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Links between microhabitat preferences and seed predation by small mammals in old fields

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Recent studies indicate that seed predation by small mammals in old fields can be intense and, in conjunction with other herbivores, may influence the rate, composition and spatial pattern of tree invasion into these systems. Patterns of seed predation in old fields may be predictable, based on the preferences herbivores exhibit for particular microhabitats. Studies testing the strength of these linkages, however, are rare. The risk of predation for foraging animals can have a considerable impact on decisions about where to feed and what to consume in particular microhabitats. We examined how an experimentally created gradient of predation risk influenced the microhabitat use and foraging behavior of white-footed mice (*Peromyscus leucopus*) in an old field in central New Jersey, USA. Specifically, we monitored the removal of seeds from dishes placed in the center of replicated treatment plots in which we manipulated ground and canopy cover, as well as distance from the forest edge. We then determined the relative importance of these factors and their interactions in explaining patterns of seed predation by mice. In addition, the distribution and abundance of small mammals were monitored and the vegetation cover in the area immediately adjacent to our experimental plots was quantified to determine how these factors were related to patterns of seed removal. Other factors evaluated included seed species, nocturnal illumination, temperature, precipitation, and time of year. Ground cover, time of day, and distance from the forest edge explained the most variation in patterns of seed predation. Ground cover, particularly proximity to vines such as *Rubus allegheniensis*, appeared to take precedence over other microhabitat variables in the decisions seed predators made about where to forage. Significantly higher nocturnal rates of seed removal, trap data, feces and seed remains left around seed dishes, reinforced previous findings which suggest that white-footed mice are the dominant seed predators in the northeastern old fields. However, spatial patterns of seed removal did not correspond with the distribution and abundance of mice as indicated by the trapping data. These results suggest that the impact of *P. leucopus* on the spatial patterns of seed survival is more dependent on the behavioral responses of individual mice than the distributions of the populations they comprise. Overall, there was little variation from general patterns of seed predation for specific tree species, suggesting that in old fields dominated by mice, there may be relatively uniform regions of high and low seed predation based on the microhabitat preferences of this seed consumer. The consequences of the interaction between old field vegetation and patterns of seed predation by mice for tree invasion and establishment in old fields are discussed.

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Small mammal preferences for particular microhabitats are well documented in a variety of ecosystems (Dueser and Shugart 1978, Alder 1985, Price and Waser 1985, Carey and Johnson 1995). In addition to being an important component of many landscape-scale models (Danielson 1991, Wiens et al. 1993, Dunning et al. 1995), microhabitat preferences have been used to help explain the coexistence of sympatric competitors (Graves et al. 1988, Montgomery 1989, Mitchell et al. 1990, Kotler et al. 1991), as well as rodent community structure and population dynamics (Price 1978, Kotler 1984, Ostfeld 1992). The microhabitat preferences exhibited by herbivorous rodents may also help elucidate temporal and spatial patterns of plant propagule survival (Gill and Marks 1991, Holt et al. 1995, Ostfeld et al. 1997).

In the eastern United States, old fields in various stages of succession make up a large and steadily increasing proportion of the landscape (Bard 1952, Pickett 1982, Glitzenstein et al. 1990). Successful invasion of tree propagules into old fields often results in rapid and significant changes in the composition and structure of surrounding vegetation (McDonnell and Stiles 1983, Myster and Pickett 1993) and may modify ecological processes operating along forest–field ecotones quantitatively and/or qualitatively (Pickett and Cadenasso 1995 and references therein); change the shape, composition, and connectivity of landscape elements (Forman 1990, Merriam 1990); and ultimately influence both local and regional biodiversity (Harris 1988, Saunders et al. 1991, Hansson 1992).

Growing evidence suggests that white-footed mice (*Peromyscus leucopus*) are the dominant consumers of seeds in old fields of eastern North America (Gill and Marks 1991, Bowers and Dooley 1993, Ostfeld et al. 1997, Manson et al. 1998) and that, together with other mammalian herbivores, may strongly influence tree invasions into these habitats (Gill and Marks 1991, Ostfeld et al. 1997). Little is known, however, about the extent to which the microhabitat use of mice can be used to predict patterns of seed predation and thus tree survival into old fields.

Traditionally, studies examining microhabitat preferences of white-footed mice and other small mammals rarely examine what these animals are actually doing in the space they occupy (M'Closkey 1975, Dueser and Shugart 1978, Kaufman et al. 1983, Buckner and Shure 1985). Seed predation studies, on the other hand, seldom adequately quantify changes in the distribution and abundance of potential consumers active at their study sites, perhaps explaining why few consistent temporal or spatial patterns of seed predation have been identified in temperate forests and adjacent old fields (Mittelbach and Gross 1984, Webb and Willson 1985, Willson and Whelan 1990, Gill and Marks 1991, Whelan et al. 1991, Myster and Pickett 1993; but see Bowers and Dooley 1993, Ostfeld et al. 1997). For example, sites that experience intense seed predation in one year may experience little the following year (Willson and Whelan 1990, Whelan et al. 1991, Ostfeld et al. 1997). Within a site, predation intensity may be highest in old fields (Willson and Whelan 1990, Whelan et al. 1991, Ostfeld et al. 1997) or in adjacent forests (Webb and Willson 1985, Whelan et al. 1991, Myster and Pickett 1993). Even within a relatively homogeneous section of the same old field habitat, seed predation may vary significantly on the order of a few meters (Mittelbach and Gross 1984). Detailed studies of the factors influencing the distribution, abundance, and foraging behavior of *P. leucopus* and other potential seed predators in old fields, in conjunction with seed predation trials, may provide a mechanistic basis by which to explain this variation.

Space use and foraging by small mammals are influenced by a variety of factors, perhaps the most pervasive of which is the risk of predation (Kotler 1984, Lima and Dill 1990). Predation risk for rodents has been shown to vary as a function of the amount of illumination and associated weather parameters (Drickamer and Capone 1977, Vickery and Bider 1981, Kotler et al. 1991, Fenn and MacDonald 1995), the density and type of ground cover (Dueser and Shugart 1978, Brown 1988, Gill and Marks 1991, Bowers and Dooley 1993), the amount of canopy cover (Cassini and Galante 1992, Lagos et al. 1995), and distance from distinct vegetation boundaries (Lima and Valone 1986, Kotler et al. 1991). In addition, competition, either through active exclusion (M'Closkey 1975, Brown and Munger 1985) or resource exploitation (Kotler and Brown 1990, Mitchell et al. 1990), may influence microhabitat use by rodents and thus seed survival in contested areas. Finally, competition may interact with predation risk to influence rodent microhabitat use and foraging behavior (Kotler and Brown 1990, Bouskila 1995). There have been few studies examining the relative importance of and interactions between the factors determining predation risk for white-footed mice, particularly as this relates to their impact as seed predators in old fields.

Working in an abandoned agricultural field in the Piedmont of central New Jersey, USA, we designed an experiment which simultaneously monitored the distribution and abundance of mice and other small mammals, as well as removal rates of tree seeds in experimentally manipulated microhabitats. We hypothesized that experimental manipulations of specific microhabitat variables would create a gradient of predation risk for foraging animals that would be reflected in the intensity of seed predation. As all previous research at our site has indicated that *P. leucopus* is the dominant granivorous small mammal (Pearson 1959, Root 1961, Bosenberg 1975, Bowker and Pearson 1975), our experimental design allowed us to test the importance of various components of predation risk in influencing the foraging behavior of mice in old fields. The main questions addressed were: 1) How do distance from forest edge, ground cover, canopy cover, and their interactions influence patterns of seed predation by small mammals? 2) Are these patterns generalizable or do they vary with individual seed species? 3) How does the structure of vegetation surrounding experimental plots influence rates of seed predation rates within them? 4) How well does the distribution and abundance of potential mammalian seed predators correspond with patterns of seed removal?

Methods

Study site

All research was conducted at William L. Hutcheson Memorial Forest (HMF) approximately 1.5 km east of East Millstone, Somerset County, New Jersey, USA (40°30′N, 74°34′W). This area consists of approximately 26 ha of mature woodlands and some 80 ha of fields in various stages of succession. Old growth forest at HMF is dominated by a *Quercus–Carya* canopy and *Cornus florida* sub-canopy (Pickett 1982). Our study site was located along the northern end of a field at HMF released from corn and soybean agriculture in 1984 and currently dominated by *Aster*, *Daucus*, and *Solidago* spp.

While white-footed mice are abundant in the fields and forests that surround the study area (Pearson 1959, Bosenberg 1975, Adams-Manson 1994), they tend to be competitively excluded from grass-dominated areas by the meadow vole, *Microtus pennslyvanicus* (Grant 1972, Bowker and Pearson 1975, M'Closkey 1975). Other potential mammalian seed predators in the region, including eastern chipmunks (*Tamias striatus*), grey squirrels (*Sciurus carolinensis*), and meadow jumping mice (*Zapus hudsonius*), were never observed or trapped within or around experimental seed plots during our study.

Experimental design

Three blocks of treatment plots were established along the eastern, northern, and western sides of the study site (Fig. 1). Within each block, treatments were randomly assigned to plots using three factors with two levels each, in all possible combinations for a total of 24 experimental plots. Treatment plots were 5 m^2 and separated from each other by similarly sized buffer plots of undisturbed vegetation. The ground cover treatment consisted of the removal of ground cover from plots by mowing every other week, leaving vegetation 5 cm high compared to control plots where vegetation height averaged 80 cm. The canopy cover treatment consisted of adding an artificial canopy to plots using 30% shade cloth attached to 1.5-m metal corner fence posts by 0.32-cm steel cable. Distance from the forest was examined by placing plots along the forest edge or 10 m into the field.

The treatment combinations were designed to create a range of predation risks for rodents, with higher predation risk predicted to result in lower seed consumption rates. As *P. leucopus* typically moves out into fields from forest edges (Ostfeld et al. 1997), predation risk for mice was predicted to be lowest in plots closest to the forest edge, with ground and artificial canopy cover present, and highest 10 m into the field, with ground and artificial canopy cover absent. Phase of the moon and cloud cover, precipitation, and temperature, by modifying the visual and auditory detectability of prey as well as the activity of predators, can also influence predation risk and, thus, the activity of rodents (Drickamer and Capone 1977, Vickery and Bider 1981, Kotler et al. 1991, Bowers and Dooley

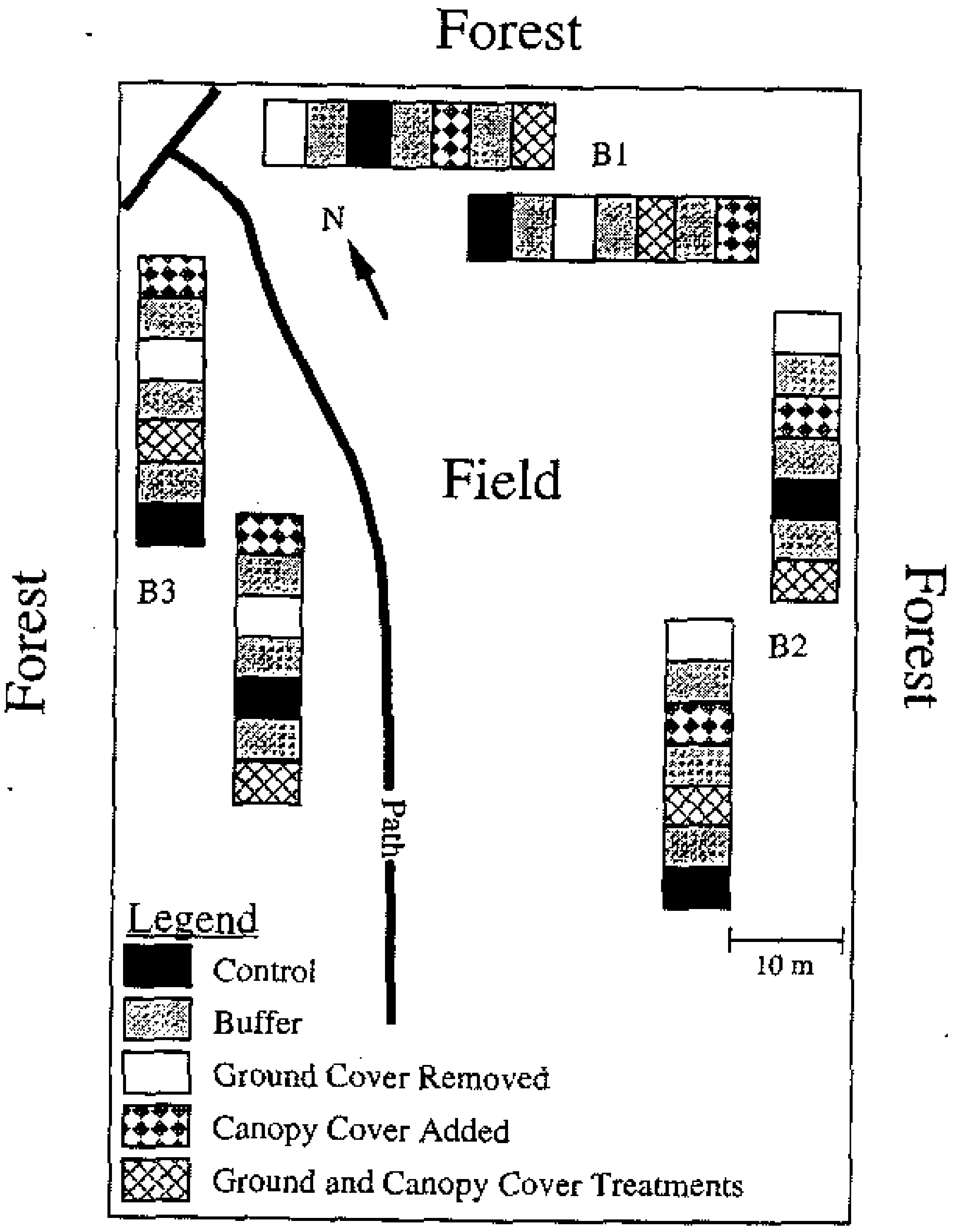

Fig. 1. The distribution of various predation risk treatment plots running along three forest-field edges at the study site following randomization within blocks (B1, B2, and B3). The path indicated on the diagram was approximately 1.5 m wide and maintained by bi-weekly mowing during the growing season. Buffer plots were used so that small mammals would treat the treatment plots as distinct foraging patches and to minimize the effects of the treatments on the natural movement patterns of these animals.

1993, Fenn and MacDonald 1995). Therefore, all of these variables were quantified during all seed predation trials to estimate their importance in influencing patterns of white-footed mouse activity and foraging in old fields.

Feeding trials were conducted from July 1992 to February 1993 to determine how patterns of seed predation in different microhabitats varied with season. Seeds of tree species common in the area were used including two native wind-dispersed species, green ash (*Fraxinus pennsylvanicus*) and box elder (*Acer negundo*), and an invasive exotic, the tree of heaven (*Ailanthus altissima*), a bird-dispersed species black cherry (*Prunus serotina*). Sunflower seeds (*Helianthus annuus*) were included to represent agricultural seed types commonly used in studies of mammalian seed predation (Kotler et al. 1991, Bowers et al. 1993). Green ash seeds were collected from trees near HMF while other seed types were obtained from F. W. Schumacher Co., Inc., Sandwich, MA.

Each of the five seed species was used separately in four feeding trials. Each trial consisted of placing 20 seeds of a single species in a dish of 12 cm diameter in the center of each treatment plot at dusk of day zero. The use of 20 seeds represented a trade-off between finding the minimum number of seeds needed to approximate continuous normal distribution (P. J. Morin pers. comm.) while simultaneously avoiding the creation a food resource that might alter the natural foraging patterns of mice. Dishes were made from heavy gauge aluminum screening which prevented seeds from washing out during periods of rain. At dawn of day one all seeds remaining in dishes were collected, counted and replenished with a fresh set of 20 seeds. In addition, the type of damage to seed remains was noted to help identify the particular seed predator involved. Seed remains were compared to those collected during laboratory feeding trials involving *P. leucopus* and *M. pennsylvanicus* (Adams-Manson 1994). This process was repeated for two consecutive days, so that seeds were exposed twice to both nocturnal and diurnal seed predators, yielding a total of 1920 feeding trials for analysis. In addition, we separated feeding trials by at least 5 days to reduce habituation of seed predators to the experimental regime and handled seeds only while wearing cotton gloves to prevent scent contamination.

To monitor small mammal activity in the vicinity of the seed dishes, we established three small mammal trapping grids of 40 traps each with one overlapping each of the blocks of treatment plots. Each trapping grid consisted of five rows of eight traps, running parallel to the forest edge. Rows and traps within rows were separated by 10 m with each grid extending 20 m into the forest and 20 m into the field. We used small (5.1 cm by 6.4 cm by 15.2 cm) Sherman live-traps supplied with oats and cotton and covered by a 20-cm^2 sheet of particle board. Trapping was conducted for three consecutive days in October, November, and December 1992 and February 1993, according to a schedule which avoided any overlap with seed predation trials. Traps were set in the afternoon and checked the following morning. Captured animals were identified to species, sexed, weighed, and, except for shrews, marked with an ear-tag for future identification.

A series of vegetation surveys was also conducted in August 1992 to examine the effects of adjacent natural vegetation on rodent activity and seed predation intensity in the different treatment plots. As mice appear highly sensitive to the structural complexity of habitats in trapping studies (M'Closkey 1975), we focussed on plant growth forms which appear most important in determining the structural complexity of old field vegetation. The percent cover of grasses, forbs, vines or vine-like shrubs, and upright woody shrubs and seedlings was measured in each buffer plot using a single, randomly placed 1-m^2 quadrat. In a second set of measurements, following the point-quadrat method outlined in Goodall (1952), a 1-cm^2, 2-m-long stick demarcated by five height classes was used to measure the vertical vegetation structure in each of the buffer plots. In each buffer plot two transects were established running perpendicular to the forest edge. At five points along each transect the stick was held vertically and the number of times and height classes in which a particular vegetation type made contact was recorded until all types touching the stick were censused.

Statistical analysis

Variation in seed predation rates across experimental manipulations was examined using the percent of seeds removed from each treatment plot per 12-h foraging period as the unit of observation. Seed dishes were placed in the center of treatment plots thus separating dishes in adjacent plots by 10 m. Combined with the small quantities of seeds used, and the temporal spacing of seed predation trials, this design presumably made foraging in one dish relatively independent of that in another. Data were $\log_{10}$ transformed and checked for normality before statistical analyses. Patterns of seed removal across treatment combinations were examined using a randomized block design ANOVA. The effects of cloud cover, phase of the moon, mean daily temperature and precipitation on seed predation patterns were analyzed in a similar but separate analysis. This analysis lumped trials from all seed species together as natural variation in these factors often resulted in inadequate representation of all levels of each factor in trials of individual seed species, thus precluding species-specific analysis. Factors with strong correlations with seed removal patterns were to be treated as covariates in analyses involving the main treatment variables. As

Table 1. Results of a randomized block ANOVA describing main treatment effects and their interactions. Values calculated from Type III sums of squares (Ground = ground cover; Distance = distance from forest edge; Canopy = artificial canopy cover; Day = time of day; Block = treatment blocks).

Factor	df	F	Prob. > F
Ground	1	101.82	0.0001
Distance	1	6.68	0.0098
Canopy	1	0.11	0.7390
Day	1	25.90	0.0001
Block	2	34.52	0.0001
Ground × Distance	1	43.66	0.0001
Ground × Day	1	5.59	0.0181
Distance × Day	1	0.01	0.9047
Distance × Ground × Day	1	0.00	0.9599
Ground × Block	2	36.52	0.0001
Distance × Block	2	4.79	0.0084
Ground × Distance × Block	2	2.23	0.1073
Day × Block	2	4.79	0.0084
Ground × Day × Block	2	0.92	0.4006
Distance × Day × Block	2	12.82	0.0001

subsequent trials for individual seed species were not independent of one another, species-specific seed predation patterns were analyzed using a repeated measures ANOVA (RMA). All factors and interactions significantly influencing seed predation rates were further examined using post hoc GT2, Scheffé, or SNK tests depending on the evenness of sample size and variance of the data set after transformation (Day and Quinn 1989). Differences in the distribution and abundance of small mammal species across the study site, as measured by the trapping data, were analyzed using Chi-square tests of homogeneity. The changes in activity of white-footed mice and meadow voles relative to each other were examined by generating a Pearson "Product-Moment" correlation coefficient on $\log_{10}$ transformed data. Percent cover and point-quadrat vegetation sampling were analyzed in an ANOVA for unbalanced designs.

Results

Seed predation patterns

In order of importance, ground cover manipulations, time of day, treatment block, and distance from the forest edge explained the majority of the variation in general patterns of seed removal at our study site (Table 1). Species-specific patterns tended to mirror general trends; however, the relative importance of particular factors or their interactions in explaining species-specific seed predation intensity varied (Table 2). While ground cover appeared to explain most of the variation in seed removal for green ash and box elder, a ground-by-distance interaction and time of day appear more important for sunflower and black cherry seeds, respectively. Overall rates of removal were the greatest for sunflower (24.1 ± 2.1%; mean percent of seeds removed from dishes per 12-h period ± 1 s.e.), followed by box elder (18.2 ± 1.8%), green ash (14.2 ± 1.6%), black cherry (10.9 ± 1.5%), and *A. altissima* (1.9 ± 0.04%).

Combining all species, rates of seed predation were significantly lower in plots with ground cover absent, 7.0 ± 0.7%, than in those with ground cover present, 20.7 ± 1.2% (Table 1). A similar pattern was observed in three of five seed species individually, with sunflower and *A. altissima* notable exceptions (Fig. 2, Table 2). There was also a significant ground cover-by-time interaction involving several seed species. Patterns of seed predation box elder and sunflower, mirrored those found for green ash, where differences in seed predation intensity between plots with and without ground cover declined through time (Fig. 3A, Table 2). Removal of *A. altissima* seed showed the opposite pattern with more seeds disappearing from plots without ground cover and this difference increasing through time. Signs of rodent foraging on *A. altissima* seeds were extremely rare during experimental trials. Thus, the effect of the ground cover treatment on the removal of this species was probably due to wind blowing these seeds out of dishes in the more exposed ground cover removal plots.

Contrary to our predictions, seed predation was greater 10 m into the field (15.8 ± 1.1%) than at the forest edge (11.9 ± 0.9%), although this general pattern was not significant for any seed species individually (Tables 1, 2). Differences in seed predation intensity between plots with and without ground cover, however, increased moving from the forest edge (14.5 + 1.5% and 9.3 + 1.2%, respectively) further out into the field (26.9 + 1.9% and 4.7 + 0.8%, respectively; Table 1) as predicted. A post hoc SNK test showed that all levels of this interaction were significantly different from one another. Species-specific patterns with respect to this interaction varied (Table 2, Fig. 2). The general pattern was mirrored in the removal patterns of green ash and black cherry seeds, with box elder seed removal show-

Table 2. Results of repeated measures ANOVA for each seed species used in seed predation trials. In this analysis days within trials were treated as separate sampling points in order to compare variation in seed predation rates within and between trials. Effects of factors and interaction terms influencing seed removal rates controlling for the effect of time (Main) as well as significant interactions involving time (Time) are reported using Type III sum of squares F values.

Factor	Green ash		Box elder		Sunflower		*A. altissima*		Black cherry	
	Main	Time	Main	Time	Main	Time	Main	Time	Main	Time
Time	–	15.63***	–	2.73*	–	15.08***	–	1.47	–	7.84**
Ground	77.52***	16.52***	37.26***	3.39*	3.13	4.82**	3.00	2.02	5.26*	2.12
Distance	2.25	0.74	3.22	0.46	0.86	2.22	0.21	1.23	0.14	1.25
Canopy	1.11	0.69	6.29*	1.26	0.19	0.59	0.82	1.66	2.00	1.51
Day	5.80*	2.69*	0.66	1.79	3.93*	3.75*	1.02	1.40	23.59***	4.20**
Block	5.55*	2.11*	8.57**	0.71	4.06*	1.98*	5.23*	2.13*	16.16***	2.48*
Ground × Distance	12.47**	0.87	3.43	1.38	15.40**	6.81**	0.86	0.84	4.31*	0.79
Ground × Canopy	0.34	1.09	4.80*	0.95	0.11	0.81	0.00	0.99	0.00	0.28
Distance × Canopy	7.94**	2.47	0.98	0.50	0.18	0.66	0.84	1.21	1.93	1.24
Ground × Distance × Canopy	7.56*	0.92	1.39	0.54	2.12	1.25	0.10	0.89	0.58	2.11
Ground × Day	1.84	4.39**	5.66*	1.49	0.01	0.53	0.30	0.85	0.17	1.20
Distance × Day	0.29	0.49	0.23	1.58	3.22	1.18	0.01	0.62	2.60	0.80
Canopy × Day	0.34	1.19	0.02	0.39	0.48	0.28	1.71	0.64	1.76	0.85
Ground × Distance × Day	0.11	1.33	0.08	1.63	0.73	0.77	3.39	0.27	0.21	0.13
Ground × Block	6.57**	2.96**	7.26**	1.33	7.82**	1.43	6.11**	0.76	6.15**	1.37
Distance × Block	3.23	1.59	0.25	1.11	0.26	1.53	0.44	2.14*	1.90	1.26
Canopy × Block	5.25*	1.24	1.46	0.86	0.72	1.26	2.72	1.94	0.19	0.70
Day × Block	1.01	0.74	0.23	1.21	1.00	1.17	3.11	2.14*	4.19*	1.22

* = $P < 0.05$; ** = $P < 0.01$; *** = $P \leq 0.0001$.

ing a similar but non-significant trend. In contrast, sunflower seeds were removed at a significantly higher rate in plots with ground cover absent along the forest edge, while this pattern was reversed 10 m into the field (Fig. 2). This pattern of removal may explain why ground cover per se appeared to have no significant effect on the removal rates of sunflower seeds (Table 2).

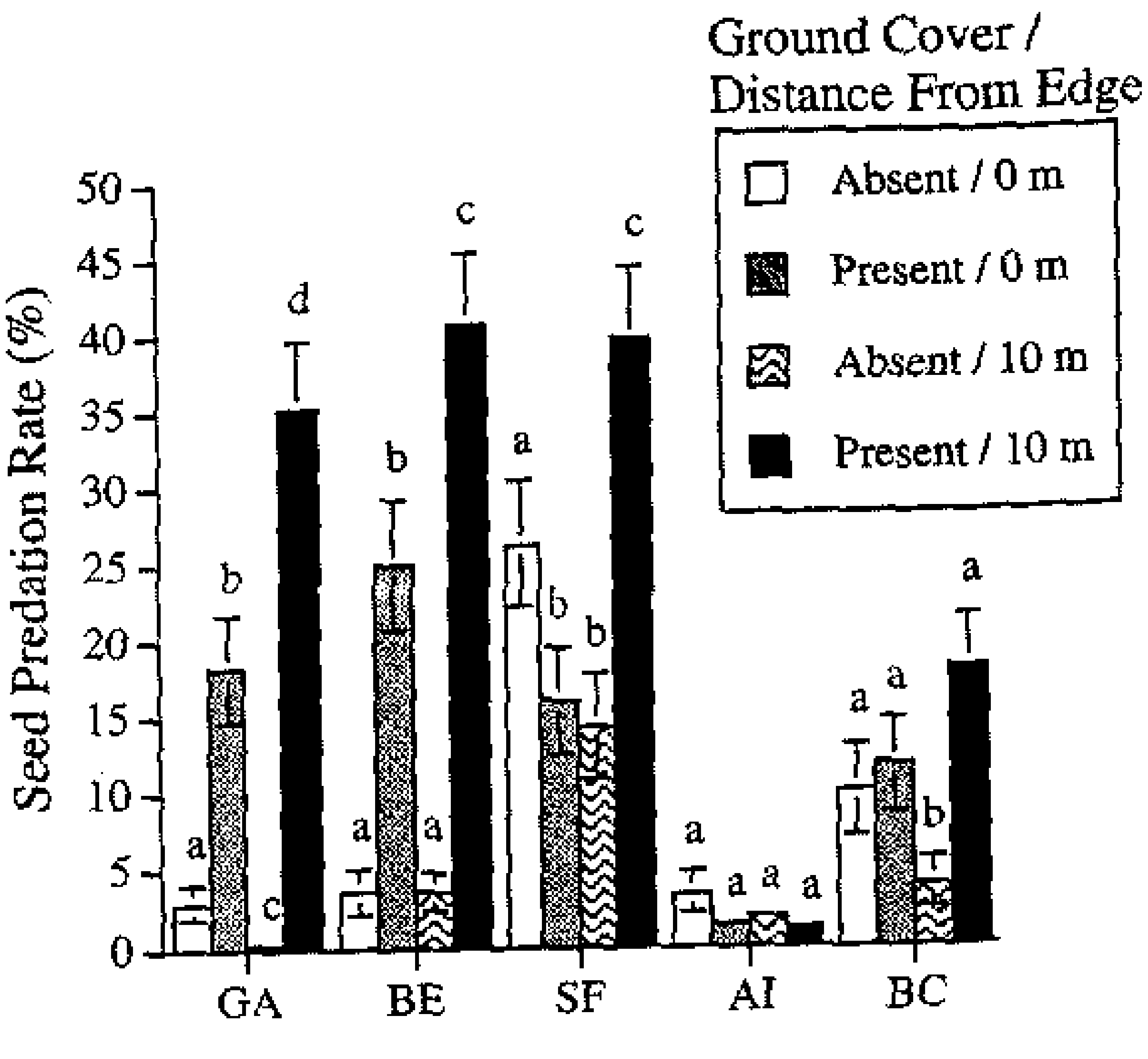

Fig. 2. Species-specific seed predation resulting from various ground cover-by-distance from the forest edge treatment combinations. Letters correspond to species-specific Scheffé tests among treatment combinations. Within each species, treatment combinations sharing a common letter are not significantly different from one another (GA = green ash, BE = box elder, SF = sunflower, AI = *A. altissima*, and BC = black cherry seeds; error bars represent ±1 s.e.; $n = 96$).

Artificial canopy cover had no significant effect on general rates of seed removal, nor were there any significant interactions involving this factor (Table 1). Removal rates for several seed species, however, were significantly affected by interactions between canopy cover and other factors (Table 2). Removal rates of box elder seeds were significantly reduced in plots with the addition of the artificial canopy (13.5 ± 2.3%) versus control plots (22.9 ± 2.8%). However, this effect of canopy cover appeared to be important for this species only in the presence of adequate ground cover (Table 2). In contrast, canopy cover appeared to have no effect on the rate at which green ash was consumed along the forest edge but significantly enhanced predation 10 m into the field (22.7 ± 3.9% vs 12.8 ± 3.2% of seeds consumed 10 m into the field with canopy cover present and absent, respectively; Table 2).

Nocturnal rates of seed predation (17.9 ± 1.2%) were significantly higher than diurnal removal rates (9.8 ± 0.8%; Table 1). Similar species-specific patterns were observed for green ash (17.9 ± 2.5% vs 10.5 ± 1.9%), sunflower (30.1 ± 3.2% vs 18.2 ± 2.5%), and in particular, black cherry seeds (18.4 ± 2.7% vs 3.4 ± 1.2%), while box elder seed removal showed a similar but non-significant trend in the same direction (Table 2). However, the effect of time of day on the removal rates of these species appeared to change over time (Table 2). Removal of green ash seed mirrored that of sunflower (Fig. 3B) with both species exhibiting higher diurnal seed removal early in the year followed by consistently higher nocturnal predation rates later, up until the final census period. In contrast, removal of black cherry seed was consistently higher at night until the final census period. Differences in seed predation rates between

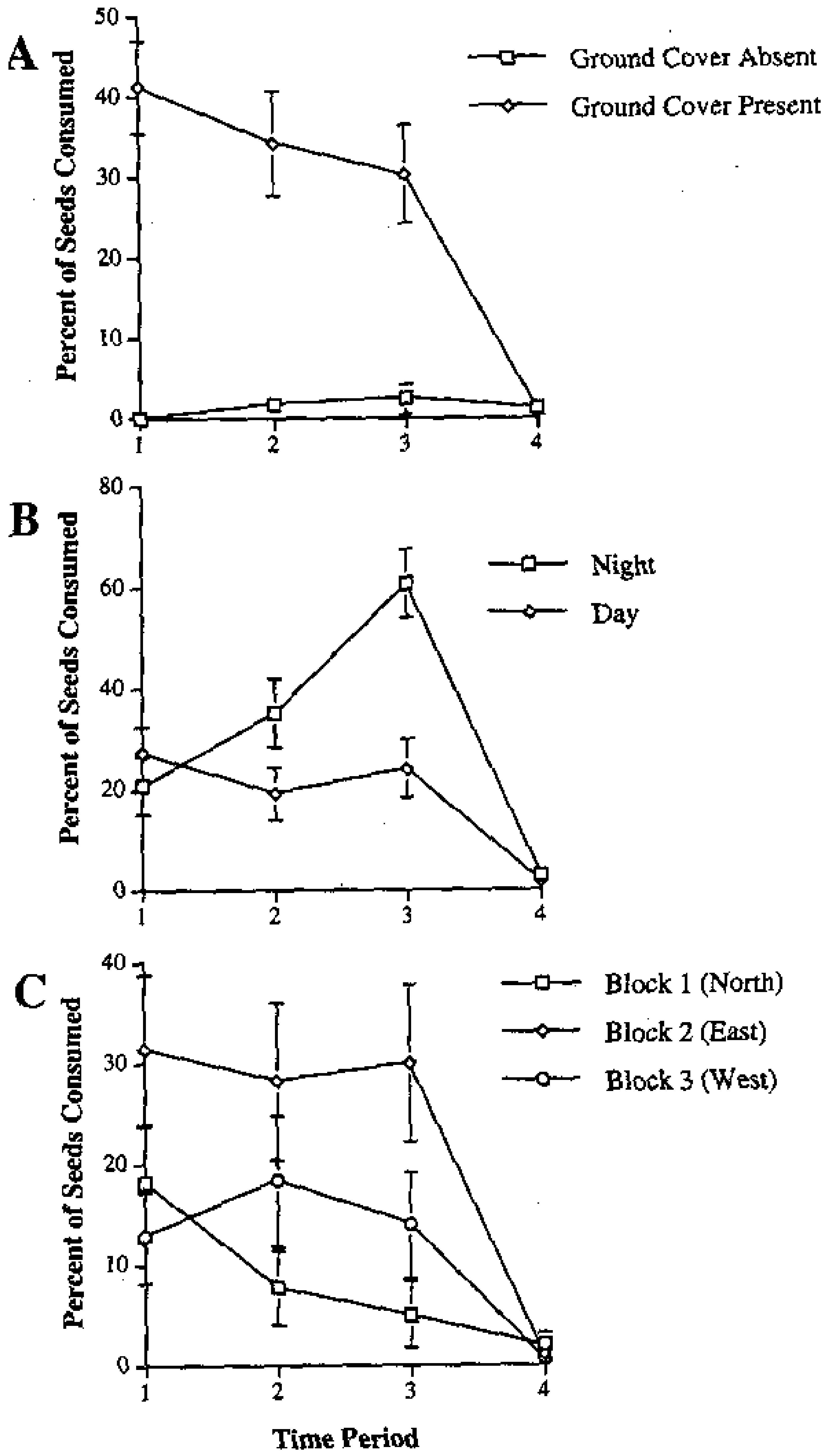

Fig. 3. Seasonal changes in the proportion of seeds consumed for, A) green ash seeds in plots with and without ground cover ($n = 48$), B) sunflower seeds at night and during the day ($n = 48$), and C) green ash seeds placed within each treatment block ($n = 32$). Approximate dates for each of these times periods can be obtained by referring to Fig. 5. Error bars represent ±1 s.e.

plots with and without ground cover were greater at night (26.4 ± 1.9% and 9.4 ± 1.2%, respectively) than during the day (15.0 ± 1.5% and 4.6 ± 0.8%, respectively; Table 1); however, this pattern was not significant for any individual seed species (Table 2).

Seed removal varied significantly with treatment block. General and species-specific seed predation rates tended to be higher in treatment blocks two and three, suggesting that many of the previously described patterns of seed predation should be interpreted in light of this block effect (Tables 1, 2). For example, seed predation 10 m into the field was greatly enhanced in block two versus other areas of the study site (Fig. 4A), although this interaction was not significant for any seed species in particular (Table 2). The enhancement of rodent seed predation in areas of high ground cover also appears to be related to an interaction of this factor with treatment block (Table 1). Ground cover had no effect on the removal rates of seed in block one; however, seed removal in other blocks, particularly in block number two, was significantly enhanced in the presence of ground cover (Fig. 4B). Similar patterns were observed for all seed species except *A. altissima*, which experienced greatest removal in block one in the absence of ground cover. Finally, nocturnal seed predation appeared to be disproportionately higher in block two compared to similar patterns of diurnal seed predation (Table 1, Fig. 4C); however, this general pattern was significant only for black cherry seeds (Table 2).

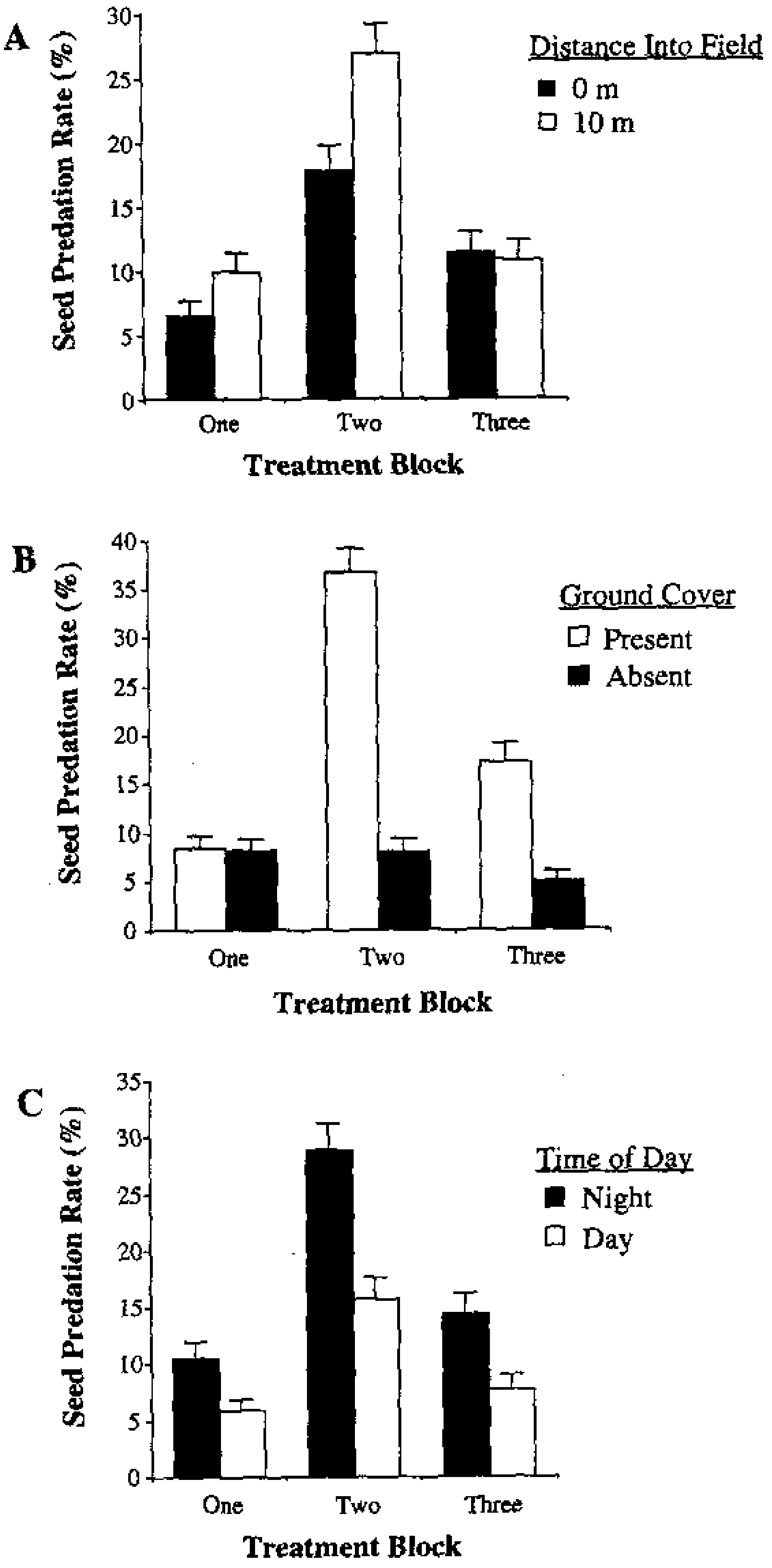

Fig. 4. Influence of treatment block on seed removal patterns with respect to, A) distance from the forest edge, B) ground cover treatments, and C) time of the day in which seeds were placed out. Error bars represent +1 s.e. ($n = 320$).

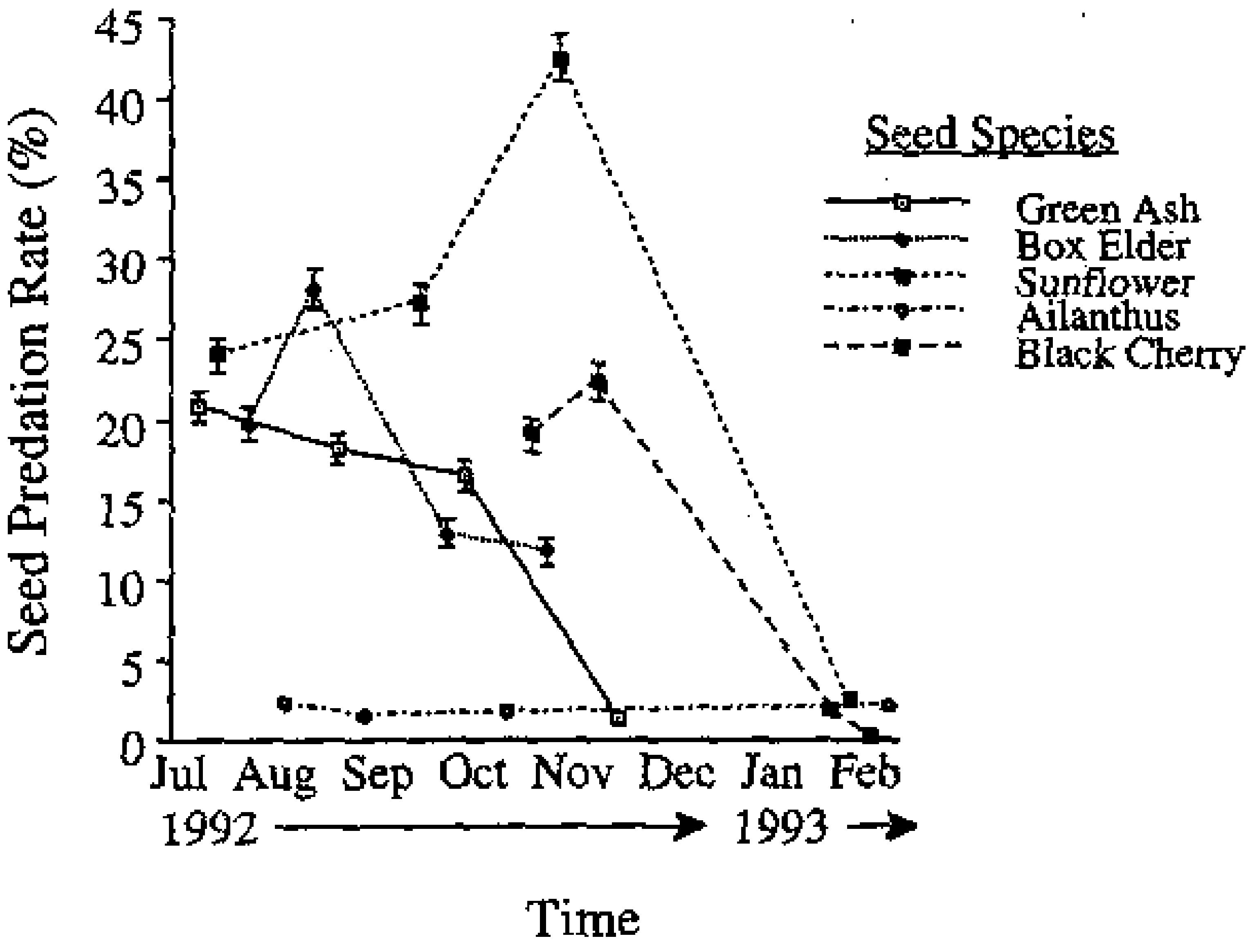

Fig. 5. Temporal patterns of seed predation intensity across trials run separately for each seed species. Each data point represents the average seed predation rate observed in dishes placed in all treatment combinations over the course of two-day trials. Error bars represent ±1 s.e. ($n = 96$).

Most seed species exhibiting changes in block-specific seed removal rates over time exhibited patterns similar to that of green ash with seed removal consistently highest in block two but varying among blocks one and three (Fig. 3C, Table 2). Again, *A. altissima* was a notable exception with seed removal highest in block one and secondarily in blocks two or three depending on the time period. In general, seed removal appeared to decline with season for all species except *A. altissima* (Table 2); however, the exact temporal pattern of removal varied on a species-specific basis (Fig. 5).

Despite a significant phase of the moon-by-time of day interaction (Table 3), there was no clear effect of phase of moon on nocturnal seed predation patterns which should be most sensitive to variation in this factor. Nocturnal seed removal during new, half and full moon phases averaged 21.2 ± 2.4%, 14.2 ± 1.5%, and 22.2 ± 2.7% of seeds placed out, respectively. A GT2 test indicated that removal during half moon periods was significantly lower than during other phases. Similarly, there was no effect of cloud cover per se on seed removal rates, and subsequent evaluation of a significant cloud-by-time of day interaction (Table 3) suggested that nocturnal seed removal was lowest during partly cloudy conditions. Seed predator activity appeared to increase significantly with temperature, leveling off above 7°C, whereas precipitation had no detectable effect on seed removal rates (Table 3). As explanations were not readily apparent for any of these patterns, we decided that further analysis of interactions between these factors and those that were experimentally manipulated during the study would not be productive.

Seed predator activity

In 1440 trap-nights only three species of small mammals were captured: white-footed mice, meadow voles, and short-tailed shrews (*Blarina brevicauda*). Mice were by far the most frequently captured small mammal ($\chi^2 = 99.2$, df = 2, $P < 0.05$) making up 140 of 214 (65.4%) total captures, followed by voles and shrews, each with 37 (17.3%) captures. Furthermore, the vast majority of seed remains found in the field showed signs of damage similar to that observed in laboratory feeding trials involving white-footed mice (Adams-Manson 1994). In these trials, *P. leucopus* consumed box elder seeds by removing them from samaras via a small hole chewed at the proximal end leaving the samara intact. Black cherry seed endosperm was removed through small (2–3 mm) circular holes scraped into the hard seed coat. Green ash and sunflower seeds were typically consumed by gnawing at the ends of the seed coats and splitting them into numerous long slivers. Feces frequently found in or around seed dishes also suggested that white-footed mice were the dominant seed predators active at our site. Although birds are capable of consuming most of the seed types used (Martin et al. 1951), only some of the remains of sunflower seeds, particularly those in plots near the forest edge with ground cover removed, showed signs of consumption by birds. In contrast to mouse consumption of sunflower seeds, bird foraging was characterized by remains of seed coats lacking tooth marks, and which were larger and less splintered than those left by their mammalian counterparts (Manson pers. obs.).

Combining all captures, small mammal activity in general did not differ between treatment blocks ($\chi^2 = 0.12$, df = 2, $P > 0.05$), nor did the activity of mice ($\chi^2 = 1.38$, df = 2, $P > 0.05$), voles ($\chi^2 = 5.58$, df = 2, $P > 0.05$), or shrews ($\chi^2 = 3.30$, df = 2, $P > 0.05$) individually. Further analysis, broken down by trap period, indicated that the activity of mice in different treatment blocks did not vary significantly with time of year (Fig. 6A). Mice ($\chi^2 = 28.9$, df = 2, $P < 0.001$) and shrews ($\chi^2 = 39.0$, df = 2, $P < 0.001$) were significantly more active along the edge of the forest while voles were most active further out into the field ($\chi^2 = 16.4$, df = 2, $P < 0.01$). However, the preferences of mice for forest edge habitat appeared to decrease with time (Fig. 6B), possibly as seasonal leaf fall decreased structural differences between edge and old field habitats. A regression of total mouse captures against total vole captures, broken down by treatment block and trapline, indicated that the spatial activity of these two species was negatively correlated ($r^2 = 0.304$, $F_{1,13} = 5.67$, $P = 0.033$). The total number of captures for all species declined significantly over the four trapping periods ($F_{3,1436} = 91.7$, $P < 0.0001$) as did the captures for each species individually.

Table 3. Results of ANOVA examining the influence of various categorical environmental factors and their interactions on seed predation rates. Factors and interactions included were those deemed most biologically relevant to the current study. See the text for further explanation. F values were calculated from Type III sums of squares (Moon = full, half, or new moon phase; Cloud = none, partial, or total cloud cover; Temperature = mean temperature intervals of −6–0, 1–7, 8–16, or 17–27°C; Precipitation = rain or snowfall of 0.0–0.2, 0.2–0.76 or greater than 0.76 cm).

Factor	df	F	Prob. > F
Day × Moon	5	3.71	0.0052
Cloud	2	0.67	0.5144
Day × Cloud	2	10.95	0.0001
Day × Moon × Cloud	8	5.31	0.0001
Temperature	3	7.99	0.0001
Precipitation	2	1.40	0.2463

The population estimator Minimum Number Alive (MNA) was calculated as an abundance estimate for mice and voles during all trapping periods. *Peromyscus leucopus* was significantly more abundant than *M. pennsylvanicus* in the field ($\chi^2 = 30.3$, df = 1, $P < 0.01$). However, whereas vole density was greatest in block one ($\chi^2 = 13.0$, df = 2, $P < 0.01$), white-footed mouse abundance did not differ significantly across treatment blocks ($\chi^2 = 1.27$, df = 2, $P > 0.05$).

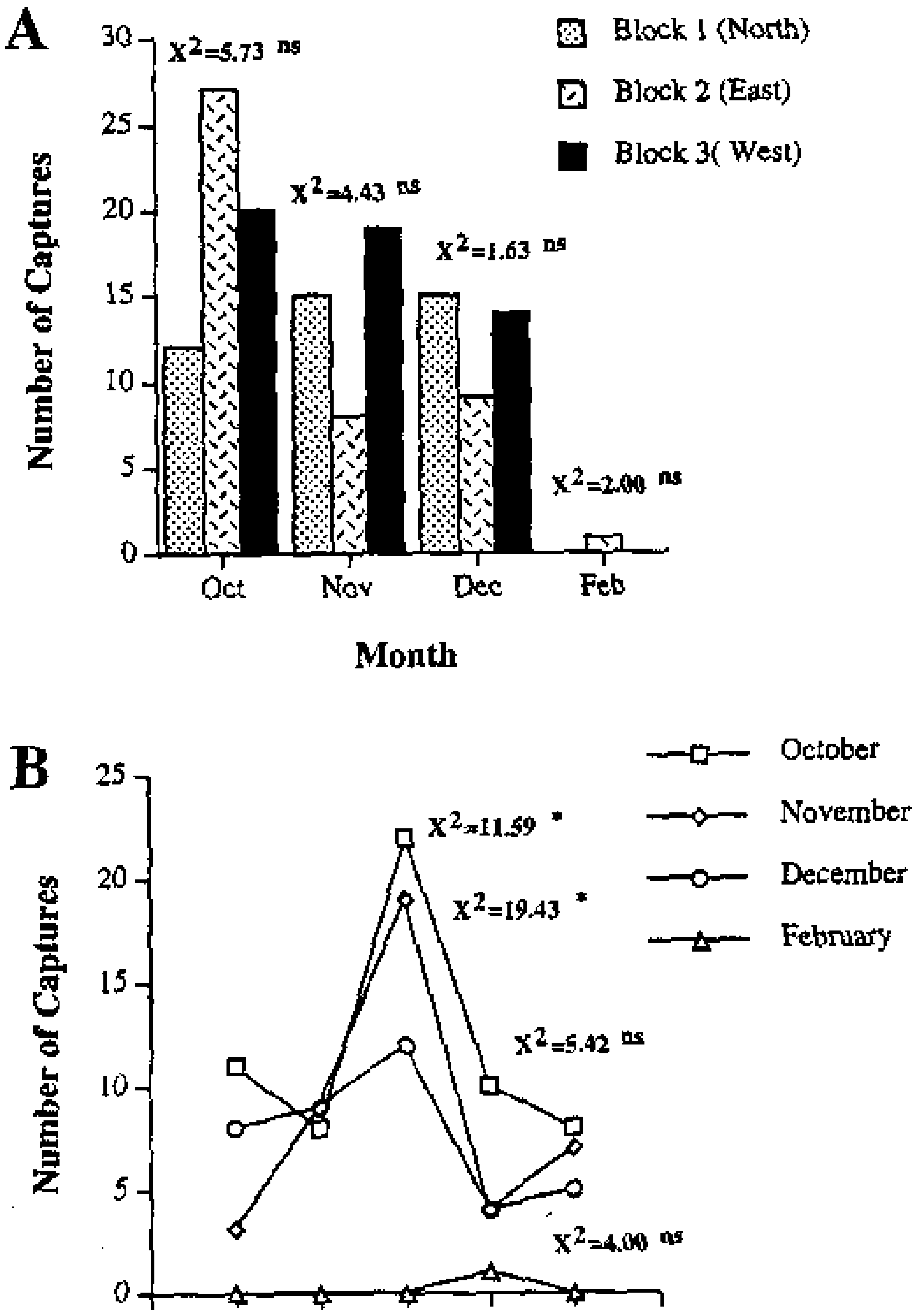

Fig. 6. Seasonal shifts in spatial activity patterns of white-footed mice at the study site represented as the sum of captures from each three-day trap session. Chi-square tests for homogeneity (alpha level = 0.025) evaluated the hypothesis that, A) activity does not differ between trapping grids (df = 2) and that, B) that activity is uniform with respect to distance from the forest edge (df = 4). Asterisks indicate significant differences existed between levels of the factor examined while non-significant patterns are indicated by "ns".

Composition of surrounding vegetation

Total cover (combining all types of vegetation cover) did not differ across treatment blocks ($F_{2,12} = 1.62$, $P = 0.239$), distance from the forest edge ($F_{1,12} = 0.17$, $P = 0.688$) or an interaction between the two ($F_{2,12} = 1.56$, $P = 0.250$). Forbs were the most dominant vegetation type, covering 47% of plots sampled, followed by vines (39%), woody shrubs and seedlings (17%), and grasses (13%). Only vine cover was found to differ significantly by treatment block ($F_{2,12} = 5.98$, $P = 0.0160$) and especially in a block-by-distance interaction ($F_{2,12} = 15.1$, $P = 0.0005$). Scheffé tests indicated that vines were significantly more abundant in block two (56.6%) vs block three (25.8%) with vine cover intermediate in block one (33.3%). Furthermore, the cover of vines was significantly greater 10 m into the field in block two vs any other block-by-distance combination, probably due to the dominance of *Rubus allegheniensis* in this area (Manson pers. obs.).

Point-quadrat sampling also indicated that vegetation cover was significantly different between treatment blocks ($F_{2,1478} = 16.8$, $P = 0.0001$). In addition, vegetation cover differed significantly between height classes ($F_{4,1478} = 3.43$, $P = 0.0006$), and exhibited block-by-distance ($F_{2,1478} = 3.68$, $P = 0.0255$) and block-by-height class interactions ($F_{8,1478} = 3.43$, $P = 0.0552$). Scheffé comparisons indicated that vegetation cover was greatest in areas surrounding the block two treatment plots, particularly 10 m out into the field. The general lack of cover at height class five (1.5–2.0 m) and the dense cover on the east side of the field, particularly in the lower height classes as indicated by a SNK test, may explain the height and block-by-height class interactions, respectively.

Discussion

Seed predation patterns

Studies examining patterns of seed predation must often contend with simultaneous consumption by multiple taxa and/or species within taxa which may have contrasting microhabitat and dietary preferences, thus making the interpretation of results difficult at best (Parmenter et al. 1984, Kelrick et al. 1986). By studying the patterns of seed predation generated by mice, largely in the absence of other seed consuming species, our study may provide valuable baseline data for interpreting patterns observed in areas with more diverse consumer guilds. Results from our study suggest that mice are sensitive primarily to the quantity and quality of ground cover in making decisions about where to forage. Seed predation was significantly higher in the presence of ground cover, particularly in areas where vine cover was dominant. These findings support previous studies which have shown that rodent abundance (M'Closkey 1975, Dueser and Shugart 1978, Kaufman et al. 1983, Buckner and Shure 1985) and seed predation intensity is greatest in areas of high structural complexity (Mittelbach and Gross 1984, Gill and Marks 1991, Myster and Pickett 1993). Small mammals are more likely to be captured by predators in microhabitats lacking complex cover (Kaufman 1974, Kotler et al. 1991).

Preferences by mice for ground cover in general, and vine cover in particular, appear to take precedence over other factors in decisions about where to forage. Seed predation rates, particularly in block two where *Rubus* cover was most abundant, increased significantly with distance from the forest edge, which was the opposite of what was predicted assuming distance from forest cover is an important variable assessed by mice. Anderson (1986) showed that foraging rodents were willing to travel over three times further than normal from preferred habitat types as long as artificial ground cover was provided. In addition to avoiding predation, using areas of high vine cover may enable mice to minimize interactions with competitively dominant meadow voles which prefer grass-dominated areas (Bowker and Pearson 1975, Ostfeld et al. 1997). Finally, the reverse distance effect observed in this and earlier studies (Ostfeld et al. 1997) may be explained by the role a predator's behavior plays in shaping the patch use and foraging decisions of its prey (Kotler 1984, Lima and Dill 1990, Cassini 1991). The presence of potential predators that focus their activity along forest edges may make foraging in open spaces in the immediate vicinity of these areas unsafe for rodents (Lima and Dill 1990). Many of the small mammal predators active in the area, including foxes (*Vulpes fulva*), house cats (*Felis cattus*), coyotes (*Canis latrans*), raccoons (*Procyon lotor*), American kestrels (*Falco sparverius*), screech owls (*Otus asio*), and barn owls (*Tyto alba*), may exhibit this type of foraging behavior along forest edges.

The artificial canopy treatment had little effect on rates of seed removal. The 30% shade used in the experiment may not have created a great enough illumination differential for mice to detect, thus failing to alter their foraging behavior. Alternatively, differential responses of mice to ground and canopy treatments may indicate something about the spatial scale at which mice assess microhabitat factors used in making decisions about where to forage (Cassini and Galante 1992). While mice have been shown to have fairly broad perceptual ranges (Lima and Zollner 1996), M'Closkey (1975) found that the foliage profile from 0 to 7.6 cm above the ground explained 76% of the variation in white-footed mouse captures. This profile is well below the height of the artificial canopy (1.5 m) used in our study.

The fact that phase of the moon, cloud cover, and their interaction did not influence seed predation rates in any biologically interpretable way may simply be an artifact of the methods employed. Nocturnal illumination varies continuously throughout the night as a function of the interaction between the phase of the moon and cloud cover. Foraging seed predators probably respond to this variation by changing their behavior frequently over the course of a single night. Therefore, the methods employed in the present study, dividing cloud cover and the phases of the moon into three discrete categories each, and only measuring these four times a day, are probably too coarse to show an effect of illumination on seed removal. To avoid this problem, studies showing an effect of illumination on rodent activity typically use artificial lighting (Brillhart and Kaufman 1991, Longland and Price 1991) or only conduct experiments on clear nights during discrete phases of the moon (Wolfe and Summerlin 1989, Bowers and Dooley 1993). However, these strategies may reveal little about the full range of foraging patterns exhibited under natural conditions. Finally, studies such as ours, conducted near urban population centers must contend with the confounding effects of artificial illumination, particularly when this illumination may be reflected off of cloud cover and thus reverse predicted light levels.

Seed predator identification

Data from seed predation trials and trapping, together with feces and seed remains in the vicinity of seed dishes, all suggest that white-footed mice were the dominant seed predators active during our study. Only three species of small mammals were captured, with white-footed mice by far the most active and abundant. Of these species, only *P. leucopus* is a well-documented seed predator (Brown 1964, Wolff et al. 1985, Zegers et al. 1991). Short-tailed shrews are insectivorous and carnivorous (Martin et al. 1951). Meadow voles consume primarily plant shoots, roots, and some monocot seeds (Lindroth and Batzli 1984, Batzli 1985) and their abundance has been shown to be negatively correlated with areas of high tree seed predation (Ostfeld et al. 1997).

White-footed mice are active mostly at night (King 1968), which may explain why more seeds were removed at night vs the day, as well as the greater sensitivity of nocturnal seed predators to the presence of ground cover. Several studies have noted bi-modal peaks of activity for rodents near dawn and dusk (Drickamer 1987, Jensen 1993), the same time period when seed dishes were checked and replenished. Thus, it is probable that some removal attributed to diurnal seed predators was in fact also due to *P. leucopus*. The seed species used in predation trials were too large to be manipulated by ants; however, birds can consume most of these species (Martin et al. 1951). In particular, removal of sunflower seeds along forest edges in areas of sparse ground cover appeared to be attributable to birds. Granivorous birds may prefer to forage in these areas as they are closer to the protective cover of the forest edges, and thus provide ready detection and routes of escape from avian predators active in old fields (Lima and Dill 1990 and references therein). Data on the removal of green ash and sunflower seeds further suggested that there may be some seasonal shifts in the importance of birds vs mice in producing the patterns of seed predation observed, particularly during the late summer. Mouse diets are thought to reflect seasonal availability (Hamilton 1941, Brown 1964) with insects consumed during the spring/summer seasons and seeds and fruit pulp during the fall/winter (Brown 1964). As mice form search images for the most abundant food type available (Greenwood 1985), they may not be important seed predators during time periods when seeds are not naturally dispersed.

The abundance of mice appears to be a poor predictor of patterns of seed predation in old fields. Assuming that the abundance of seed predators in a given area should influence the probability of seed removal there, the trap data suggest that seed predation should have been relatively constant across our old field study site and particularly intense along the edge of the forest where *P. leucopus* is most active. However, seed removal was consistently greater on the eastern side of the field, particularly 10 m from the forest edge. Unmeasured seasonal changes in the vegetation cover or natural levels of seed input at our study site may explain some of these results. However, both the spatial patterns of seed predation and mouse abundance were fairly constant through time suggesting these changes, if they occurred, played a relatively minor role. Our findings suggest that the habitat factors influencing the overall distribution and abundance of mice in an area, or those determining the size and dimensions of mouse home ranges, may not be the same as those used secondarily by mice in making decisions about which microhabitat patches to forage in and, thus, may need to be examined independently in future studies.

The trap data also suggested a negative spatial correlation between mice and voles. Previous studies have suggested that this pattern may emerge as a result of competitive exclusion of mice by voles (Bowker and Pearson 1975, Ostfeld et al. 1997), and that the presence of voles may, therefore, have an indirect positive effect on seed survival in areas of high vole density (Ostfeld et al. 1997). Results from the current study, however, only partially support these findings. While seed removal rates were significantly lower in treatment block one, where voles were most abundant, this did not result from a significant decrease in mouse abundance in this area.

It is extremely difficult to compare the rates of seed removal documented in this study with those conducted in similar habitats (Mittelbach and Gross 1984, De Steven 1991, Gill and Marks 1991, Myster and Pickett 1993, Reader 1993, Ostfeld et al. 1997). Seed predation studies employ a wide variety of experimental techniques, as well as different seed species, microhabitats, and times of year in measuring rates of seed removal. This and other recent studies (Ostfeld et al. 1997) suggest that a significant portion of the variation observed between studies may be also due to changes in distribution and abundance of the seed predators active in experimental areas. Only by standardizing many of these sources of variation, and combining seed predation trials with simultaneous studies of the distribution and abundance of potential consumers, will it be possible to state whether observed variation in seed survival is due to, 1) an overall greater abundance of seed predators in a given area, 2) changes in the foraging behavior of individual seed predators in different microhabitats, or 3) different seed predators active in different areas. Answering these types of questions appears crucial for defining the role of seed consumers in plant population and community dynamics (Kelrick et al. 1986, Davidson 1993, Hulme 1993, Holt et al. 1995, Ostfeld et al. 1997).

Individual seed species

Patterns of seed predation for different species of trees in particular microhabitats appeared to largely mirror general patterns with several notable exceptions. Significantly more sunflower seeds were removed with ground cover absent along the forest edge, while this pattern was reversed 10 m into the field, probably reflecting the foraging preferences of birds and mice, respectively. This conclusion is supported by the seasonal shifts observed in the predator guilds foraging on this species as well as the lack of a significant time of day effect on seed removal rates suggesting that both nocturnal and diurnal seed predators shaped the survival patterns of this species. A highly significant effect of time of day on the removal of black cherry seed suggests that this species is consumed primarily by mice, which can easily penetrate the hard seed coat of this species by gnawing with their incisors. *A. altissima*, an introduced exotic species, appears to experience little seed predation regardless of microhabitat. Together with the allelopathic effects of its tissues (Mergen 1959, Heisey 1990, Lawrence et al. 1991), the lack of seed predation may provide this species with a competitive advantage over native species, helping to explain the rapid spread of *A. altissima* in eastern North America following its introduction earlier this century. Taken together, results from this study suggest that seed survival in old fields dominated by white-footed mice may be largely dependent upon where seeds are dispersed in the matrix of vegetation patch types that characterize this habitat. Furthermore, these vegetation-mediated gradients in the probability of seed consumption were fairly uniform for a number of different tree species that typically colonize old fields.

Tree invasion dynamics

The levels of seed predation observed in this and other recent studies (Manson et al. 1998, Ostfeld et al. 1997) suggest that mice, in conjunction with other mammalian herbivores, may significantly influence tree invasion dynamics in old fields. Previous research has indicated that both the relative and absolute abundance of white-footed mice and meadow voles in old fields may influence the rate, species composition, and spatial pattern of tree invasion into these systems (Ostfeld and Canham 1993, Manson et al. 1998, Ostfeld et al. 1997). Furthermore, these effects may be negative or positive depending on the behavior of the particular seed predator involved. White-footed mice and other rodents are known to actively store seeds in scattered surface caches or ground nests for future consumption (Vander Wall 1990). While the majority of these seeds are ultimately consumed, those that survive are often left in ideal microhabitats for germination and thus may comprise a substantial proportion of the seedlings successfully recruiting into subsequent generations (Abbot and Quink 1970, Vander Wall 1990). Birds, particularly nutcrackers and jays (Tomback 1982, Johnson and Adkisson 1985), are also known to cache seeds but not those used in this study.

Results from our study further suggest that the effects of mice on the spatial patterns of seed predation observed in old fields may be related to the matrix of vegetation patch types found there. In particular, the sensitivity mice exhibited to the overall quantity and quality of ground cover in making decisions about where to forage, highlights a mechanism by which earlier seral stages may facilitate or inhibit the establishment of later successional species (sensu Connell and Slatyer 1977; but see Pickett et al. 1987) as well as the need for more research exploring these connections (see Gill and Marks 1991). Our results suggest that factors influencing the pattern of *R. allegheniensis* establishment in old fields may ultimately modify the pattern of forest encroachment by creating a gradient in rodent seed predation intensity. However, as seed predation is but one of many factors influencing tree seedling establishment in old fields, more studies are needed examining both the relative importance of these factors and how their effects change through time.

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