

SEASON AND DISTANCE FROM FOREST - OLD FIELD EDGE AFFECT SEED PREDATION BY WHITE-FOOTED MICE

JAMES T. MCCORMICK^{1,2} AND SCOTT J. MEINERS¹

Abstract - We studied the spatial pattern of seed predation across a forest-old field edge in both fall and winter to assess the potential for seed predators to influence plant spatial patterns. We used a 100 x 100 m grid that began 30 m inside the forest and extended 60 m into the old field. Inside this grid we placed seed stations at regular 10 m intervals and monitored seed removal. Seed predation varied significantly across the edge gradient in both fall and winter with the highest rate of seed removal at the edge in both trials. The spatial pattern of seed predation also differed between seasons. The field portion of the site (≥ 30 m from the edge) was characterized by high seed removal rates in winter and low removal rates in fall. This spatial and temporal variation may alter tree establishment, causing long-term changes in plant community composition and structure.

INTRODUCTION

To understand vegetation dynamics in fragmented landscapes, it is necessary to understand the mechanisms by which edges affect plant community development. Factors that affect the invasion and establishment of woody plants are especially important in old field succession, as they may cause changes in community structure that persist for long periods (Myser and Pickett 1993). Seed predation by mammals is one factor that may limit the establishment of woody plants in successional habitats (De Steven 1991, Gill and Marks 1991, Manson et al. 1998). As edges may alter habitat use by seed predators (Cummings and Vessey 1994, Manson and Stiles 1998), edges may indirectly alter tree invasion dynamics by altering the spatial pattern of seed predation.

Seed predation can have strong influences on the pattern of seedling establishment, but may vary greatly in time and space (Willson and Whelan 1990). This variation in the temporal and spatial pattern of seed predation can be caused by fluctuations in predator populations, fluctuations in seed availability, and selective use of habitat by predators (Gill

¹ Department of Ecology, Evolution, and Natural Resources, Rutgers University, 1 College Farm Road, New Brunswick, NJ 08901-1582; meiners@rci.rutgers.edu. ² Current address: Department of Biological Sciences, State University of New York, 1400 Washington Avenue, Albany, NY 12222.

and Marks 1991, Mittelbach and Gross 1984, Whelan et al. 1990, Willson and Whelan 1990). Time of seed dispersal may also affect the predation intensity a species is subjected to as predator activity often declines in winter (Whelan et al. 1990, Kollmann et al. 1998). Seed predation rates may vary spatially as predators respond to small scale heterogeneity such as logs, woody cover, and vegetation patches (Bowman and Casper 1995; Briggs 1986; Manson and Stiles 1998; Schupp 1988 a, b) or large-scale landscape elements such as edges (Holl and Lulow 1997, Murcia 1995, Sork 1983). This variation in seed predation intensity can determine the spatial pattern of establishment of a plant species.

In eastern deciduous forests, the main predator of woody plant seeds is the white-footed mouse, *Peromyscus leucopus* Rafinesque (Manson and Stiles 1998, Myster and Pickett 1993), which is abundant in both old fields and forests (Cummings and Vessey 1994, Manson and Stiles 1998). *Peromyscus leucopus* prefer to forage in areas of high structural complexity, particularly under woody cover (Briggs 1986, Manson and Stiles 1998) that provides protection from avian and mammalian predators (Lima and Dill 1990). The selective use of habitat by this species is thought to be the dominant factor that determines the spatial pattern of seed predation in abandoned agricultural land (Gill and Marks 1991, Manson and Stiles 1998).

Peromyscus leucopus has also been shown to adjust diet seasonally in response to food availability and dietary needs. Hamilton (1941) examined *Peromyscus leucopus* diets in New York and found that between May and October, only 21% of their diet consisted of seeds, while between November and April, 44% of their diet was comprised of seeds. Such seasonal dietary shifts could impact seed predation as alternative food items may be eaten at other times. *Peromyscus leucopus* behavior differs seasonally in that they cache seeds during the fall (Sanchez and Reichman 1987), which may alter the spatial pattern and rate of seed removal. This behavior could lead to increased removal during the fall, when the dispersal of the majority of woody plants occurs.

We employ a gradient approach to examine the spatial pattern of predation across a forest - old field edge. As animal activity may change seasonally, this experiment was replicated in fall and winter. This experiment was designed to answer the following questions: 1) Does seed predation vary in response to the edge gradient? 2) Do seed predation rates vary between fall and winter? and 3) Does the spatial pattern of seed predation change between seasons? Based on previously published studies we predict: 1) seed predation will be greater in the forest and close to the edge based on habitat selection by *P.*

leucopus, 2) predation rates will be higher in fall when animals are caching seeds, and 3) the spatial pattern of seed predation will be similar between seasons because the habitat preferences of *P. leucopus* will not change.

METHODS

Field site description

The study site, consisting of an old field (last tilled and farmed in 1986) and the adjacent second-growth forest, was at the Hutcheson Memorial Forest Center (HMFC), located approximately 10 km east of New Brunswick, NJ. The forest edge used in this study faced south-east. Herbaceous cover in the field was dominated by several species of *Solidago* spp., *Aster* spp., and *Fragaria virginiana* Duchesne and contained a few scattered trees and shrubs, including a few large *Juniperus virginiana* L. and *Rosa multiflora* Thunb. (Meiners and Pickett 1999). The canopy of the forest was dominated by *Acer rubrum* L. and *Quercus palustris* Muenchh., with a few scattered large *Quercus rubra* L. The understory vegetation of the forest was very sparse with little herbaceous cover. The vegetation at the forest edge was dominated by exotic species, largely *Rosa multiflora* and *Lonicera japonica* Thunb., and the overhanging forest canopy.

The dominant seed predators at the site are white-footed mice, *Peromyscus leucopus* (Manson and Stiles 1998). Other potential seed predators observed at the site include: gray squirrels (*Sciurus carolinensis* Gmelin), white-throated sparrows (*Zonotrichia albicollis* (Gmelin)), song sparrows (*Melospiza melodia* (Wilson)), and house finches (*Carpodacus mexicanus* (Müller)). *Sciurus carolinensis* is largely restricted to forest habitat and often forages preferentially on acorns, while the seed-eating birds forage on smaller-seeded herbaceous species (S.J. Meiners, pers. obs.).

Study species

We used *Acer rubrum* as a test species for seed predation. *Acer rubrum* is a common tree species in old field succession (Buell et al. 1971, Myster and Pickett 1992, Peroni 1994, Pickett 1982) and a dominant species within the second growth forest at HMFC. *Acer rubrum* is a spring-dispersing species, though seeds of this species can still be found on the ground in the fall and winter and are readily taken by seed predators (Myster and Pickett 1993). *Acer rubrum* seeds are easily distinguishable from fall-dispersed seeds within the site. Manson and Stiles (1998) found no differences in the spatial pattern of seed predation among seed species, so the selection of *Acer rubrum*

as a prey species should be indicative of more general patterns of seed predation.

Experimental Design

In a one-hectare portion of the site, one hundred 1 m² plots were arranged in a regular pattern (Fig. 1). Approximately 20 m beyond the innermost forest plots, the second-growth forest abuts the old-growth stand. Plots were restricted to the first 30 m to avoid the influence of changing forest structure. A petri dish filled with 15 *Acer rubrum* seeds was placed within each plot, for a total of 1,500 seeds. A hole was drilled in the center of each dish to allow for drainage. All seeds were sorted before deployment to remove undeveloped or damaged seeds in order to minimize the number of seeds rejected due to food quality. Experiments were initiated on 23 October 1997 and on 9 February 1998. Dishes were monitored on days 5, 10, 15, 20, 30, 40 and 50 in the fall, and weekly in the winter to determine seed removal. Sampling periods differed between trials because seed predation was initially expected to be lower during winter. To account for seeds or seed husks blown out of the dish, a 30 cm radius was searched around each dish for missing seeds at each census. Seeds were generally found within 10 cm of the dish while husks tended to move greater distances. Located seeds were checked for mammal damage and replaced in the dish. The number of husks and partially eaten seeds was also recorded to verify predator activity. The winter trial was stopped at day 28 because of extremely high predator activity.

Because the winter trial was stopped at day 28, only data through day 30 were used in the survival curve analysis (PROC LIFETEST; SAS Institute Inc. 1989) to compare seed removal between seasons. Mean

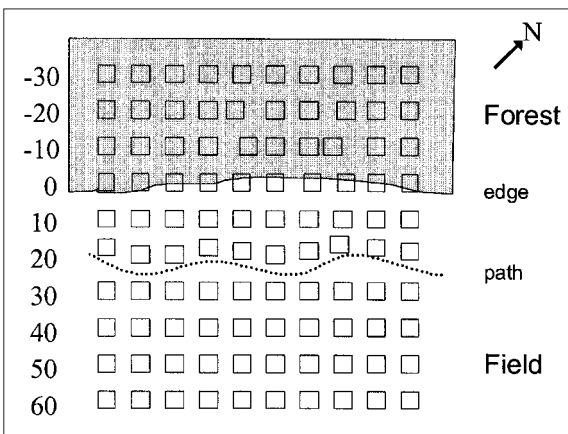


Fig. 1. Map of the study site showing the actual positions of each seed dish (not drawn to scale). The plot extends from 30 m inside the forest to 60 m into the field. Dishes were placed to avoid the mown path that crossed the grid (shown as a dashed line).

survival time was defined as the average minimum number of days seeds survived in each dish and included the entire fall data set. Spatial variation in mean survival time across the edge gradient, between seasons, and similarity between the spatial pattern of seed predation in the fall and winter trials was analyzed with ANOVA (PROC GLM; SAS Institute Inc. 1989). Because data did not conform to normality assumptions of ANOVA, the data were rank-transformed prior to analysis.

RESULTS

The seed removal curves for fall and winter were significantly different, with the winter having a higher rate of seed removal (log-rank=529.269; $P=.0001$; Fig. 2). The percentages of seeds remaining at day 28-30 of the fall and winter trials were 28 and 4%, respectively. Animal activity, as assessed by the presence of seed remains at a station, was found in 86% of the dishes in fall and 91% of the dishes in winter. Seed remains were found for 60% of removed seeds in the fall trial and 55% in the winter trial. All seed remains found had damage consistent with that caused by *P. leucopus* predation.

Mean survival time varied spatially across the edge gradient in both seasons (Fig. 3). Mean survival times were lowest (rapid seed removal) near the edge during fall, while values were lowest at the edge and ≥ 30 m into the field in the winter trial. ANOVA significantly explained the seasonal and spatial pattern of seed predation ($F^{19,180}=12.91$; $P=0.0001$; $R^2=0.58$) with significant distance from the edge, distance \times season interaction terms (all $P = 0.0001$).

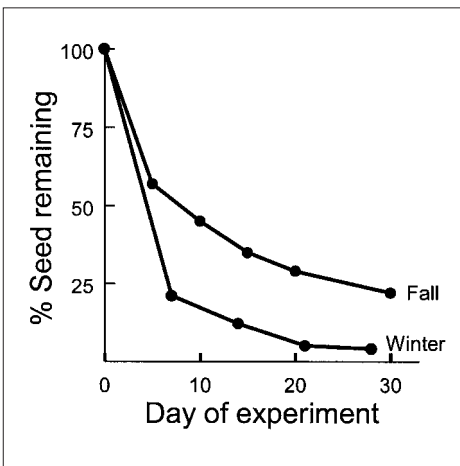


Fig 2. Survival curves for all seeds in the fall and winter trials. Fall experiment continued to day 50, while winter experiment was stopped at day 28.

DISCUSSION

The effects of seasonality upon seed predation were striking. Seed predation occurred at a higher rate and at a different spatial pattern in winter than during the fall. These seasonal changes suggest that seeds dispersing in the fall will suffer lower predation rates than those dispersing in winter. Fall-dispersing seed may escape later predation by falling into soil crevasses or by becoming buried under leaf litter, which may reduce seed encounter (Bowman and Casper 1995, Hulme 1994). Persistent snow cover, which did not occur during the study period, may reduce winter predation rates when present.

A relatively unstudied aspect of edges are their effects on plant - animal interactions (Murcia 1995). This study found a strong effect of distance from the edge on seed removal rates. Heavy predation at the

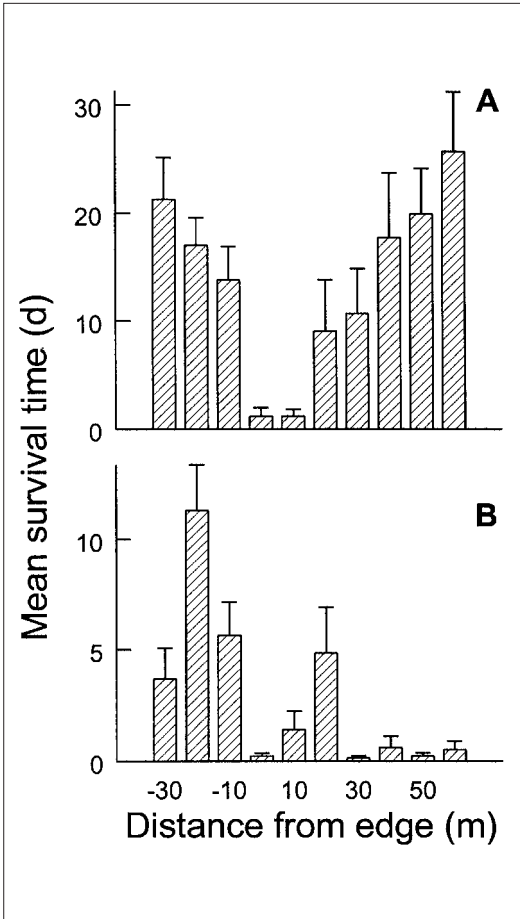


Fig 3. Response of mean survival time to distance from the forest edge for the fall (A) and winter (B) trials. Negative distances represent positions in the forest and positive distances represent spatial position on the field side of the edge. Bars represent mean \pm 1 SE.

edge should be expected as the edge is dominated by *Rosa multiflora*, which would provide cover for predator avoidance (Barnum et al. 1992). The consistently heavy fruit production of *R. multiflora* would also provide a large source of seeds that are preferred food items for *P. leucopus* (Drickamer 1970). Cover of *R. multiflora*, the dominant shrub, declined with distance into the field (Meiners and Pickett 1999), providing a gradient of cover for foraging. As fall seed predation levels are low in the area of the field ≥ 40 m from the edge, and since establishment and survivorship of a tree seedling are much more likely in such an open area (Gill and Marks 1991), the probability of establishment would be expected to increase with distance into the field (Manson et al. 1998). However, winter seed predation patterns would act against this trend. In both seasons the edge had very low seed survival, making edge habitat a consistently poor site for tree establishment.

Behavioral changes in *P. leucopus* may explain seasonal changes in the spatial pattern of seed predation. Although *P. leucopus* spend 85% of their time on the ground (Graves et al. 1988), they spend more time foraging in trees in fall than in winter (McMillan and Kaufman 1995). Increased foraging on the ground by predators would increase encounter rates with dispersed seeds. In addition, shifts in home range occur in winter, when *P. leucopus* form communal underground nests (Wolff and Durr 1986), which would affect habitat utilization. Areas near communal nests would be expected to have very low rates of seed survival.

The fall experiment displayed a slower rate of *A. rubrum* seed removal than the winter experiment, which may indicate a decrease or shift in food resources during the winter trial. In the winter, most of the seeds from a dish were eaten during one census period, even in areas with little cover from predators. This behavior contrasts with the fall trial, when complete seed removal in one period only occurred under *Rosa multiflora*. Similarly, in an experiment conducted in a grassland from winter to early spring, all seeds were removed upon encounter (Hulme 1994). Although *P. leucopus* typically cache seeds, which would increase seed removed in the fall trial, these caches may be depleted by the winter trial (Wolff and Durr 1986). The mild winter during this study may also have resulted in more active mice, further increasing the need for food. Based on comparison with seed predation rates from other years, the *P. leucopus* population appeared to be relatively large during this study (Meiners, Unpublished data). In years with smaller population size, the observed shift in foraging may be less dramatic.

Another possible reason for such a large increase in the winter predation rate is the beginning of breeding for *Peromyscus leucopus*. Breeding season generally occurs from March until November, with

peaks in April-June and September through October (Wolff 1985). However, reproductive *P. leucopus* males were captured in another part of HMFC at the beginning of the winter trial (K. LoGiudice, New Brunswick, NJ pers. comm.). *P. leucopus* compensates for the increased energy demands of breeding by increasing energy intake (Jacquot and Vessey 1998). Although the early portion of the winter experiment was performed before the first peak in breeding normally occurs, the mild winter may have initiated early breeding (Briggs 1986). Winter breeding is also possible in years of good food availability (Wolff and Durr 1986).

The rate and spatial pattern of tree invasion into an old field can be significantly altered by post-dispersal seed predation. This study documents the potential for seasonal shifts in the magnitude and spatial pattern of seed predation. Fall-dispersing seeds were much more likely to survive than winter-dispersing seeds. Furthermore, there appears to be no spatial refugia from predation during winter. In order to understand the effects of seed predation on forest dynamics in fragmented habitats, an understanding of the seasonal and spatial activities of seed predators is necessary.

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