeld, Manson & Canham, 1997).

We observed a strong negative effect of vole density on the abundance of mice across all enclosures during the seed predation trials ($F_{1,19} = 8.27$; $P = 0.0101$). The vole density treatment resulted in significantly fewer mice in the high (1.30 ± 1.15 [SD] mice) *versus* the low (4.40 ± 2.17 mice) vole density treatments ($F_{1,19} = 15.87$; $P = 0.0009$). Similarly, vole abundance ranged from 11.70 ± 4.19 to 6.10 ± 4.65 individuals in the high and low vole density treatment, respectively ($F_{1,19} = 8.00$; $P = 0.0112$).

SEED DENSITY EXPERIMENTS

The proportion of seeds consumed within experimental plots was high, ranging from 76.5 to 100% by the end of the 6-week census period. There were no significant differences among sites in overall seed or seedling consumption rates, so they were lumped together in all subsequent analyses

(Table I). Within the set of three adjacent plots (H, M, L1), an average 99.3 ± 6.6% of seeds were consumed and the seed-density treatment had no significant effect on seed predation patterns (Table Ia; Figure 2a). In contrast, significantly fewer seeds were consumed in isolated low-density plots (L2: 89.0 ± 31.4%) than in the low-density plots adjacent to the higher density treatments (L1: 99.0 ± 10.0%; Table Ib).

Averaging across all plots, the intensity of seed predation was significantly lower ($Q_{MH} = 0.011$, df = 1) in the high (94.5 ± 5.70%) *versus* low vole density enclosures (99.0 ± 2.24%). However, despite the fact that vole density appeared to repress mouse abundance within our enclosures, neither enclosure-specific vole density ($F_{1,9} = 2.70$; $P = 0.1390$) nor mouse density ($F_{1,9} = 0.444$; $P = 0.524$) *per se* was correlated with overall seed survival. Higher vole density resulted in a significant difference between L1 and L2 seed density treatments (Figure 2b; Table Ib), however vole density did not influence the intensity of predation within adjacent treatment plots (H, M, and L1; Table Ia). The proportion of seeds consumed ranged from 82.0 ± 5.5% in L2 plots compared to 98.0 ± 2.0% in L1 plots under the high vole density treatment.

SEEDLING DENSITY EXPERIMENTS

The proportion of seedlings consumed was also high, ranging from 60 to 100% per plot by the end of the 6 week census period. Seedling predation was significantly lower in plots with a high density of seedlings (78.4 ± 4.2%) than in plots of medium (89.9 ± 3.0%) and low seedling density (92.6 ± 2.7%; Table Ic; Figure 3). Although enclosure-specific density of meadow voles appeared not to explain a significant amount of the variation in the overall proportion of seedlings killed within enclosures ($F_{1,8} = 0.504$; $P = 0.4980$; Table Ic), there was a trend for higher seedling mortality in areas of high vole density (89.7 ± 2.5% *versus* 84.1 ± 3.0% of seedlings consumed in high and low vole density treatments, respectively). Finally, while seedling survival was

TABLE I. Results from contingency table analysis of the seed and seedling density experiments. Two separate analyses were performed on the seed data; a) effects of seed density *per se* using data from the seed density plots in close proximity to one another (H, M and L1) while excluding the isolated low density plots (L2), and b) effects of proximity to a hypothetical seed source, controlling for seed density by entering only on L1 and L2 into the analysis. All three seedling density treatments were included in a single contingency table analyses (c)

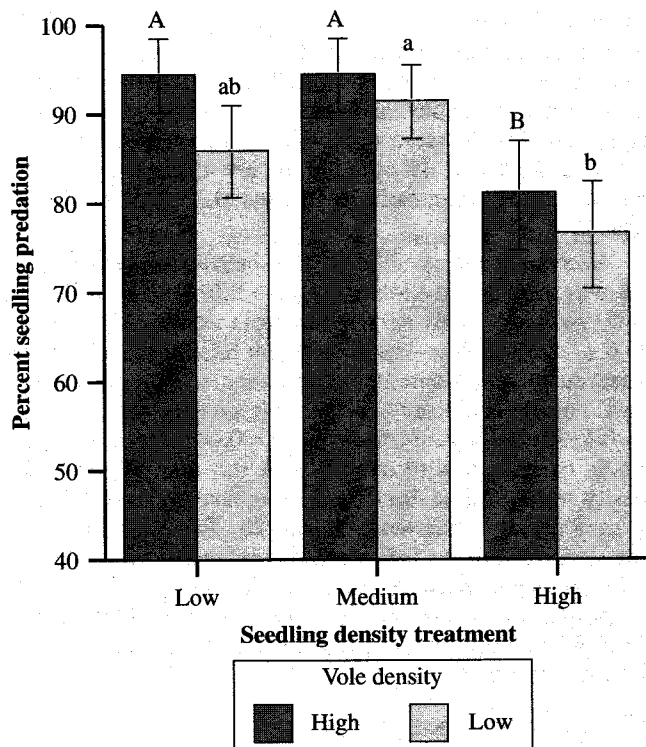|	Treatment	df	Chi-square	Alpha Level
a)	Seed density	2	$Q_{MH} = 1.629$	0.443
	Site	4	$Q_{MH} = 1.003$	0.316
	Seed × vole density	2	$G^2 = 1.007$	0.604
b)	Seed proximity	1	$Q_{MH} = 8.821$	0.003
	Site	4	$Q_{MH} = 2.939$	0.086
	Proximity × vole density	1	$G^2 = 9.033$	0.003
c)	Seedling density	2	$Q_{MH} = 8.485$	0.004
	Vole density	1	$Q_{MH} = 1.931$	0.165
	Site	4	$Q_{MH} = 0.445$	0.505
	Seedling × vole density	2	$G^2 = 9.418$	0.009

FIGURE 3. Mean (± 1 SE) proportion of seedlings depredated in the three seedling density treatments, controlling for vole density. Means sharing the same letter were not significantly different from one another while those demarcated by letters of similar case were analyzed in the same contingency table analysis. Calculation of means and standard errors proceeded after converting the categorical herbivory data (yes/no) into 1/0 analogs.

consistently higher in the high-seedling-density plots, this pattern was more pronounced in enclosures with a high density of voles than in low-vole-density enclosures (Table Ic; Figure 3).

Discussion

Patterns of seed predation by white-footed mice were consistent with the escape hypothesis but not with the predator satiation hypothesis. In accordance with escape hypothesis predictions (Janzen, 1970), mice consumed a smaller proportion of seeds in low-density plots that were distant from a large source, than in low density plots close to a dense seed source. However, in contrast to the predator satiation hypothesis (Janzen, 1971; Silvertown, 1980), they consumed similar proportions of seeds in high-, medium-, and low-density plots that were closely juxtaposed. Our data suggest that mouse foraging in old fields should generate a hyperdispersed pattern of seed survival with isolated pockets of low seed density having the highest survival probabilities and contributing most to the colonization of old fields. Isolated areas of low seed density are expected to occur at the tail end of seed shadows (Portnoy & Willson, 1993) or where seeds are secondarily dispersed by scatter-hoarding animals (Vander Wall, 1992).

In contrast, our data on seedling herbivory by voles suggest that seedling survival should be greatest in areas of high seedling density. Our results indicate that voles are satiated by high seedling density, a result that is consistent with predictions of the predator satiation hypothesis. Vole foraging should therefore lead to a clumped distribution of young seedlings, a pattern that has been observed in previous studies in old fields (Rankin & Pickett, 1989).

The responses of mice and voles to tree propagule density in old-fields varied with vole density. Both the distance-responsive pattern of mouse foraging and the satiation exhibited by voles were accentuated in the high-vole-density treatments. When vole density was low, mice consumed nearly all seeds regardless of the seed-density treatment or proximity to high densities of seeds. However, when voles were abundant, mice concentrated their foraging in neighborhoods of high seed density. Because voles appear to be behaviorally dominant to mice (Grant, 1972; Bowker & Pearson, 1975; Ostfeld, Manson & Canham, 1997), mice in plots with high vole density may be forced to reduce foraging activity and concentrate only on the most profitable patches. If so, interspecific competition with voles may produce or reinforce foraging patterns by mice that result in tree recruitment peaks distant from seed sources.

It is unclear why voles were satiated by plots of high seedling density. Voles did not consume all the seedlings they clipped. Approximately 10-25% of clipped stems were found lying near the spot where they were planted (R.H. Manson, pers. observ.). If voles typically rely on small seedlings as a food source, then satiation may be explained by previous work that has shown that voles are sensitive to the levels of plant secondary compounds in their forage (Bélanger & Bergeron, 1987; Marquis & Batzli, 1989; Hjalten & Palo, 1992) and may employ a cut-and-wait strategy which reduces the concentrations of volatile compounds prior to consumption (Roy & Bergeron, 1990). However, if meadow voles do not use small tree seedlings as food at times when other, more nutritious, plants are available (Lindroth & Batzli, 1984; Batzli, 1985), then areas of high seedling density may signal poor forage and thus be avoided by voles.

The unique response of mice and voles to seed and seedling density, respectively, in old fields reinforces previous findings that suggest that these animals are not functionally redundant in their effects on tree propagule survival in old fields (Ostfeld, Manson & Canham, 1997). Meadow voles are known to exhibit 3-5 year fluctuations in population density (Tamarin, Reich & Moyer, 1984; Batzli, 1992) and recent work has shown that white-footed mice can exhibit regular population fluctuations as well, primarily in response to oak masting (Ostfeld, Jones & Wolff, 1996; Wolff, 1996). Multi-annual population fluctuations, together with the unique patterns of mouse and vole foraging, may provide temporal and spatial windows of opportunity for tree colonization of old fields (Ostfeld, Manson & Canham, 1997). Results from this study and others (Ostfeld & Canham, 1993; Ostfeld, Manson & Canham, 1997) suggest that when both mouse and vole populations are at peak densities in old fields, virtually all seeds and seedlings will be consumed, resulting in uniformly low recruitment and the maintenance of distinct forest-field edges. During periods of high mouse density and low vole density, the tendency for mice to forage along edges (Ostfeld, Manson & Canham,

1997), should result in little seedling recruitment at the edge but potentially higher recruitment in the field interior due to distance-responsive foraging by mice (this study), their sensitivity to the risk of predation (Anderson, 1986; Lima & Dill, 1990), and low seedling consumption rates by voles (Ostfeld *et al.,* 1997). With high vole density and low mouse abundance, however, we predict that seed survival will be highest along edges, leading to dense concentrations of seedlings. As voles are satiated by high seedling density and predation on seedlings is relaxed near the forest edge (Ostfeld *et al.* 1997), we predict a flush of tree propagule recruitment and subsequent expansion of the forest edge under these conditions.

Our experiments suggest that both the escape hypothesis and predator satiation hypothesis may be operational in old fields. However, the relative importance of these hypotheses may vary with the spatial and temporal patterns of seed input, particularly as they interact with the population fluctuations of rodents. Factors influencing seed and seedling densities in old fields and gaps appear more variable than those assumed to be operating in forests (Janzen, 1970; Augspurger & Franson, 1988). The magnitude and spatial distribution of seed input in old fields during a given year may vary depending on the composition of seed-producing trees along the forest edge (Greene & Johnson, 1996), prevailing wind patterns (Augspurger & Franson, 1987; 1988; Hill, Canham & Wood, 1995), modes of seed dispersal (Janzen, 1970; Howe and Smallwood, 1982; McDonnell & Stiles, 1983), and the size of the old field or forest gap into which seeds are dispersed (Hill, Canham & Wood, 1995). The escape hypothesis and the predator satiation hypothesis were originally developed to predict patterns of tree propagule survival in forests. Results from this study highlight the need for further studies to determine the relative importance of these hypotheses in predicting the recruitment patterns of trees in adjacent habitats where patterns of seed input and consumer communities may differ substantially from those in forests.

Acknowledgements

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