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Tree seedling establishment under insect herbivory: edge effects and inter-annual variation

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Abstract

As the density and species composition of insects may change in relation to distance from the forest edge, the role of herbivory in tree establishment may also change across edges. To determine the importance of insect herbivory in tree establishment, insect densities were experimentally altered at different distances from the forest edge. Plots were established at three distances from the edge, with plots located in forest, edge, and field habitats. In half of each plot, insect densities were reduced by insecticide application. Seeds of two tree species, *Acer rubrum* and *Fraxinus americana*, were planted into each plot in 1995. The experiment was repeated in 1996 with the addition of *Quercus palustris* and *Quercus rubra*.

Distance from the forest edge was the most important factor in determining seedling emergence and mortality. Overall seedling performance increased from field to edge to woods, although responses varied among species. In 1995, a drought year, insect removal increased emergence and decreased mortality of tree seedlings. In 1996, a year with normal precipitation, insect removal had much less effect on *A. rubrum* and *F. americana*. For the two *Quercus* species, mortality was reduced by insect removal. The tree species differed in their susceptibility to insect herbivory, with *Acer rubrum* the most susceptible and *Fraxinus americana* the least. Herbivory by insects was shown to have the potential to affect both the composition and spatial pattern of tree invasions. Herbivore importance differed greatly between the two years of the study, making the interaction between insects and tree seedlings variable both in space and time.

Introduction

Insects have been shown to exert strong effects on herbaceous stages of old field succession (Malone 1969; Shure 1973; Brown 1985; Brown & Gange 1992), although their role in the establishment of woody species has been little studied. Invertebrates can alter herbaceous species composition and diversity through selective herbivory (Malone 1969; Shure 1973; Brown & Gange 1992; Hulme 1996), which may change successional rates or trajectories (McBrien et al. 1983; Brown & Gange 1992). However, for woody seedlings in old field communities, insects are rarely found to affect survival or growth (Myster & McCarthy 1989; Inouye et al. 1994; McCarthy 1994). This is contrasted by mammalian herbivory, which, through more extensive removal of leaf and stem tissue, can reduce or even eliminate woody plant regeneration (Ostfeld & Canham 1993; Inouye et al. 1994; McCarthy 1994). This has led to the generalization that mammal herbivory determines the rate of tree establishment in old fields, while insects have little or no impact.

The lack of demonstrated effects of insect herbivory on tree establishment in old fields may be artifactual. In most studies, the tree seedlings used to assess the impacts of insects are well established and often a few years old (Myster & McCarthy 1989; McCarthy 1994; Inouye et al. 1994). This is problematic because the susceptibility of a seedling to herbivore damage, and the impacts of that damage, change with the development of the seedling (Dirzo 1984; Hendrix 1988; Hanley et al. 1995; Karban & Thaler 1999). Herbivory occurring before a seedling's emergence or on young cotyledons can have catastrophic effects on survival (Facelli 1994), while insect herbivory on established seedlings often has no measurable effect (Myster & McCarthy 1989; McCarthy 1994). To adequately assess the role of insects in tree establishment, the earliest demographic stages must be included.

Successional dynamics are further complicated by the spatial heterogeneity caused by habitat edges. Forest edges cause gradients in microclimate (Matlack 1993; Chen et al. 1995; Cadenasso et al. 1997) which can affect the growth or establishment of plants along the edge. Species abundances near edges may either increase or decrease due to their physiological responses to abiotic factors (Sork 1983; Williams-Linera 1990; Chen et al. 1995), resulting in altered physical structure of the edge vegetation. Since the animal species that interact with plants may themselves respond to edges, there is the potential for indirect biological effects on tree seedling establishment (Louda 1989; Murcia 1995; Didham et al. 1996). Insect species may also respond directly to small changes in microclimate (Shure & Phillips 1991; Burger & Louda 1994; Murcia 1995). These direct and indirect responses may lead to changes in insect community composition along edges (Harman & Harman 1987; Bellinger et al. 1989; Didham et al. 1996; Jokimäki et al. 1998), resulting in differing herbivory rates across the edge gradient (Didham et al. 1996).

This study examined the effects of insect herbivores on the emergence and establishment of tree seedlings along the gradient from forest interior to open field. Tree seedling establishment may respond directly to a change in microclimate, to a change in herbivore pressure, or to both. This study was designed to address the following questions: (1) Does herbivory by insects affect the establishment of woody seedlings in old fields? (2) Does distance from the forest edge influence tree establishment? (3) Do the effects of insects on tree seedling establishment change in relation to the forest edge?

Methods

Study site

This research was conducted in an old field (last tilled and farmed in 1986) and adjacent forests at the Hutcheson Memorial Forest Center near East Millstone, Somerset County, NJ (40°30′ N, 74°34′ W). The old field was bordered on three sides by forest and contained a few scattered trees and shrubs including a few large *Juniperus virginiana* L. and *Rosa multiflora* Thunb. The forest edges used in this study faced southeast (both years) and northwest (1996 only). The northwest edge was added in the second year of the study to increase statistical power.

Herbaceous cover in the field was dominated by several species of *Solidago* L. and by *Fragaria virginiana* Duchesne. The canopy of the forest was dominated by *Acer rubrum* L. and *Quercus palustris* Muenchh. with scattered large *Quercus rubra* L. The understory of the woods 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. Nomenclature follows Gleason & Cronquist (1991).

Study species

In 1995, *Fraxinus americana* L. and *Acer rubrum* were used in the field experiment. Two oak species, *Quercus rubra* and *Quercus palustris* were added to the experiment in 1996. *Fraxinus americana* and *Acer rubrum* are the most frequent invaders in the study site while the two oak species have only limited establishment (Meiners, unpublished data). Seeds of all species were collected from sources within central New Jersey and were stratified as necessary (Young & Young 1992). Insect larvae were killed in *Quercus rubra* seeds before stratification by immersing the seeds in 49 °C water for 40 min.

Experimental design

A series of 2.75 × 4.5 m plots was established at three distances from the forest edge (−10, 2, and 10 m) resulting in treatments within the forest, at the edge, and in the open field respectively (Figure 1). The forest edge is defined here as the base of the trees that formed the original fencerow. Within each half plot, 50 seeds of *Acer rubrum* and *Fraxinus americana*, and in 1996, 20 seeds of each *Quercus* species were planted.

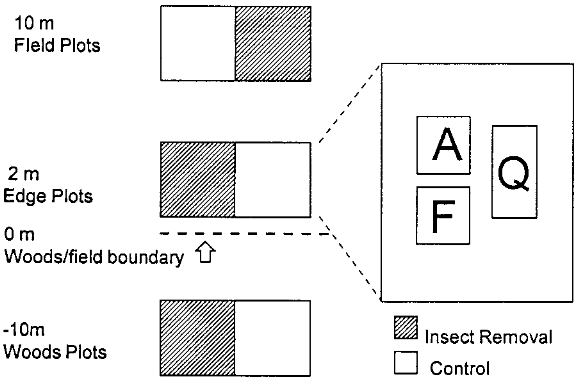

Figure 1. Diagram of the experimental design of one transect in the field experiment. Distances are relative to the forest edge with −10 being inside the forest. A, F, and Q refer to plantings of *Acer rubrum*, *Fraxinus americana*, and both *Quercus palustris* and *Q. rubra,* respectively. *Quercus* seed were placed in hardware cloth exclosures to prevent mammalian seed predation. Diagram is not to scale.

To prevent seed predation, the *Quercus* acorns were planted into a cage of 1.4 cm hardware cloth, anchored with two metal pins. A total of 12 experimental plots along 4 transects was used in 1995. Because of low seed availability, only 727 seeds of *Fraxinus americana* were used in 1995. In 1996, the experimental design was replicated on the opposite side of the field using a northwest facing edge. One transect that had unexplainably low germination in 1995, was not used in 1996 resulting in a total of 9 plots along 3 transects on each side of the field.

Half of each plot had insect densities reduced by periodic application of both soil and foliar insecticides (Brown & Gange 1992). Soil insecticide (chlorpyrifos) was applied monthly in a granular form (100 mg ai m^2) and foliar insecticide (dimethoate) was applied as a spray every two weeks (33.6 mg ai m^2). Equivalent amounts of deionized water were sprayed on control plots (Brown et al. 1987). Pesticide application was done on windless mornings with a backpack sprayer at low pressure to minimize drift onto control portions of the plot. All treatments were surrounded by poultry netting to reduce mammalian exposure to pesticides. This fencing had mesh large enough to allow access by the dominant seedling predator in the site, *Microtus pennsylvanicus* (Manson et al. 1998). Large *R. multiflora* shrubs prevented access to portions of three plots in 1995, so shrubs in all plots were clipped and removed.

Data collection and analysis

Each week, all plots were censused and seedlings were marked with plastic toothpicks. Once emergence was complete, censuses switched to biweekly. At week four, herbivory was assessed visually as the percentage of cotyledon tissue removed in 5% increments. Emergence and mortality were analyzed with log-linear analysis (Proc CATMOD; SAS Institute Inc. 1989), which allows analyses similar to ANOVA to be performed on categorical data. Herbivory data were analyzed with split-plot ANOVA, in which significance of the site term was determined with an F-test using the transect × site interaction as the error mean square. Plot means of percent cotyledon herbivory were used to avoid problems of large numbers of zeros in the data.

To assess the effectiveness of the insecticide applications, pitfall trapping was done monthly in 1995 (July and August) and 1996 (June–August). Trap exposure time was one day in 1995 and was increased to 3 days in 1996. A cover was added to the 1996 traps to exclude flying insects. All insects >2 mm were recorded. The total number of insects captured was pooled for each trap across all sampling dates within each year. Insect herbivores were rarely found on the experimental seedlings, so direct estimation of herbivore loads was not possible.

Phytotoxicity of insecticides

To assess the direct effects of the insecticides on the study species, a 2 × 2 complete factorial experiment was performed with the foliar and soil insecticides as the treatments. Pots of greenhouse soil were planted with 20 seeds of *Fraxinus americana* or *Acer rubrum*, or 15 seeds of *Quercus palustris* and were thinned to the first 10 individuals emerging. Each treatment was replicated 6 times for each species (a total of 72 pots). The pots were placed on an elevated bench outside and were watered as necessary.

The soil of pots receiving soil insecticide was treated monthly with an equivalent amount of chlorpyrifos granules to the field application. Foliar insecticide treatments were sprayed every two weeks with dimethoate solution at the same concentration as field applications. Foliar insecticide control pots were sprayed with equivalent amounts of deionized water at the same time as insecticide application. After 60 d, the plants were harvested, dried, and weighed.

Results

The insecticide treatments significantly reduced insect abundances in both years as assessed by the pitfall traps (Wilcoxon rank-sum test; 1995 $P=0.0277$, 1996 $P=0.0491$). Average insect captures/trap were: 1995 – control 21.3±2.0, removal 15.3±1.6; 1996 – control 35.2±3.3, removal 26.2±2.4. The two years of the experiment differed greatly in precipitation, with 1995 being a severe drought and 1996 having average rainfall. Average (10 yr) rainfall is 514 mm for May–September but was only 371 mm (72% of normal) in 1995 and was 489 mm (95% of normal) in 1996. Precipitation data were collected from the Hutcheson Memorial Forest Center weather station.

Acer rubrum performance

The emergence of *A. rubrum* was increased by insect removal in 1995, while there was no significant effect in 1996 (Figures 2a and 2b, Table 1). Site was a significant factor in both years (Table 1); however, the spatial relationship changed. Emergence decreased from field to edge to woods in 1995, while it increased from field to woods in 1996. Overall, emergence was lower in the 1995 drought (G test of independence; G = 289.9 1 df, $P=0.001$).

High mortality of *A. rubrum* in 1995 prevented log-linear analysis for all factors except site, which was insignificant (Figure 2c, Table 1). In 1996 only site was significant with increasing mortality from field to woods (Figure 2d; Table 1). Mortality across all treatments was higher in the drought year (G test of independence; G=86.6 1 df, $P=0.001$). Insecticide application reduced cotyledon herbivory in 1995 but had no significant effect in 1996 (Table 1). Herbivory was greatest in the edge plots in 1995, but showed no clear spatial pattern for 1996 (Figures 2e and f).

Fraxinus americana performance

The emergence of *F. americana* was significantly higher in the insect removal treatment in 1995 (Table 2, Figure 3a) but was unaffected by insecticide application in 1996 (Figure 3b). Site was the only significant factor in the 1996 analysis (Table 2), although the site × treatment interaction was nearly significant ($P=0.0514$; Table 2). Emergence was increased by insecticide application in the field and woods plots but decreased in the edge plots (Figure 2b). Overall emergence was higher in the dry year when compared to the average year (G test of independence; G = 5.5, 1 df, $P=0.019$).

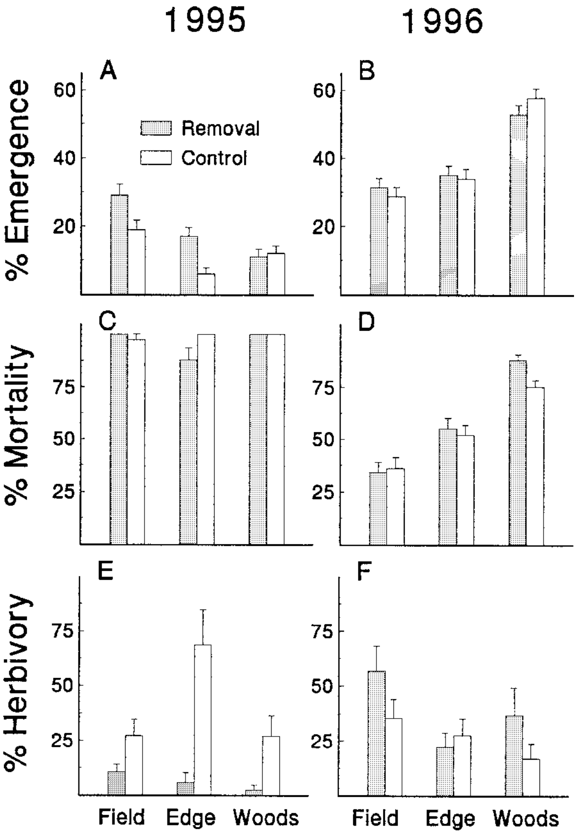

Figure 2. Effects of insect herbivory and spatial position on the emergence (A, B), mortality (C, D) and cotyledon herbivory (E, F) of *Acer rubrum* in the field experiment for 1995 and 1996. Herbivory data is presented as average plot mean for percent cotyledon removal. Error bars represent one standard error.

Mortality was decreased by insecticide application in 1995 and increased from field to edge to woods (Figure 3c, Table 2). All terms were significant in 1996, including the site × treatment interaction (Table 2). There was a slight increase in mortality from field to edge to woods (Figure 3d). Overall mortality was much lower during the year with average precipitation (G test of independence; G = 102.3, 1 df, $P=0.001$). Cotyledon herbivory of *F. americana* was significantly reduced by insecticide application in 1995 (Figure 3e, Table 2). In 1996, the only significant factor for herbivory was the transect effect (Figure 3f, Table 2).

Table 1. Analysis of *Acer rubrum* seedling performance from the field experiment. Categorical data (emergence and mortality) were analyzed with a log-linear model. Values shown are χ^2-square statistics (df). Herbivory data were analyzed with split-plot ANOVA. Values shown are F-statistics (df).

	Site	Treatment	Site×Treatment	Transect
1995				
Emergence	$32.30^{***(2)}$	$10.00^{***(1)}$	$6.97^{*(2)}$	
Mortality	$2.03^{(2)}$	—	—	
Herbivory	$0.22^{(2,5)}$	$88.41^{***(1,6)}$	$7.55^{*(2,6)}$	$6.16^{*(3,6)}$
1996				
Emergence	$87.85^{***(2)}$	$0.01^{(1)}$	$2.05^{(2)}$	
Mortality	$103.65^{***(2)}$	$3.23^{(1)}$	$5.65^{(2)}$	
Herbivory	$3.08^{(2,10)}$	$0.48^{(1,12)}$	$0.72^{(2,12)}$	$4.86^{*(5,12)}$

$^{*} = P<0.05$; $^{**} = P<0.01$; $^{***} = P<0.001$.

Table 2. Analysis of *Fraxinus americana* seedling performance from the field experiment. Categorical data (emergence and mortality) were analyzed with a log-linear model. Values shown are χ^2-square statistics (df). Herbivory data were analyzed with split-plot ANOVA. Values shown are F-statistics (df).

	Site	Treatment	Site×Treatment	Transect
1995				
Emergence	$3.89^{(2)}$	$14.26^{***(1)}$	$3.36^{(2)}$	
Mortality	$99.08^{***(2)}$	$8.80^{**(1)}$	$0.80^{(2)}$	
Herbivory	$39.08^{**(2,3)}$	$0.07^{(1,4)}$	$1.04^{(2,4)}$	$0.51^{(2,4)}$
1996				
Emergence	$22.94^{***(2)}$	$0.77^{(1)}$	$5.94^{(2)}$	
Mortality	$7.65^{*(2)}$	$45.55^{***(1)}$	$54.94^{***(2)}$	
Herbivory	$3.08^{(2,10)}$	$0.48^{(1,12)}$	$0.72^{(2,12)}$	$4.86^{*(5,12)}$

$^{*} = P<0.05$; $^{**} = P<0.01$; $^{***} = P<0.001$.

Quercus performance

The emergence of *Q. palustris* was significantly increased in the insecticide treatment, while the emergence of *Q. rubra* was unaffected (Figures 4a and 4b, Table 3). In both species, emergence decreased from field to edge to woods. Mortality was decreased by insect removal at most sites in both species (Figures 4c and d, Table 3). The intensity of the insecticide effects changed with distance from the edge for both species, resulting in a significant site × treatment interaction (Table 3). Mortality was higher in the insecticide treatment for *Q. rubra*. Because no seedlings died in the field insecticide treatment, the site term could not be evaluated in the log-linear analysis.

Phytotoxicity experiment

Insecticide application affected the emergence of some of the species tested. *A. rubrum* emergence was decreased by all insecticide application treatments (Figure 5a, Table 4). *Q. palustris* emergence was increased by nearly 8% in the presence of both the soil and foliar insecticides (Figure 5a), but was unaltered by either insecticide alone. *Fraxinus americana* emergence was unaffected y the presence of the insecticides. Insecticides reduced the growth of seedlings for both *Acer rubrum* and *Fraxinus americana* with no significant interaction between soil and foliar applications (Figure 5b, Table 4). *Quercus palustris* seedlings did show some reduction in growth but this was not significant at $P<0.05$. Similar phytotoxic effects were observed for the growth of all species in the field experiment. For this reason growth data are not presented.

Table 3. Analysis of *Quercus palustris* and *Quercus rubra* seedling performance from the field experiment. Categorical data (emergence and mortality) were analyzed with a log-linear model. Values shown are χ^2-square statistics (df).

	Site	Treatment	Site×Treatment	Transect
Q. palustris				
Emergence	$9.38^{**(2)}$	$18.59^{**(1)}$	$3.14^{(2)}$	
Mortality	—	$120.13^{***(1)}$	$133.14^{***(2)}$	
Q. rubra				
Emergence	$19.61^{***(2)}$	$0.79^{(1)}$	$1.03^{(2)}$	
Mortality	—	$45.55^{***(1)}$	$54.94^{***(2)}$	

$^{**} = P<0.01$; $^{***} = P<0.001$.

Table 4. Summary of emergence and growth responses of seedlings to foliar and soil insecticide application in the control experiment. Emergence data were analyzed with a log-linear model. Values shown are χ^2-square statistics (df). Growth data were analyzed with ANOVA. Values shown are F-statistics (df). Data were log-transformed as necessary to conform to assumptions of ANOVA.

	Foliar insecticide	Soil insecticide	Interaction
Acer rubrum			
Emergence	$25.72^{***(1)}$	$9.68^{**(1)}$	$13.39^{***(1)}$
Growth	$6.27^{*(1,154)}$	$4.27^{*(1,154)}$	$0.82^{(1,154)}$
Fraxinus americana			
Emergence	$0.09^{(1)}$	$0.34^{(1)}$	$2.59^{(1)}$
Growth	$45.33^{***(1,235)}$	$3.83^{*(1,235)}$	$0.00^{(1,235)}$
Quercus palustris			
Emergence	$0.52^{(1)}$	$3.11^{(1)}$	$3.92^{*(1)}$
Growth	$3.51^{(1,205)}$	$3.83^{(1,205)}$	$0.00^{(1,205)}$

$^{*} = P<0.05$; $^{**} = P<0.01$; $^{***} = P<0.001$.

Discussion

Insect herbivory on tree establishment

Below-ground herbivores appear to have the strongest effects on tree seedlings very early in establishment. In the 1995 drought, the main difference between insecticide treatments and controls was in emergence for *A. rubrum* and *F. americana*. For herbivory to influence emergence, it would have to occur on emerging radicles or on cotyledons, possibly while they remain in the seed coat (Dirzo 1984; Facelli 1994). As all of the effects in the phytotoxicity experiment were negative, the significance of the positive effects of insect removal on *Acer rubrum* in the field experiment are not compromised (Gange et al. 1992). Insect herbivory was also found to reduce the emergence of *Ailanthus altissima*, an exotic invasive tree species, in another HMFC field (Facelli 1994).

The two *Quercus* species had little leaf tissue removed by herbivores (S. Meiners, personal observation) but still showed significant effects of insect removal. This could be caused by soil insects feeding on the large cotyledons, which remain below ground in *Quercus* species. Sap-feeding insects could also reduce survival without causing leaf damage (Shure 1973); however, sap-feeding insects were not observed on the experimental seedlings. *Quercus palustris* emergence was increased approximately 8% in the phytotoxicity experiment by the combined insecticide treatment. This beneficial effect of the insecticide does not appear to be sufficient to explain the entire increase in emergence in the field experiment for this species, which exceeded 20% in one treatment.

All species tested showed beneficial effects of insect removal in at least one year of the experiment. Species differed in their susceptibility to insect damage with *Acer rubrum* the most susceptible and *Frax-*

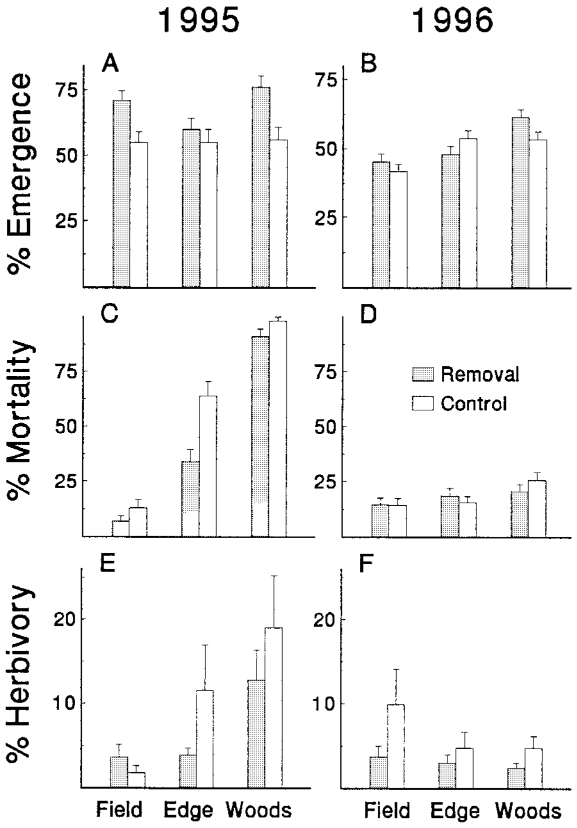

Figure 3. Effects of insect herbivory and spatial position on the emergence (A, B), mortality (C, D) and cotyledon herbivory (E, F) of *Fraxinus americana* in the field experiment for 1995 and 1996. Herbivory data is presented as average plot mean for percent cotyledon removal. Error bars represent one standard error.

inus americana the least affected. These differences in herbivore susceptibility may lead to changes in the species composition of the invading plant community (Davidson 1993; Hanley et al. 1996). Species subjected to higher levels of herbivory would be less likely to successfully invade an old field, either through direct mortality from herbivore damage (Hendrix 1988), or from reduced competitive abilities (Hulme 1996; Frost & Rydin 1997).

Edge effects on tree establishment

Emergence was greater in the woods plots for *Acer rubrum* and *Fraxinus americana* in 1996. This is probably a response to cooler, moister conditions of the forest floor providing better conditions for germination. Burton & Bazzaz (1991) found that the response of *F. americana* emergence to local vegetation changed from year to year with higher emergence under tree canopies in one year, and higher emergence

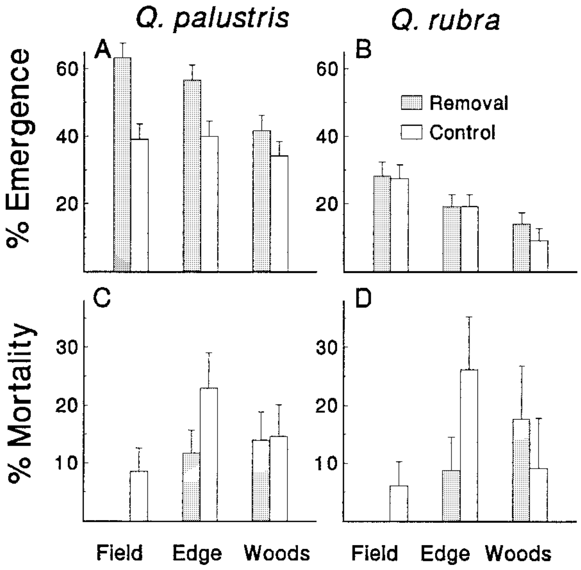

Figure 4. Effects of insect herbivory and spatial position on the emergence (A, B) and mortality (C, D) of *Quercus palustris* and *Quercus rubra* in the field experiment for 1996. Error bars represent one standard error.

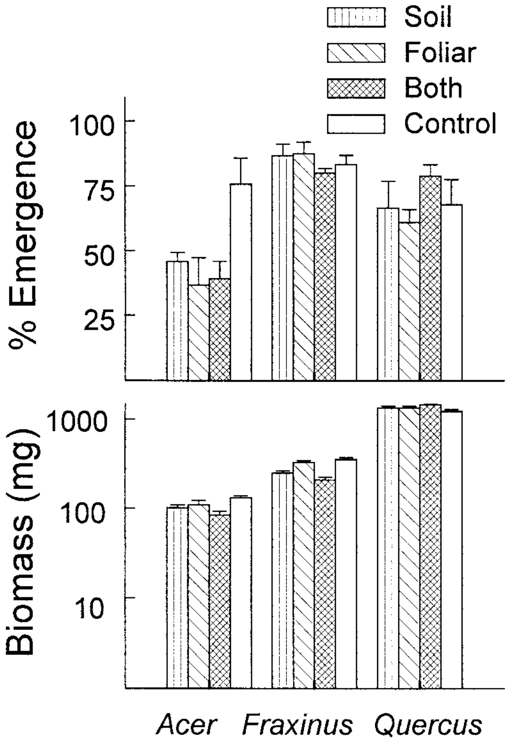

Figure 5. Effects of insecticide application on emergence (A) and growth (B) of *Acer rubrum*, *Fraxinus americana*, and *Quercus palustris* in the phytotoxicity experiment. Growth is plotted on a log scale to allow comparison between species. Error bars represent one standard error.

in herbaceous vegetation in another. This variation can be seen in this study with significant position effects in 1996 but not in 1995 for *F. americana* and a reversal of the edge response between the two years for *A. rubrum*. This variation probably results from changes in germination constraints caused by rainfall differences between the two years of the study (Burton & Bazzaz 1991). *Quercus* species, which would need less moisture for establishment because of their large seeds (Jurado & Westoby 1992), probably responded to higher soil temperatures in sites exposed to direct sunlight (Figures 4e and 4f). Similarly, Callaway (1992) found that *Quercus lobata* and *Q. douglassii* emergence was lower in the shade of shrub canopies.

Overall, tree seedling mortality increased from field to edge to woods. This suggests that light availability may be limiting to tree seedling establishment (Kobe et al. 1995). The tree species used in this experiment are all relatively shade-intolerant (USDA 1990) and would be expected to perform poorly in shade. Shade-tolerant species may have no response, or respond negatively to higher light levels near the edge and in the old field (Whitney & Runkle 1981; Chen et al. 1992).

The direct responses of tree seedlings to the forest edge have been largely ignored in ecological studies. The majority of studies focus on forest edges as a source of seeds, proposing that it is the spatial pattern of seed dispersal that determines the spatial pattern of tree establishment (Johnson 1988; Hughes & Fahey 1988; Hughes & Bechtel 1997). For seed dispersal to determine seedling establishment, the likelihood of seedling establishment must be constant across the edge (Johnson 1988). This study clearly shows that establishment rates are affected by the presence of edges. For this reason, future studies of tree establishment in fragmented successional systems must include the influence of edges.

Edge effects on insect herbivory

A relatively unknown impact of forest fragmentation is the effect of edges on plant-herbivore interactions (Didham et al. 1996). Herbivore activity, as measured by cotyledon removal, changed with position along the edge during the drought year. The intensity of the effects of insect removal on plant performance also changed with position relative to the forest edge, as shown by the significance of the site∗treatment interaction in several analyses. These biological edge effects may be caused by shifts in the insect community across the edge in response to changes in microclimate (Burger & Louda 1994; Didham et al. 1996; Jokimäki et al. 1998). Changes in herbivore density or species composition can result in changes in herbivore load, and consequently the amount of herbivory to which a seedling is subjected. These differences in herbivore impacts across the forest edge gradient show the potential for herbivorous insects to alter the spatial pattern of tree establishment (Louda 1989).

The spatial variation in the amount of herbivory and in the effects of herbivory on tree seedlings empahsizes the importance of spatial context in herbivory studies. Mammalian herbivory and seed predation have been found to vary between edge and non-edge habitats in *Carya* spp. (Sork 1983; Myster and McCarthy 1989; McCarthy 1994). Likewise, insect herbivores respond to small scale environmental variation, damaging plants in some locations while others are left undamaged (Burger & Louda 1994, 1995). In this study the effects of herbivory changed dramatically over a small spatial scale (20 m from field to woods plots). If the effects of herbivory on tree seedlings were studied in only one habitat, the conclusions reached would be quite different, ranging from no effect to strong negative effects on establishment.

Inter-annual variation in establishment

The difference in rainfall between the two years of this experiment allows the role of regional weather patterns in plant/herbivore interactions to be addressed. For the two species used in both years of the experiment, *Fraxinus americana* and *Acer rubrum*, insect removal had greater beneficial effects during the drought year. There are two mechanisms that could explain this pattern. (1) Insect densities were higher in the drought year. However, based on cotyledon herbivory data, herbivore activity was greater in the normal year, suggesting densities were not greater during the drought. Because of changes in trap design and exposure period, direct comparisons of pitfall data are inappropriate. (2) Seedlings were water-stressed during the drought and were less tolerant to herbivory. Stressed plants may have fewer resources, limiting recovery from herbivory and increasing the likelihood of mortality (Rosenthal & Kotanen 1994). Furthermore, any below-ground herbivory would directly interfere with the ability of the seedlings to attain water during a drought. This interaction between soil moisture and root herbivory has been shown in dipterocarp seedlings, which had higher mortality from root herbivory in drier sites (Itoh 1995).

The strong differences seen between years in the spatial pattern of cotyledon herbivory and seedling mortality have large implications for the establishment of tree seedlings across the edge. Particularly for *F. americana*, mortality was strongly site-dependent in 1995, closely following the spatial pattern of cotyledon herbivory. In contrast, mortality and cotyledon herbivory did not vary spatially and insect herbivory was unrelated to seedling mortality in 1996. This inter-annual variation in the factors that limit tree establishment not only leads to a change in the number of seedlings establishing in a site, but also to a change in the spatial pattern of those seedlings between years.

Conclusions

Edges represent complex environmental gradients along which both physiology and herbivory function to limit the invasion and establishment of trees into adjacent old fields (Louda 1989). The magnitude of this limitation depends on the species of tree and the spatial position of the seedling in the landscape. The limitation is also correlated with yearly fluctuations in rainfall at this site. As the time window of invasion for a tree species may be short (Rankin & Pickett 1989), the specific conditions of a site during that temporal window will determine the extent of insect effects on establishment. The effects of forest edges on the interactions between insect herbivores and their host plants is a relatively unknown impact of forest fragmentation, but this study suggests that this interaction may be biologically significant (Didham et al. 1996). Furthermore, studies on the importance of insect herbivores in limiting woody plant establishment should be focused at early demographic stages. This will allow more accurate generalizations to be made about insect herbivory as a limiting factor in tree establishment.

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