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Survival of and Herbivore Damage to a Cohort of Quercus rubra Planted Across a Forest—Old-field Edge

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ABSTRACT.—Forest edges are known to affect plant community composition and habitat use by animals. However, the direct influence of edges in determining patterns of tree regeneration is poorly understood. Survival of and herbivore damage to *Quercus rubra* seedlings were experimentally determined for seedlings planted across a forest—old-field edge gradient. Seedling survival was lowest inside the forest (1%), intermediate at the edge (25%) and highest within the old-field portion of the gradient (49%). Deer herbivory decreased with increasing distance into the old field. Seedling survival increased under *Rosa multiflora* and decreased in plots with mammalian herbivory. Seedling height was significantly affected by distance from the edge but was unaffected by mammalian herbivory. Based on our results, herbivore effects on *Quercus rubra* growth and survivorship appear secondary to influences of distance from the forest edge.

INTRODUCTION

As landscapes become increasingly fragmented, it is critical that we understand the effects of anthropogenic habitat edges on vegetation dynamics. Although patterns associated with edges have been described for many systems, the ecological function of these landscape features has not been adequately determined. Edges have the potential to control the movement and establishment of plants within fragmented ecosystems (Pickett and Cadenasso, 1995). However, the role of edges in regulating forest regeneration within fragmented landscapes is poorly understood.

The best understood characteristic of edges is their impact on local microclimate. At boundaries between deciduous forests and abandoned agricultural land, edge environments have higher light, wind speed and soil temperature and lower relative humidity relative to the adjacent forested patch (Matlack, 1993; Forman, 1995; Cadenasso *et al.*, 1997). However, the spatial position and abruptness of the transition from field to forest conditions differs greatly among environmental variables (Cadenasso *et al.*, 1997). Although the largest changes in microclimate may occur on the field side of the edge (Cadenasso *et al.*, 1997), detectable changes in microclimate may extend 50 m into deciduous forest stands (Matlack, 1993). This complex environmental gradient may influence the spatial pattern of tree seedlings within forest remnants (Wales, 1972; Whitney and Runkle, 1981; Meiners *et al.*, 2000). However, experimental studies examining the direct response of tree seedlings to this environmental gradient are few.

Edges also alter habitat use by animals. Both insect and mammalian communities change with distance from the forest edge (Linzey, 1989; Jokimäki *et al.*, 1998). Foraging patterns may also vary in response to the presence of edges (Cadenasso and Pickett, 2000; McCor-

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mick and Meiners, 2000). For this reason, there is the potential for indirect edge effects on the plant community through altered spatial patterns of herbivory or predation (Louda, 1989; Murcia, 1995; Meiners *et al.*, 2000). Despite the potential importance of edges in determining plant-animal interactions, these interactions are poorly known in the context of habitat fragmentation. In combination, these direct and indirect effects of edges may regulate the spatial pattern of tree invasion into successional sites.

Throughout the eastern deciduous forest, oak regeneration has been declining and is considered a problem by land managers (Lorimer, 1981; Crow, 1988; Pallardy *et al.*, 1988; Abrams and Downs, 1990). The major postdispersal factors implicated in the lack of regeneration of *Quercus* species are: (1) light limitation in closed canopy forests (Carvell and Tryon, 1961; Lorimer, 1981; Johnson, 1984; Crow, 1992), (2) contemporary decreases in fire frequency (Crow *et al.*, 1994; Brose *et al.*, 1999), (3) increases in herbivore pressure associated with expanding deer populations (Bowers, 1997; Lawson *et al.*, 1999; Canham *et al.*, 1999) and (4) competition with herbaceous and woody vegetation (Carvell and Tryon, 1961; Lorimer *et al.*, 1994; Brose *et al.*, 1999; George and Bazzaz, 1999a, b). *Quercus rubra* has historically established in successional sites following clearing (Foster, 1993; Gilliam *et al.*, 1995; Lawson *et al.*, 1999) and is an important component of old growth and successional forests in the Piedmont region of New Jersey. For these reasons, we selected *Quercus rubra* as a suitable test species to examine oak regeneration across edges.

Most studies of edge effects focus on the forest fragment side of the edge, ignoring edge effects extending into the surrounding matrix. Because the majority of tree regeneration in agricultural clearings occurs near edges (Myster and Pickett, 1992; Inouye *et al.*, 1994), the potential for edges to regulate tree establishment is great. Using *Quercus rubra* as a test species, this study addressed the following questions: (1) How does *Q. rubra* survival and growth vary across an edge gradient?, (2) Does insect and mammalian herbivory on *Q. rubra* vary in response to edges?, (3) How does feeding by different herbivores affect seedling survivorship? and (4) Does competition with shrubs affect seedling growth and survivorship?

MATERIALS AND METHODS

Study site and species.—The research site was an old field and adjoining early successional forest at the Hutcheson Memorial Forest Center (HMFC) near East Millstone, New Jersey (40°30′N, 74°34′W) with a southeast facing forest edge. The young forest was dominated by *Fraxinus americana*, *Acer rubrum* and *Quercus palustris* and was on land that was abandoned in the 1950s. The field had been used to grow corn and had been abandoned 12 y at the beginning of this study. Herbaceous perennial species dominated the vegetation of the old field with scattered trees and shrubs (Meiners and Pickett, 1999). *Rosa multiflora* was the most abundant shrub species across the entire site, dominating local areas. Deer populations in adjacent natural areas were estimated at $>90/\text{km}^2$ in March 1999 (L. S. Katz, pers. comm., based on infrared censuses).

Experimental design.—We established a 90 × 90 m grid across the forest edge that began 30 m inside the forest and extended 60 m into the old-field. Within this grid, we placed 100 1 m^2 plots at regular 10 m intervals (Fig. 1). Plot position was shifted when necessary to avoid other experimental projects or trails. Wherever possible, we held distance from the forest edge constant within each distance interval, shifting plot position parallel to the edge. We defined the forest edge as a straight line that approximated the most recent plow line. The vegetation within each plot was sampled between 29 June–2 July 1996 (Meiners and Pickett, 1999). With the aid of a sampling frame, the percent cover of all species present

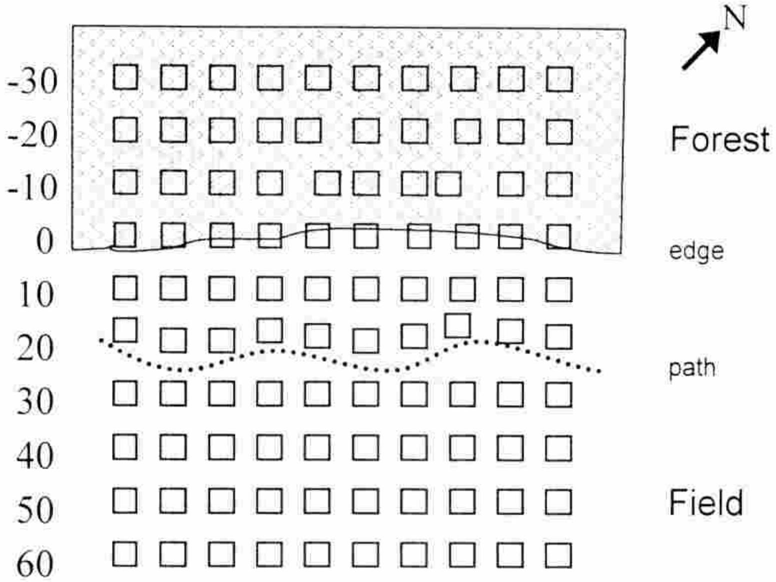

FIG. 1.—Map of the study site showing the actual positions of each seedling plot (not drawn to scale). The grid extends from 30 m inside the forest to 60 m into the field. Plots were placed to avoid the mown path that crossed the grid (shown as a dashed line)

was visually estimated to the nearest 1%. Cover of *Rosa multiflora* in each plot was used to assess the influence of shrub competition on *Quercus* survival and growth.

On two sides of each plot, five bare-root seedlings, principally of *Quercus rubra*, were planted in May 1996. Seedlings were from the New Jersey State Tree Nursery and were 2–3 y old and 30–50 cm tall. We monitored plots twice a year (June and September) for survivorship over 4 y. At the first census, it was discovered that the seedlings contained a small number (<5%) of other *Quercus* species, *Q. bicolor*, *Q. prinus* and *Q. velutina*. Because it was unknown how many seedling of the original planting were not *Q. rubra*, and some mortality had already occurred, survival measures include all *Quercus* species. Height measurements were taken in September 1999 for *Quercus rubra* seedlings only.

Seedlings were assessed for herbivore damage to determine the spatial pattern of plant-animal interactions across the edge gradient. The prevalence of insect damage was measured in July 1996 as the percent of leaves on each *Quercus rubra* seedling that showed signs of insect herbivory, generally leaf tissue loss. Overwinter damage to stems by mammalian herbivores was assessed in June 1997 and separated into deer (*Odocoileus virginianus*) browse and rabbit (*Sylvilagus floridanus*) clipping based on stem damage characteristics. Seedlings were classified as damaged or undamaged for mammalian herbivores. A few seedlings showed girdling by voles (*Microtus pennsylvanicus*) but these were too few for analysis. Most *Quercus* seedlings were too large to have been clipped by voles (Ostfeld *et al.*, 1997). Because of high mortality of forest seedlings in the first year, herbivore damage was assessed only once during the study.

Data analysis.—Cox regression was used to determine the effects of distance from the edge, *Rosa multiflora* cover and herbivore damage on seedling mortality, (Proc PHREG, SAS; Allison, 1995). A second Cox regression was conducted to calculate survival model parameters for each distance from the forest edge relative to seedlings at the edge. The

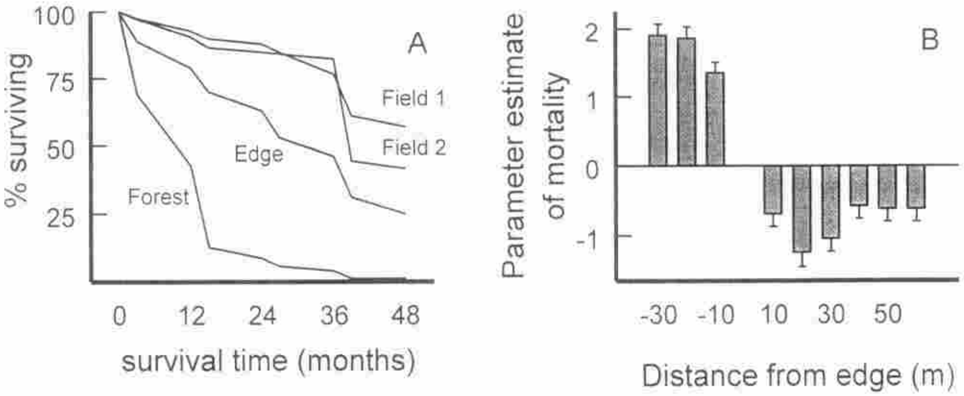

FIG. 2.—Effects of distance from the forest edge on *Quercus* seedling survival. (A) Survival curves are for forest plots (distance −30 to −10 m), edge plots (distance 0 m only), field 1 (distance 10 to 30 m) and field 2 (distance 40 to 60 m). (B) Regression coefficients from Cox regression for mortality at each distance class (compared to distance = 0). Positive parameter estimates indicate increases in mortality relative to seedlings at the edge. Bars represent mean = 1 SE of the coefficients

significance of variation in herbivore damage across the edge gradient was evaluated with ANOVA for each herbivory type (Proc GLM, SAS Institute, Inc., 1989). The effects of herbivore damage, *R. multiflora* cover and distance from the forest edge on seedling height were analyzed with ANCOVA, using distance from the edge as a categorical variable and *R. multiflora* cover and herbivore damage as covariates (Proc GLM, SAS Institute, Inc., 1989). The relationships between *R. multiflora* cover and herbivore damage were assessed with Spearman correlations (Proc CORR, SAS Institute, Inc., 1989).

RESULTS

Survivorship differed dramatically across the edge gradient (Fig. 2A.). Four years after planting, survival was lowest in the forest portion of the site, intermediate at the edge and highest in the old field. During a severe drought in 1999, seedlings 40–60 m into the old field had higher mortality than those at 10–30 m. Parameter estimates from the Cox regression of mortality for seedlings within the forest were approximately twice that of edge seedlings (Fig. 2B). Seedlings within the field portion of the site were much less likely to die (*i.e.*, a negative regression coefficient) than seedlings at the edge or within the forest. Overall, seedling mortality decreased with increasing *Rosa multiflora* cover and across the edge from forest to field (Table 1). Seedling mortality increased with increasing herbivore pressure from deer browse and rabbit clipping, but was unaffected by levels of insect damage.

Seedling height was greatest 20 m into the old field, and decreased both farther from, and closer to, the edge (Fig. 3). Distance from the edge and increasing *Rosa multiflora* cover were associated with increases in seedling height (Table 2). Plots with more insect damage also had taller seedlings, whereas deer and clipping damage had no significant relationship to seedling height. All interaction terms were nonsignificant and were dropped from the model.

Herbivore damage varied significantly across the edge gradient for both insect and mammalian herbivores (Fig. 4). Insect herbivory varied irregularly with distance from the edge ($F_{9,89} = 2.96$; $P = 0.004$; $R^2 = 0.23$). Rabbit damage was lowest in the field 10 to 30 m from

TABLE 1.—Effects of distance from edge, *Rosa multiflora* cover, and herbivore damage on the survival of *Quercus* seedlings. Parameter estimate is per unit change in source variable (*e.g.*, per 1% increase in *R. multiflora* cover)

Source	Df	Wald χ^2	*P*	Parameter estimate
Distance from edge	1	202.11	0.0001	−0.029
Rosa multiflora cover	1	19.15	0.0001	−0.006
Insect herbivory	1	1.97	0.1597	0.004
Rabbit clipping	1	19.83	0.0001	0.006
Deer browse	1	12.83	0.0004	0.008

the edge and was almost twice as frequent at all other distances ($F_{9,87} = 3.01$; $P = 0.0036$; $R^2 = 0.24$). Deer browse was highest 20 m into the forest and decreased with distance into the old field ($F_{9,87} = 3.24$; $P = 0.0019$; $R^2 = 0.25$). Deer browse estimates are likely conservative because rabbit damage generally resulted in the seedling being chewed off 2–3 cm above the soil surface. This damage made deer browse on seedling tops undetectable. Although *Rosa multiflora* cover was significantly associated with seedling height, it was not related to any measure of herbivore activity (insect damage: $r_S = -0.04$, $P > 0.05$; rabbit clipping: $r_S = -0.0001$, $P > 0.05$; deer browse: $r_S = 0.04$, $P > 0.05$).

DISCUSSION

Seedling performance.—Distance from the forest edge was the principal factor in determining both survivorship and height of *Quercus* seedlings. Although not directly measured in this study, light availability changes abruptly across forest-old-field edges, with significant changes in light occurring on both sides of the edge (Matlack, 1993; Cadenasso *et al.*, 1997). Growth of first year *Q. palustris* seedlings also increased with distance into the field, reach-

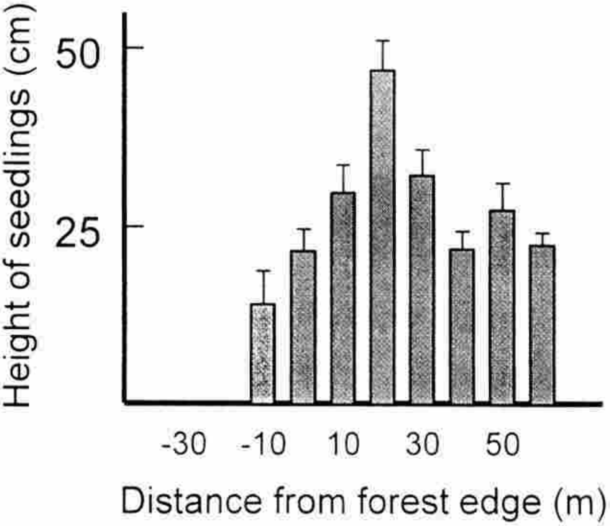

FIG. 3.—Effect of distance from the forest edge on *Quercus rubra* height, four years after planting. Bars represent mean = 1 SE for plots at each distance class

TABLE 2.—ANCOVA results for the effects of distance from the forest edge, *Rosa multiflora* cover, and herbivore damage on seedling height. Overall model was significant ($F_{11,56} = 6.17$; $P = 0.0001$; $R^2 = 0.55$)

Source	Parameter estimate	df	MS	F	P
Distance from edge	—	7	505.16	5.47	0.0001
Rosa multiflora cover	0.14	1	852.82	9.23	0.0036
Insect herbivory	0.21	1	376.13	4.07	0.0485
Rabbit clipping	−0.09	1	269.35	2.91	0.0933
Deer browse	−0.07	1	62.26	0.67	0.4153

ing a maximum 40 m into the field (Meiners, 1999). These data are consistent with the hypothesis that low light is limiting for *Quercus* regeneration (Carvell and Tryon, 1961; Johnson, 1984; Crow, 1992).

A severe drought in 1999 generated further responses to the edge in seedling survivor-

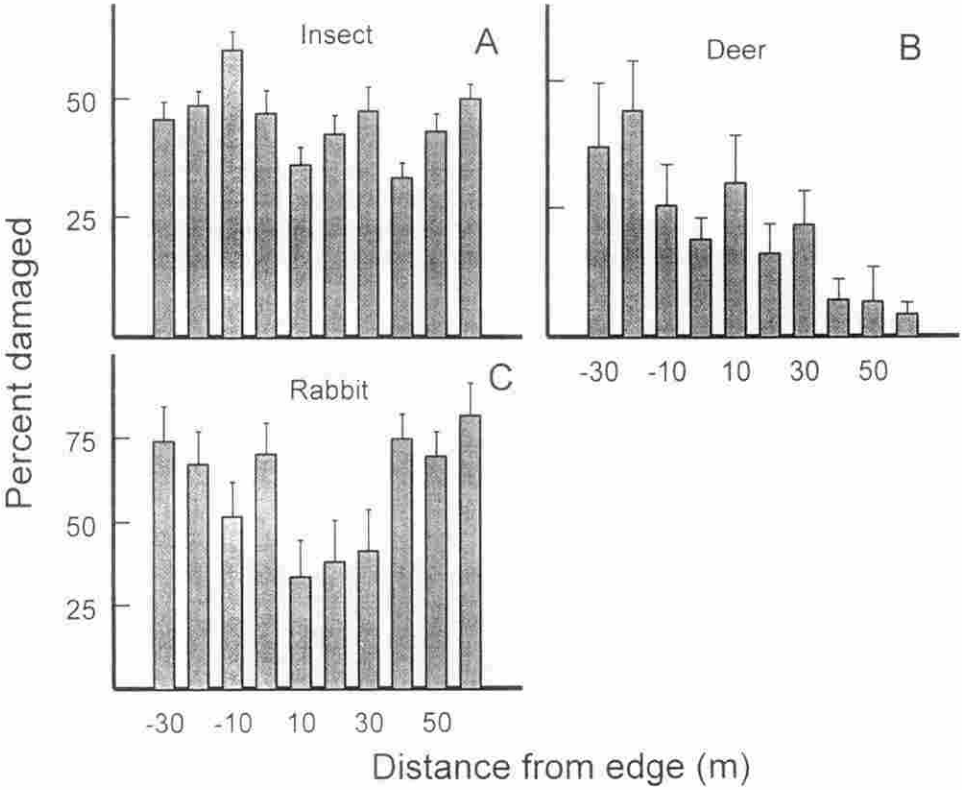

FIG. 4.—Effects of distance from the forest edge on the spatial patterns of insect (A), deer (B) and rabbit (C) damage on *Quercus rubra* seedlings. Insect damage expressed as the percent of leaves showing damage. Rabbit clipping and deer browse are shown as percent of seedlings showing each damage type. Bars represent mean ± 1 SE for plots at each distance class

ship. Seedlings planted 40–60 m into the old field had greater mortality than those at 10–30 m. Drought stress may have been more severe for seedlings farthest from the forest edge because they were beyond ameliorating effects of the edge such as shading (Cadenasso *et al.*, 1997). The vegetation of the site also suggests that the area 40–60 m into the old field was drier than areas closer to the forest. The plots 40–60 m into the old field were dominated by *Solidago juncea*, while plots closer to the forest were dominated by *S. canadensis* (Meiners and Pickett, 1999). These species are known to assort along moisture gradients, with *S. juncea* occupying drier microsites and *S. canadensis* occupying more mesic areas (Potvin and Werner, 1983). *Quercus rubra* seedlings respond to drought stress by closing stomata, leading to a reduction in growth (Cavender-Bares and Bazzaz, 2000). The combined response to drier conditions in the field center and light limitation near the edge may account for the peak in seedling height at intermediate distances into the field.

Competitive effects.—While competition with associated vegetation can have strong effects on *Quercus* regeneration (Carvell and Tryon, 1961; Lorimer *et al.*, 1994; Brose *et al.*, 1999; George and Bazzaz, 1999a, b), the influences of *Rosa multiflora* in this study were not consistent with this expectation. *Quercus* seedlings grew taller and were more likely to survive as *Rosa* cover increased. The dense thorny canopy of *R. multiflora* could have protected associated seedlings from mammalian herbivores, however herbivore activity was not statistically related to *Rosa* cover. For this reason the mechanism resulting in beneficial effects on *Quercus* seedlings is not clear.

Herbivore effects.—Although the prevalence of insect damage changed spatially, there was no clear response to the edge gradient. The spatial pattern of insect damage may have been driven by changes in insect community composition or activity across the edge (Jokimäki *et al.*, 1998; Meiners *et al.*, 2000). While there were no detectable insect effects on seedling survivorship, insect herbivory was positively associated with seedling height. This association may have been caused by insects selectively feeding on larger individuals. Although insect herbivory rarely affects survivorship or growth of older seedlings such as those used here (Inouye *et al.*, 1994; McCarthy, 1994), insects are important in seedling establishment at HMFC (Facelli, 1994; Meiners *et al.*, 2000).

In contrast to insect herbivory, mammalian herbivores had significant influences on *Quercus* survivorship in this site. Damage by deer and rabbits was associated with higher levels of mortality, but did not influence seedling height. Herbivory by mammals is generally thought to limit tree regeneration in successional areas of eastern North America (Inouye *et al.*, 1994; McCarthy, 1994; Ostfeld *et al.*, 1997), particularly with contemporary increases in deer populations (Bowers, 1997; Alverson *et al.*, 1998). We found that herbivore effects on both height and surviorship were much smaller than edge effects on seedling performance. This suggests that herbivore activity can reduce *Quercus* regeneration, but that it is secondary to edge effects within in the site (Bowers, 1997). Direct manipulation of herbivore activity is needed to fully evaluate this observation.

Mammalian herbivores selectively used habitat in relation to the edge gradient. Deer browsed preferentially on seedling within the forest and those closer to the forest edge, resulting in a gradient of herbivore pressure (Strange and Shea, 1998; Cadenasso and Pickett, 2000). Clipping damage was consistently high within the site except for 10-30 m from the edge. This area was dominated by dense stands of *Solidago canadensis* (Meiners and Pickett, 1999), which may have prevented rabbits from accessing seedlings. This is contrast to areas farther from the edge, which were dominated by shorter plants, such as *S. juncea* and *Fragaria virginiana* (Meiners and Pickett, 1999) that would allow rabbits to move easily. Similar influences on tree regeneration have been found in long term studies at HMFC, with seedlings palatable to herbivores clustered close to forest edges (Myster and Pickett, 1992).

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