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Effects Of Forest Edges On Population Dynamics In A Successional System

Kimberly Anne Lang

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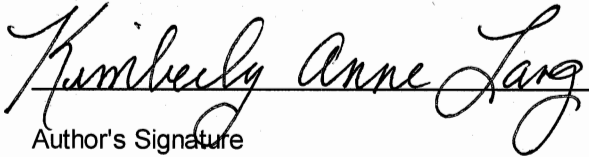
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EFFECTS OF FOREST EDGES ON POPULATION DYNAMICS
IN A SUCCESSIONAL SYSTEM

BY

KIMBERLY ANNE LANG

THESIS

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF

MASTER OF SCIENCE – BIOLOGICAL SCIENCES


IN THE GRADUATE SCHOOL, EASTERN ILLINOIS UNIVERSITY
CHARLESTON, ILLINOIS

2010

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ABSTRACT

Abandoned agricultural land is often bound by remnant woodlands which may locally influence successional dynamics. The primary objective of this study was to examine the effect of an old-growth forest edge on plant population dynamics within a successional system. Data from the Buell-Small Succession Study (BSS) in New Jersey were used to analyze population dynamics in relation to the forest edge during the first 50 years of succession following agriculture. It was hypothesized that edge responses would be driven by either differential colonization (dispersal and establishment) or differential performance (increase within plots).

By looking at individual species' edge responses, I worked toward understanding the role the forest edge plays in regulating successional patterns. Individual species edge patterns were determined for 75 species by looking at the year of peak cover (highest percent cover over the first 50 years) and determining the edge association by performing an analysis of covariance to quantify the field and distance from the forest edge effects for each species. The role of mechanistic processes, differential colonization and differential performance, in generating species' edge responses were analyzed by performing a logistic regression or analysis of covariance, respectively.

Large amounts of variation were found among species in both the direction and magnitude of edge responses. Of the species analyzed, approximately 27% were more abundant closer to the forest edge, 39% were more abundant farther from the edge, and 34% had no discernable edge response. Edge responses were not directly associated with plant traits. Mechanistic analyses of species edge responses found that some were driven by differential dispersal, some by differential performance, and some by both

mechanisms. Though both were important, differential colonization (53% of species) influenced spatial patterns nearly twice as often as differential performance (29% of species). Despite its prevalence, differential colonization was not associated with any of the plant traits. In contrast, differential performance was associated with clonality, dispersal mode, and peak year in succession.

There was no overriding pattern that connected edge response with species traits that would allow prediction of an association with distance from the edge for groups of species. However, species varied individualistically in response to edges and no one mechanism (differential colonization or performance). Overall, the presence of habitat boundaries had a large but unpredictable effect on population dynamics and spatial patterns within the successional system. Understanding succession of plant communities is important for management of this ecosystem altered by cultivation and fragmentation.

DEDICATION

I would like to dedicate my thesis manuscript to my boyfriend, Daniel Pelphrey, for all his encouragement, support, love, advice, and motivation during my two years at Eastern Illinois University. I could not have done this without you.

I would also like to dedicate my thesis manuscript to my parents for introducing me to and keeping me connected to nature through our annual camping trips. And to my sister for exploring those natural areas with me.

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I would like to thank my advisor, Scott Meiners, for mentoring me in all aspects of my Master's degree. Because of him I have excelled in research, academics, and my duties as a teaching assistant.

I would like to thank my committee members, Barbara Carlsward and James Novak, for their insightful contributions to my thesis.

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I could not have accomplished this without the undying support and motivation from my parents, Marianne and Gary, my sister, Kaitlin, and my boyfriend, Dan. Thank you so much!

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TABLE OF CONTENTS

ABSTRACT	i
DEDICATION	iii
ACKNOWLEDGEMENTS	iv
LIST OF TABLES	vi
LIST OF FIGURES	vii
INTRODUCTION	1
METHODS	8
RESULTS	14
DISCUSSION	25
CONCLUSIONS	33
LITERATURE CITED	35

LIST OF TABLES

TABLE 1. Species analyzed for their forest edge response including their nativity, edge response category, year of peak cover, and number of fields included in the analysis. The distance β is the regression coefficient of distance from the forest edge on species abundance during the peak year of cover. Distance β s were used to clarify species edge response.	17
TABLE 2. Field and distance from the forest edge effects for mechanistic processes of colonization and performance of all species with positive or negative edge responses.	19

LIST OF FIGURES

- FIGURE 1.** Layout of the 10 fields of the BSS. 13
- FIGURE 2.** Variation in species characteristics among edge response groups. 21
- FIGURE 3.** Proportion of negative and positive edge associated species that were significantly driven by differential colonization and performance. 22
- FIGURE 4.** Subset of species of varying life forms, vegetative reproduction status and dispersal mode that were driven by differential colonization and performance. 23
- FIGURE 5.** Probability of species of varying peak year of cover, seed mass and specific leaf area that were driven by differential colonization and performance. 24

INTRODUCTION

Forest clearcutting during the early 19th century has left fragmented remnants of forests throughout the northeastern United States (Abrams et al. 1997, Cadenasso et al. 1997, Goldblum and Beatty 1999, Cadenasso and Pickett 2000, Foster et al. 2004). Increased prevalence of forest edges is directly associated with this forest fragmentation. Boundaries of fragmented ecosystems are structurally different from adjacent forest and nonforest habitats. This difference in structure, as well as the orientation of the edge, alters the amount of light, moisture, and wind across the edge. The unique microclimate present at the edge supports a different suite of species than the surrounding habitat, commonly referred to as an “edge effect” (Leopold 1933, Wales 1972, Fraver 1994, Chen et al. 1995, Cadenasso et al. 1997, Tulloss 2006). The alteration of habitat by edges may contribute to loss of biodiversity and forest degradation in fragmented landscapes (Gascon et al. 2000, Harper et al. 2005).

Typically, edge effects refer to the influence of the nonforest habitat on the species composition and ecological processes of the adjacent forest. However, Cadenasso et al. (1997) state that most research on edge effects has been constrained by this conceptual approach and therefore has overlooked important functional aspects of edges. One such aspect is that edge effects can also alter the nonforest patches by extending forest interior conditions into the nonforested environment (Williams-Linera 1990, Brothers and Spingarn 1992, Carmago and Kapos 1995). Adjacent patches exchange energy, materials, information or organisms across their boundary (Murcia 1995, Cadenasso and Pickett 2000, Harper et al. 2005, Tulloss 2006). Both abiotic and biotic factors are altered across boundaries by these four types of flows, which link

habitat patches and may affect community dynamics within both (Cadenasso and Pickett 2000, Cadenasso et al. 2003, Harper et al. 2005).

Edges are important drivers of ecological patterns and processes within remnant habitats, but they may also be important in the dynamics of matrix habitat. In the northeastern United States, abandoned agricultural land is often bounded by remnant forests or hedgerows. Over time, the vegetation of abandoned agricultural land would change composition through successional processes (Bard 1952, Bazzaz 1968, Lawson et al. 1999). Edges influence vegetation dynamics by serving as a source of colonists and by generating environmental gradients which may alter the successional trajectory of the abandoned field. Abiotic parameters, such as nutrients or water availability, influence the course of succession (Parrish and Bazzaz 1982, Tilman 1985, Carson and Pickett 1990, Kupfer and Runkle 2003) by determining the species that dominate under those conditions. Together environmental effects of proximity to the forest (Williams-Linera 1990) along with species dispersal patterns (Myster and Pickett 1992, Kupfer and Runkle 2003) can affect the composition of the regenerating successional system. Initially forest edges are characterized by an abrupt change in structure, composition, and abiotic conditions which allows the successional system to be open to new colonizers (Cadenasso and Pickett 2000). However, over time the edge becomes less noticeable as the matrix vegetation regenerates into forest, reducing the steepness of the environmental gradient (Fraver 1994).

Succession is a spatio-temporal process controlled by the continuous colonization and extinction of a site by plant populations (Bazzaz 1979) and in general terms is a type of vegetation dynamics (Pickett and Cadenasso 2005). Dispersal patterns and local

environmental gradients are two of the main factors that contribute to species distribution and diversity (Cook et al. 2005, Flinn 2007) as well as change in species composition over time (Pickett and Cadenasso 2005). Dispersal can be limited by the distance a patch is from the seed source. Many studies have found that as distance from the seed source increases, seedling density decreases (Buell et al. 1971, McDonnell 1986, McClanahan and Wolfe 1987, McClanahan and Wolfe 1993, Ribbens et al. 1994). This pattern is not ubiquitous because small or bird dispersed seeds may colonize open areas quickly with little seed limitation (Garcia et al. 2010). Later successional species, in contrast, tend to have larger seeds, which have more limited dispersal, which increases the time they take to colonize and generates strong spatial patterns (Cook et al. 2005). A species' ability to disperse to an area may be independent from its survival potential as local variation in the environment regulates species composition (Matlack 1994a). The complex biotic and abiotic gradient of an ecotone influences vegetation patterns and generates edge effects. While it is important to document the pattern in vegetation generated by edges, it is also necessary to understand the community dynamics that generate those patterns.

Drivers of Community Dynamics

Vegetation composition is determined by the individual capacities of species to disperse, grow, survive, and reproduce under current environmental conditions. As environmental conditions change, species composition will also change, resulting in community dynamics. Community dynamics are regulated by three fundamental processes: site availability, differential colonization, and differential performance (Pickett and McDonnell 1989, Pickett and Cadenasso 2005).

Site availability begins successional processes. Disturbance events disrupt the current vegetation and alter resource availability yielding a site that is open to the colonization of new species. The intensity of disturbance events varies greatly in how much vegetation is removed and how much the substrate is altered. The site characteristics following disturbance greatly impacts how new plants will establish and grow within the area (Myster and Pickett 1990, LePage et al. 2000).

The second process, differential colonization, is highly dependent upon individual species' life history traits. Plant species that initially dominate the new community either were able to persist through the disturbance or dispersed to and established in the area quickly after the disturbance. Plants can survive disturbance as seeds, vegetative fragments, or even adult plants (Parrish and Bazzaz 1982, Bazzaz 1996). Plants species disperse from seed sources at varying distances to the disturbed site. The further the seed source, the more likely dispersal will be limited by distance (McDonnell 1986, McClanahan and Wolfe 1987, McClanahan and Wolfe 1993, Ribbens et al. 1994). Finally, the characteristics of the site following disturbance determine the differential establishment and survival of species once they are dispersed.

The third process, differential performance, represents the ecological sorting of species once established at the site (Pickett and Cadenasso 2005). Performance includes acquisition of resources, growth, and reproduction. How well a species does at a site is dependent on that species' suite of life history traits, physiological attributes, and interactions with other species. For example, light levels are high early during succession compared to the low light levels of closed canopy systems characteristic of later successional communities (Bazzaz 1996, Pickett and Cadenasso 2005). Because of the

shift in light levels during succession, species that are typically dominant early in succession utilize high light levels for maximum growth rates and species that are dominant later in succession perform better under lower light conditions (Tilman 1985). Nutrient variability within the community can be another driver of differential species performance (Parrish and Bazzaz 1982, Carson and Pickett 1990). Substrates of newly disturbed, successional communities may lack large nutrient pools which makes species that can fix nitrogen, successful colonizers within early successional communities. Naturally, species that are dominant later in succession take advantage of the increased nitrogen level available as a result of nitrogen fixation by early succession species (Tilman 1985, Bazzaz 1996, Pickett and Cadenasso 2005). By understanding the relative contributions of these mechanisms in generating edge effects, the underlying causation of the spatio-temporal patterns created by succession can be determined.

Linking Edges with Community Dynamics

The goal of this thesis is to use long term, permanent plot data to document the influence of an old-growth forest on population dynamics within successional fields. The different successional fields all share the same soil type (Penn silty clay loam; Bard 1952) and are within close proximity to one another. The close proximity of the study sites minimizes abiotic variation among sites. The fields vary in their agricultural history, which translate to variation in community structure and function among fields (Buell et al. 1971, Connell 1980, Pickett 1982, Keever 1983, Myster and Pickett 1990). Incorporating field identification into my analyses accounted for difference in pre-abandonment agriculture, minimizing the effects of differential site availability.

Instead, I focused on biotic responses to the forest edge as measured by the mechanistic processes of differential colonization and differential performance. Differential colonization of species occurs when propagules survive the disturbance and re-establish or new individuals disperse into the site and successfully establish. Differential colonization integrates local patterns of dispersal and the biotic and abiotic constraints on establishment. Therefore it combines differential dispersal with the early establishment and success of species from the general model of community dynamics. Differential performance spatially sorts species along the edge through acquisition of resources, growth, and reproduction once established in the site. In both processes, environmental variation and biotic interactions within the successional field determines which species become dominant, however they affect different phases of the life cycle.

Often successional systems are under restoration plans which manipulate vegetation dynamics in order to achieve a desired successional stage (Clements 1935, Pickett et al. 2001, Cramer et al. 2008). Given this relationship between vegetation dynamics and restoration, succession research contributes to the field of restoration ecology by revealing the patterns of change in natural systems and the mechanisms that control this change. Knowledge of species assembly helps to evaluate whether habitat modification is beneficial in achieving restoration goals. Because of the prevalence of fragmentation, realistic estimates of edge effects on succession are vital to the preservation and restoration of fragmented forest ecosystems (Matlack 1994b, Cramer et al. 2008).

In order to understand the influence of forest edges on regeneration, the effects of the forest on the nonforest environment must be studied. The objectives of this study

were (1) to determine the edge response of individual species within a successional plant community, (2) to understand the plant life history traits that determine individual species' edge response, (3) to identify the mechanisms driving spatial patterns at the community scale, and (4) to relate species' life history traits to the mechanisms that generate edge responses.

METHODS

Study Site & Data Collection

This research was conducted at the Hutcheson Memorial Forest Center (HMFC) located in East Millstone, New Jersey, USA (40°30'N, 74°34'W). Since 1958, HMFC has been the site of the Buell-Small Succession Study (BSS, www.ecostudies.org/bss), a long-term study of successional vegetation dynamics within the Piedmont region of New Jersey (Pickett 1982). The BSS consists of 10 agricultural fields that were abandoned as pairs during alternate years from 1958 to 1966. Before abandonment, all fields had been under continuous agricultural production since the mid 1700s and therefore lacked trees when succession began (Buell et al. 1971, Myster and Pickett 1992). However, Myster and Pickett (1990) found large compositional variation among the fields based on year of abandonment in conjunction with pre-abandonment treatment (season of abandonment, final crop, and final soil treatment). Most of the fields abut the old-growth forest of HMFC which consists of a *Quercus-Carya* canopy and historically a *Cornus florida* subcanopy (Bard 1952, Monk 1961).

Within each of the fields, 48 permanent plots are arranged in rows horizontal to the old-growth forest edge, with the spacing between rows differing with the size of the field. At each sampling, the percentage cover of all species present was visually estimated in each permanently marked, 0.5 x 2.0 m plot. Data collection occurred every year after the release from agriculture, until 1979, when sampling switched to alternate years. These data represent the longest continuous data set on successional change known. Nomenclature follows Gleason and Cronquist (1991).

Total Species Pool

To assess the effects of the old-growth forest edge on plant population dynamics in this successional system, the six fields with a single boarder with the old-growth forest edge were selected (Figure 1). Individual species' responses to the edge were determined for 75 of the most abundant (cover and frequency) species within the BSS. I examined the spatial patterns of these species when each was at its peak cover. For a field to be included in the analyses, the species had to have at least an average cover of 2% in that field to account for variability among fields and remove uncolonized fields (Yurkonis et al. 2005). Individual species' edge responses were determined using an ANCOVA, which quantified the influence of field (categorical) and distance from the forest edge on plant cover at population peak. Variability among fields was removed by using field as a categorical variable. The beta values for distance from the edge in the ANCOVA were used to divide species into three edge response groups: negative, neutral, and positive. Species with negative edge responses had a distance beta of -0.10 or less and species with a positive edge response had a distance beta of 0.10 or greater. Those species with a distance beta between 0.10 and -0.10 were categorized as neutral edge responders, indicating they had no response to the edge. The cover of negatively associated species decreased with distance from the forest edge, into the open field. Likewise, positively associated species were those whose cover increased with distance from the forest edge. For simplicity I will refer to these as negative and positive edge responses, respectively.

To understand the characteristics that determine species' edge responses, plant traits were compared among the three edge response groups. Differences among groups were assessed with a chi-square test for the categorical variables (life form, clonality, and

dispersal mode) and an ANOVA for the continuous plant trait variables (peak year in succession, seed mass, and specific leaf area). These six plant traits were selected because they each provide insight into the factors controlling plant growth and success.

The categorical plant traits of life form, clonality, and dispersal mode are common life history traits analyzed for successional systems. Life form was separated into three broad categories short-lived (herbaceous annuals and biennials), perennial (herbaceous), and woody. Life form can indicate under what conditions a species may dominate and captures fundamental differences among species. For example, annuals and biennials are short-lived, weedy plants that typically thrive in an open, unshaded area further from the forest edge. Clonal species often produce many genetically identical individuals which can allow expansion within an area where an individual is already established.

Vegetative reproduction is an aggressive, competitive strategy that plants employ to secure acquisition of local resource pools (Grime 1979, Bazzaz 1996). Dispersal mode (abiotic vs. biotic) is a classic plant trait in studying how spatial patterns develop over time. Typically, biotic dispersal is associated with the forest edge or other structural features, such as perches. The shelter provided by these structures allows dispersers to move across habitats (McDonnell 1986, Myster and Pickett 1992, Garcia et al. 2010).

The continuous traits of peak year in succession, seed mass, and specific leaf area also capture important aspects of species biology. Peak year in succession indicates whether the species is an early, mid, or late successional species. Early successional species would be a more weedy plant that may have greater performance in open areas further from the forest edge. On the other hand, late successional species come in when other plant species are already established, and therefore may be able to survive better in

shaded areas closer to the forest edge. Seed mass is closely related to dispersal mechanism. Larger seeds disperse more poorly (McEuen and Curran 2004, Cook et al. 2005) but can also establish in poor conditions (Westoby 1998). Specific leaf area is a measure of leaf thickness, calculated by dividing the area of a leaf by the mass of that leaf. Species with high specific leaf area typically have high growth rates and therefore perform best in resource rich environments (Wilson et al. 1999).

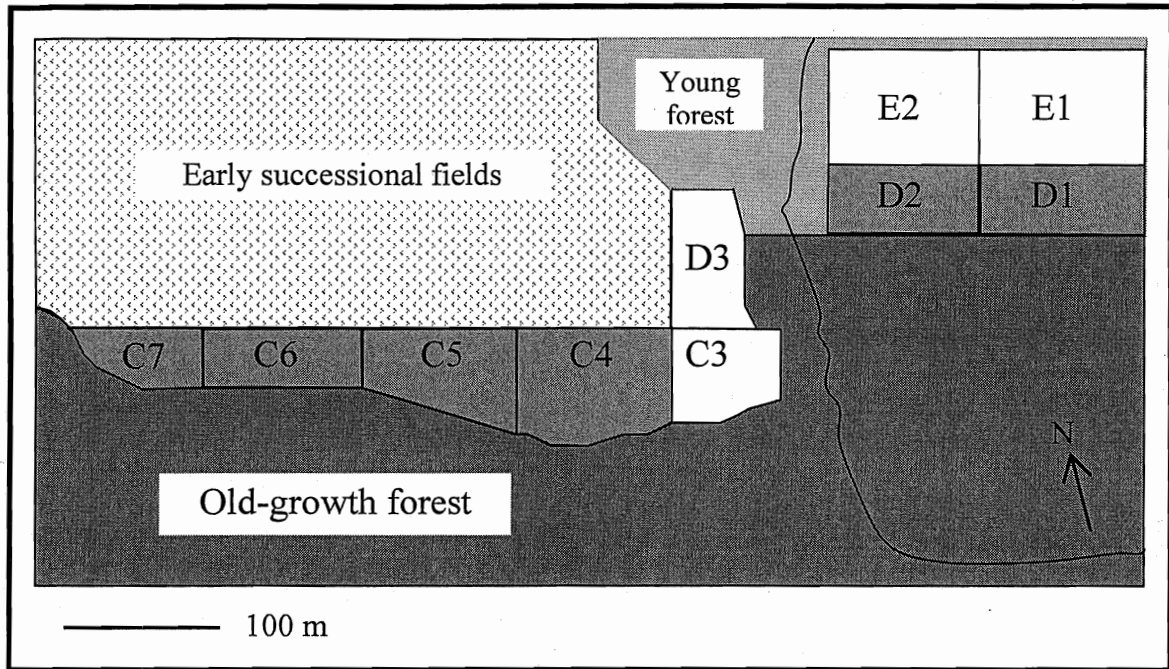
Dynamics Behind the Edge Response of Species

A second set of analyses was run to determine the population level dynamics that generated each species' response to distance from the forest edge. For this reason, only species with a negative or positive edge response were used. The two mechanisms evaluated that determine population dynamics were differential colonization and performance. By selecting only colonized fields, I have minimized the influence of different sites and their history. Differential colonization determines where in a landscape a species will occur (spatial location) and is controlled by the dispersal traits and establishment requirements of the species (Pickett and Cadenasso 2005). Colonization combines both differential species availability and the interaction of species with the local environment. Differential performance refers to the ability of a species to grow, persist, and eventually reproduce in those spatial locations that are colonized. Performance represents the ecological sorting of species through how the species perform once established at the site.

The relative importance of differential colonization and performance in determining the spatial pattern of each species with an edge response were assessed with

a logistic regression and an ANCOVA, respectively. In both analyses, field identity was included as a categorical variable to account for differences among fields and distance from the edge was included as a continuous variable. To relate species characteristics to the importance of differential colonization and performance in generating edge responses, species traits were again related to population dynamics. A logistic regression was performed for the continuous variables (peak year in succession, seed mass, and specific leaf area) while a chi-square test was performed for the categorical variables (life form, clonality, and dispersal mode).

Figure 1. Layout of the 10 fields of the BSS. Successional fields C4, C5, C6, C7, D1, and D2 were included in the analysis. Fields C3 and D3 have edges adjacent to the old-growth forest, but those fields either had multiple edges adjacent to the old-growth forest (C3) or the edge adjacent to the old-growth forest was not entire (D3).



RESULTS

Total Species Pool

Seventy-five species met the criteria of having one or more fields where their average cover was at least 2% during their peak year of succession. The total species pool contained a diversity of life forms and peak year in succession (Table 1, Figure 2). Sixty-four percent of these species were native. Individual species varied greatly in the direction and magnitude of edge responses (Table 1). Based on the distance beta cutoff of 0.10, 27% of the species were negatively associated with distance from the forest edge (decreased with distance into field), 34% of species had no response to the edge (neutral), and 39% were positively associated with distance from the forest edge (increased with distance into the open field).

The plant traits examined revealed no difference among edge groups for all traits (Figure 2, life form: $X^2 = 5.8973$, d.f. = 4, $p = 0.2069$; presence of clonal growth: $X^2 = 1.5633$, d.f. = 2, $p = 0.4577$; dispersal mode: $X^2 = 0.8200$, d.f. = 2, $p = 0.6637$; year of peak cover: $F_{2,74} = 1.53$, $p = 0.2239$; seed mass: $F_{2,74} = 0.72$, $p = 0.4919$; specific leaf area: $F_{2,74} = 1.16$, $p = 0.3197$). Perennials were the most common life form in all three edge response groups (negative: 45%, neutral: 46%, positive: 52%). Despite the lack of a significant influence of seed mass on the edge responses of species, the average seed mass varied greatly among and within the three edge groups (negative: 135.4 mg, neutral: 384.4 mg, positive: 8.4 mg). A nonparametric analysis was also performed with the same result as the parametric tests (Kruskal-Wallis $X^2 = 3.4997$, d.f. = 2, $p = 0.1738$) as seed mass distribution could not be normalized.

Dynamics Behind Edge Response of Species

When looking at the role of mechanistic processes in edge responses, the non-edge-responders (neutral species) were dropped from the analysis because distance from the edge did not generate spatial patterning in those species. This subset of the total species pool consisted of 20 negatively and 29 positively associated species. Seventy-two percent of species showed field effects for colonization, and 53% of species showed field effects for performance. For both negative and positive edge responders, colonization influenced spatial patterns for half the species, nearly twice as often as performance (Table 2, Figure 3). Fifty percent of negative species and 55% of positive species' population dynamics were influenced by colonization. In contrast, 30% of negative species and 28% of positive species were influenced by performance. Thirty percent of negative species were influenced by both colonization and performance, and 21% of positive species were influenced by both mechanisms. Species that had both significant differential colonization and performance occurred more often than would be expected, indicating that colonization and performance were not independent ($X^2 = 9.4407$, d.f. = 1, $p = 0.0021$).

To understand species traits that might determine the mechanism of edge response, the traits of the negative and positive edge responders were related to differential colonization and performance. Life form was not related to either differential colonization ($X^2 = 2.3139$, d.f. = 2, $p = 0.3144$) or performance ($X^2 = 6.6967$, d.f. = 2, $p = 0.0529$). However, those species influenced by differential performance showed an interesting trend. Woody species had a lower proportion of performance impacts, though sample size was small (Figure 4). Clonality was not associated with significant

colonization effects ($X^2 = 0.4949$, d.f. = 1, $p = 0.4817$), but it was for performance ($X^2 = 5.5764$, d.f. = 1, $p = 0.0182$). The spatial patterns of clonal species were less likely to be driven by differential performance (Figure 4). Dispersal mode had similar results to clonality. Colonization was unrelated to dispersal ($X^2 = 0.2940$, d.f. = 1, $p = 0.5877$), while performance varied significantly for dispersal ($X^2 = 4.4100$, d.f. = 1, $p = 0.0357$) with biotically dispersed species less likely to be driven by performance (Figure 4).

The analyses of the three continuous plant trait variables did not show any significant association with differential colonization (Figure 5, peak year - Wald $X^2 = 0.0034$, d.f. = 1, $p = 0.9536$; seed mass - Wald $X^2 = 0.1258$, d.f. = 1, $p = 0.7228$; specific leaf area - Wald $X^2 = 0.3896$, d.f. = 1, $p = 0.5325$) or performance except for the relation of peak year in succession with differential performance (Figure 5, peak year - Wald $X^2 = 4.2892$, d.f. = 1, $p = 0.0384$; seed mass - Wald $X^2 = 0.9629$, d.f. = 1, $p = 0.3264$; specific leaf area - Wald $X^2 = 0.7875$, d.f. = 1, $p = 0.3749$). As the year in which a species peaked in succession increased, the proportion of species impacted by differential performance decreased. Seed mass showed a similar trend for differential performance but it was not significant.

Table 1. Species analyzed for their forest edge response including their nativity, edge response category, year of peak cover, and number of fields included in the analysis. The distance β is the regression coefficient of distance from the forest edge on species abundance during the peak year of cover. Distance β was used to clarify species edge response. Distance β values above 0.10 and below -0.10 fell into the edge response category + (positive) and - (negative) respectively, and those in between were denoted 0 (neutral) edge responses. The fields had to have an average of at least 2% cover of the species in order to be included in the analyses.

Species	Edge Response (+, 0, -)	Year of Peak Cover	Number of fields	Distance β
<i>Acalypha rhomboidea</i> (N)	0	1	2	-0.088
<i>Acer negundo</i> (N)	+	20	1	0.357
<i>Acer rubrum</i> (N)	-	35	6	-0.338
<i>Achillea millefolium</i> (N)	0	12	1	0.034
<i>Agrostis hyemalis</i> (N)	+	5	1	0.120
<i>Allaria petiolata</i> (E)	0	37	5	0.032
<i>Ambrosia artemisiifolia</i> (N)	+	1	5	0.319
<i>Apocynum cannabinum</i> (N)	+	15	1	0.146
<i>Aster ericoides</i> (N)	+	6	2	0.100
<i>Aster lanceolatus</i> (N)	0	6	5	-0.096
<i>Aster lateriflorus</i> (N)	+	8	1	0.185
<i>Aster pilosus</i> (N)	+	11	5	0.495
<i>Barbarea vulgaris</i> (E)	0	2	5	0.036
<i>Bromus racemosus</i> (E)	-	10	1	-0.797
<i>Calystegia sepium</i> (N)	+	6	4	0.102
<i>Carex</i> spp. (N)	+	38	2	0.133
<i>Centaurea dubia</i> (N)	+	26	2	0.169
<i>Cerastium vulgatum</i> (E)	0	10	1	0.019
<i>Chenopodium album</i> (E)	+	1	3	0.298
<i>Chrysanthemum leucanthemum</i> (E)	0	8	2	0.018
<i>Circaea lutetiana</i> (N)	-	33	1	-0.173
<i>Cornus florida</i> (N)	+	35	6	0.226
<i>Cornus racemosa</i> (N)	+	32	3	0.136
<i>Dactylis glomerata</i> (E)	-	1	2	-0.381
<i>Daucus carota</i> (E)	0	4	6	0.006
<i>Digitaria sanguinalis</i> (E)	-	1	2	-0.120
<i>Elytrigia repens</i> (E)	-	6	2	-0.219
<i>Erigeron annuus</i> (N)	0	2	5	0.020
<i>Eupatorium rugosum</i> (E)	-	42	5	-0.132
<i>Euthamia graminifolia</i> (N)	0	14	6	-0.093
<i>Fragaria virginiana</i> (N)	+	12	6	0.261
<i>Fraxinus americana</i> (N)	-	37	6	-0.248
<i>Hedeoma pulegioides</i> (N)	-	4	2	-0.112
<i>Hieracium caespitosum</i> (E)	+	10	6	0.461

<i>Hieracium pilloselloides</i> (N)	0	12	2	0.061
<i>Juglans nigra</i> (N)	0	38	3	-0.039
<i>Juncus</i> spp. (N)	+	3	1	0.275
<i>Juniperus virginiana</i> (N)	+	39	5	0.618
<i>Lepidium campestre</i> (N)	0	4	1	0.010
<i>Lolium perenne</i> (E)	+	1	1	0.308
<i>Lonicera japonica</i> (E)	+	18	6	0.300
<i>Oenothera biennis</i> (N)	0	7	1	-0.097
<i>Oxalis stricta</i> (N)	0	3	5	0.010
<i>Parthenocissus quinquefolia</i> (N)	—	20	4	-0.762
<i>Phleum pratense</i> (E)	0	8	2	0.002
<i>Plantago lanceolata</i> (E)	+	3	2	0.826
<i>Plantago rugelii</i> (N)	—	3	4	-0.335
<i>Poa compressa</i> (E)	0	17	3	0.028
<i>Poa pratensis</i> (E)	+	12	3	0.266
<i>Polygonum pensylvanicum</i> (N)	0	1	2	-0.015
<i>Potentilla simplex</i> (N)	+	9	3	0.356
<i>Prunella vulgaris</i> (N)	—	4	3	-0.566
<i>Prunus serotina</i> (N)	0	35	3	0.021
<i>Quercus rubra</i> (N)	—	42	1	-0.659
<i>Raphanus raphanistrum</i> (E)	—	1	6	-0.104
<i>Rhus glabra</i> (N)	+	20	1	0.726
<i>Rosa multiflora</i> (E)	0	28	6	-0.096
<i>Rubus allegheniensis</i> (N)	—	16	4	-0.154
<i>Rubus flagellaris</i> (N)	+	18	1	0.155
<i>Rumex acetosella</i> (E)	0	4	3	-0.050
<i>Rumex crispus</i> (E)	0	3	1	-0.079
<i>Setaria faberii</i> (E)	0	1	1	0.099
<i>Silene latifolia</i> (E)	+	3	2	0.129
<i>Solanum carolinense</i> (N)	0	10	4	0.002
<i>Solidago canadensis</i> (N)	+	19	6	0.101
<i>Solidago gigantea</i> (N)	—	16	4	-0.119
<i>Solidago juncea</i> (N)	+	17	5	0.274
<i>Solidago nemoralis</i> (N)	0	10	2	-0.013
<i>Solidago rugosa</i> (N)	—	16	5	-0.179
<i>Toxicodendron radicans</i> (N)	—	22	6	-0.222
<i>Trifolium hybridum</i> (E)	—	4	2	-0.160
<i>Trifolium pratense</i> (E)	+	7	1	2.003
<i>Verbascum blattaria</i> (E)	0	4	1	0.071
<i>Viburnum prunifolium</i> (N)	—	28	1	-0.734
<i>Vitis</i> spp. (N)	+	37	5	0.128

Table 2. Field and distance from the forest edge effects for mechanistic processes of colonization and performance of all species with positive or negative edge responses. Significance indicated by symbols * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, and **** $p < 0.0001$. No values for fields are reported in species which only occur in sufficient abundance in one field.

Species with Negative Edge Response	Colonization		Performance	
	Field	Distance	Field	Distance
<i>Acer rubrum</i>	60.017****	0.003	4.980***	0.653
<i>Bromus racemosus</i>	-	3.475	-	0.1
<i>Circaea lutetiana</i>	-	9.482**	-	0.486
<i>Dactylis glomerata</i>	0.008	0.492	60.736****	1.308
<i>Digitaria sanguinalis</i>	7.688**	7.081**	5.956*	7.000**
<i>Elytrigia repens</i>	4.330*	0.072	0.052	0.667
<i>Eupatorium rugosum</i>	23.935****	7.115**	10.519****	0.578
<i>Fraxinus americana</i>	10.618	4.243*	1.909	4.244*
<i>Hedeoma pulegiodes</i>	0.473	2.376	1.324	0.002
<i>Parthenocissus quinquefolia</i>	14.331**	38.976****	11.249****	7.270**
<i>Plantago rugelii</i>	4.798	4.980*	64.145****	28.238****
<i>Prunella vulgaris</i>	11.395**	28.139****	4.380*	10.475**
<i>Quercus rubra</i>	-	2.393	-	2.672
<i>Raphanus raphanistrum</i>	21.050***	6.705**	19.760****	4.682*
<i>Rubus allegheniensis</i>	19.730***	0.149	0.278	2.414
<i>Solidago gigantea</i>	5.989	2.349	0.986	0.994
<i>Solidago rugosa</i>	10.451*	2.542	1.724	0.208
<i>Toxicodendron radicans</i>	9.738	5.376*	8.292****	3.214
<i>Trifolium hybridum</i>	15.846****	1.986	7.722**	0.777
<i>Viburnum prunifolium</i>	-	4.083*	-	0.075
Species with Positive Edge Response				
	Field	Distance	Field	Distance
<i>Acer negundo</i>	-	3.005	-	0.171
<i>Agrostis hyemalis</i>	-	1.585	-	0.333
<i>Ambrosia artemisiifolia</i>	4.421	9.419**	73.41****	8.740**
<i>Apocynum cannabinum</i>	-	0.283	-	9.627**
<i>Aster ericoides</i>	24.597****	1.424	1.202	1.264
<i>Aster laterifolius</i>	-	9.284**	-	1.022
<i>Aster pilosus</i>	20.054***	13.498***	1.656	14.939***
<i>Calystegia sepium</i>	16.897***	2.091	13.279****	0.414

<i>Carex</i> spp.	8.161**	11.286***	0.036	0.195
<i>Centaurea dubia</i>	1.909	3.3	2.9	0.013
<i>Chenopodium album</i>	0.004	2.155	4.839**	14.526***
<i>Cornus florida</i>	16.228**	3.493	2.16	0.085
<i>Cornus racemosa</i>	3.83	3.866*	0.33	0.084
<i>Fragaria virginiana</i>	41.822****	1.199	4.280***	2.586
<i>Hieracium caespitosum</i>	35.768****	7.867**	9.504****	4.459*
<i>Juncus</i> spp.	-	0.025	-	1.451
<i>Juniperus virginiana</i>	13.761**	19.230****	5.974***	2.213
<i>Lolium perenne</i>	-	4.476*	-	0.006
<i>Lonicera japonica</i>	16.969**	9.565**	8.835****	3.016
<i>Plantago lanceolata</i>	3.866*	13.433***	0.068	8.520**
<i>Poa pratensis</i>	39.656****	11.049***	11.371****	0.086
<i>Potentilla simplex</i>	16.559***	0.351	0.75	3.637
<i>Rhus glabra</i>	-	4.309*	-	0.003
<i>Rubus flagellaris</i>	-	5.346*	-	0.082
<i>Silene latifolia</i>	9.964**	10.383**	3.967	0.208
<i>Solidago canadensis</i>	16.881**	3.368	3.117*	0.012
<i>Solidago juncea</i>	18.673***	16.639****	1.179	4.277*
<i>Trifolium pratense</i>	-	5.782*	-	14.903***
<i>Vitis</i> spp.	13.464**	0.798	1.701	0.901

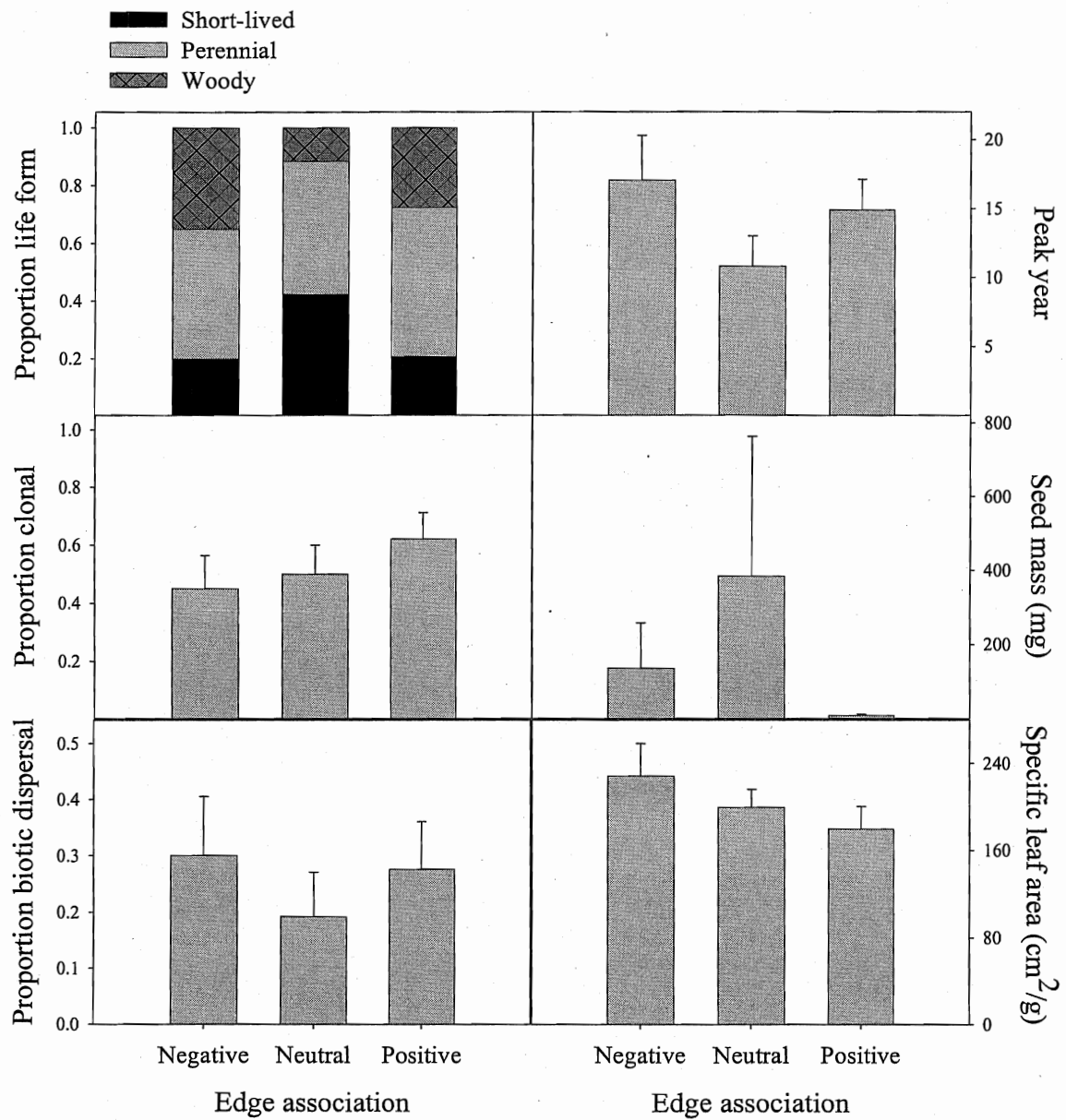


Figure 2. Variation in species characteristics among edge response groups. Variables in the left column are proportions of species with a characteristic in each edge response group. Variables in the right column are means of the quantitative measure within each group. Peak year is the year when each species reached its maximum abundance.

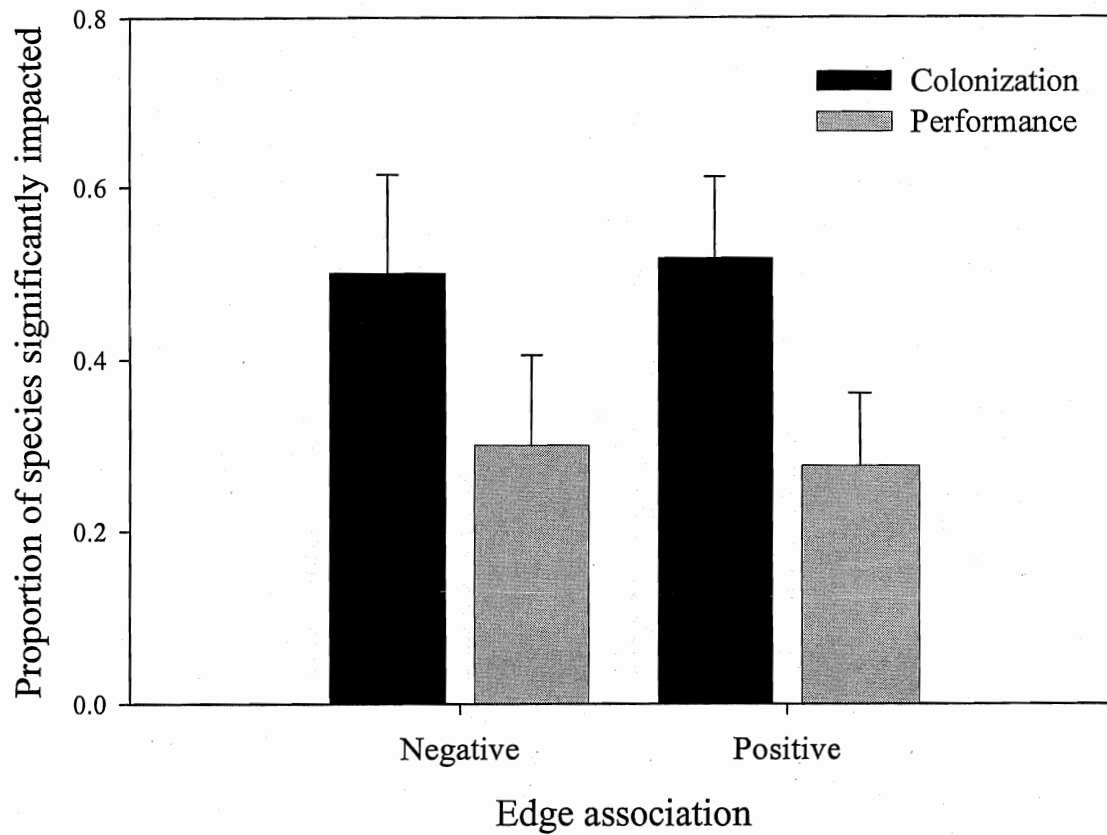


Figure 3. Proportion of negative and positive edge associated species that were significantly driven by differential colonization and performance. Negative colonization/performance were species whose cover decreased with distance from the forest edge. Positive colonization/performance were whose cover increased with distance from the forest edge.

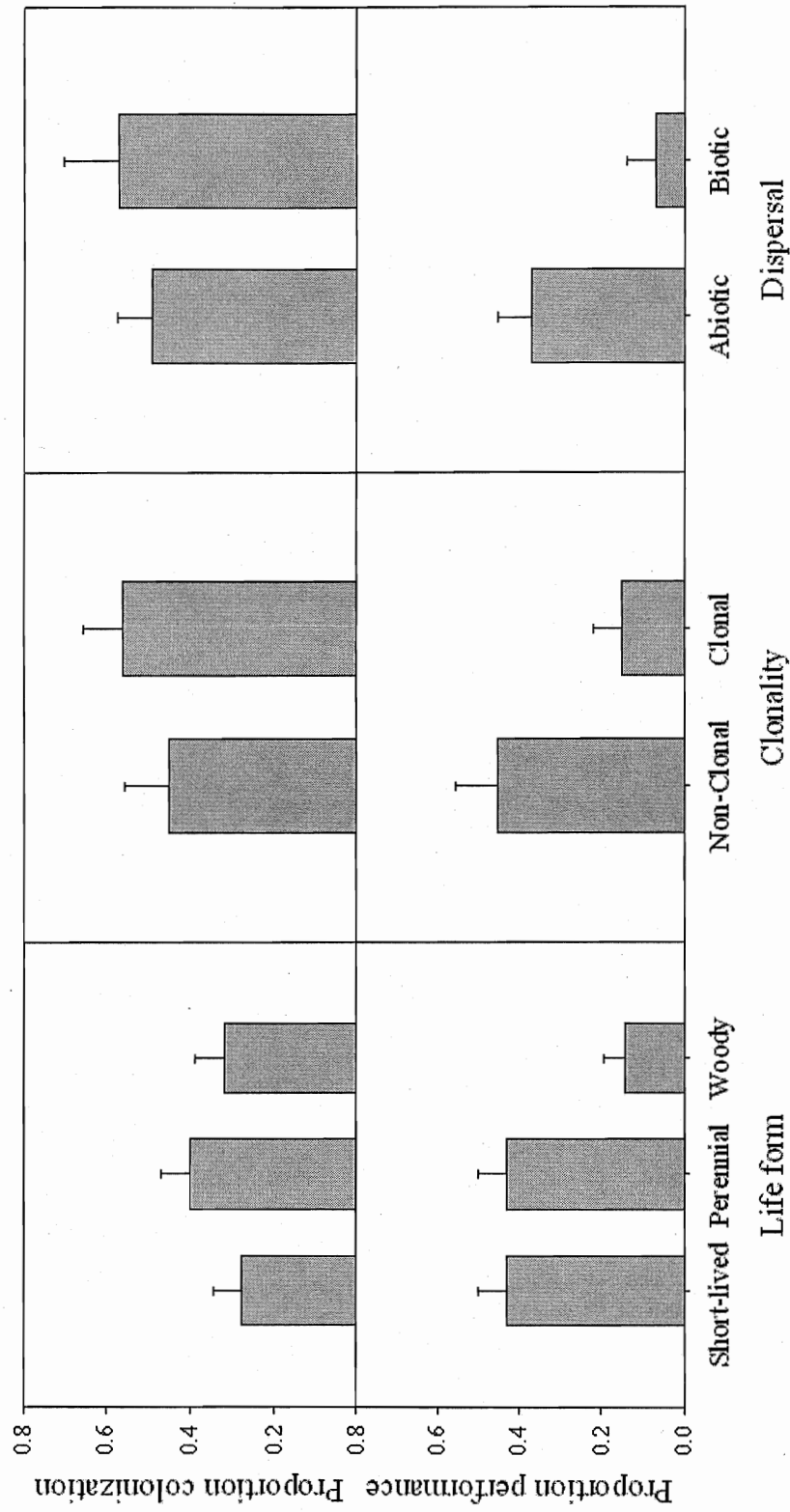


Figure 4. Subset of species of varying life forms, vegetative reproduction status, and dispersal mode that were driven by differential colonization and performance.

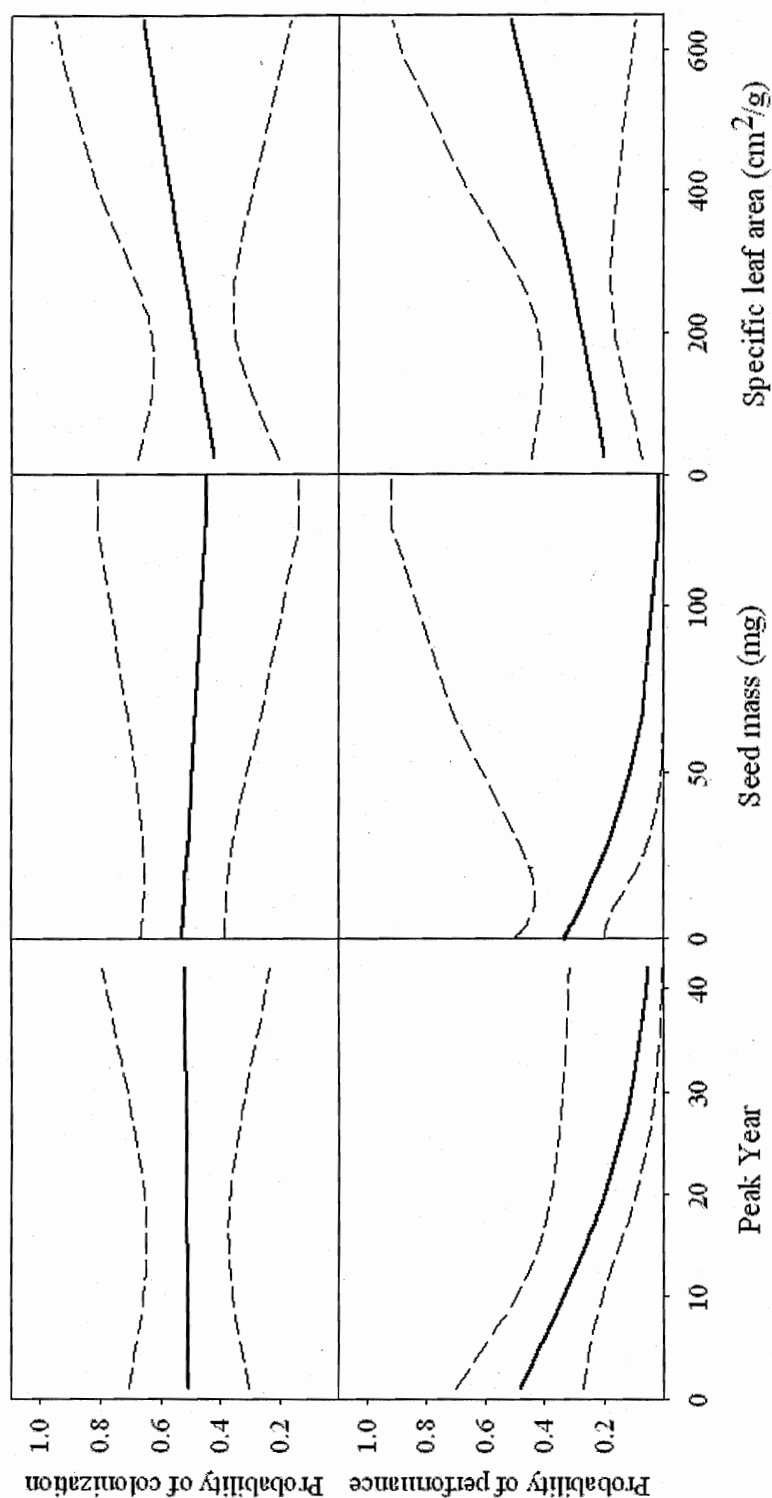


Figure 5. Probability of species of varying seed mass, specific leaf area, and peak year of cover that were driven by differential colonization and performance. Data plotted are predictions for a logistic regression (solid lines) with a 95% confidence interval (dotted lines).

DISCUSSION

Succession impacts many interactions, including facilitation, inhibition, selective herbivory, and competition-colonization tradeoffs (Bard 1952, Buell et al. 1971, Tilman 1993, Cook et al. 2005, Pickett and Cadenasso 2005). These interactions are strong determinants of population dynamics in succession. The combination of all these individual interactions, along with a plants' response to environmental factors, controls the vegetation composition of successional systems (Bazzaz 1968, Bazzaz 1979, Grime 1979). Therefore, it is not only distance from the forest edge that impacts plant population dynamics, but also the many complex interactions occurring throughout this ecosystem (Chen et al. 1992).

Individualistic Edge Responses of the Total Species Pool

There were a diversity of edge responses, in both direction and magnitude, within the total species pool (Table 1). Positive edge responding species (39%) were more common than those species that were negatively (27%) or neutrally associated (34%) with the edge. Despite the great variety of edge responses, no life history traits were able to predict the direction of a species' response to the edge (Figure 2). These results provide evidence for strong influence of the edge on spatial patterning but not for structural or physiological characteristic that drive species' responses.

Because of the variability in species' edge responses, associations with plant traits which determine plant performance, would be expected (Prach 1997). The most abundant life form across edge response groups were perennials. The dominant life form changes with succession, short-lived species (annuals and biennials) are quickly replaced

by perennials (Bazzaz 1968, Myster and Pickett 1988, Bazzaz 1996). Perennials are dominant during mid-succession, and because of the dominance of perennials in this analysis the average peak year was between years 10 and 20 (Cook et al. 2005, Meiners et al. 2007). The edge responses of species were not influenced by life form because those patterns are more strongly influenced by the temporal dynamics of successional systems. The full range of species' edge responses were observed within each life form. Thus, the life form grouping may be too coarse for delineating edge response patterns. Around 50% of species for the three edge response groups were clonal. Clonality is an important plant strategy which greatly impacts the spatial distributions of plant communities (Grime 1979, Bazzaz 1996). As clonality would allow species to dominate resource patches, the lack of edge response is surprising.

Approximately 25% of the species' pool had biotic dispersal. Dispersal mode and seed mass are evolutionarily related to each other, and typically abiotically dispersed seeds are smaller (Harper et al. 1970, Tackenberg et al. 2003). Surprisingly, there were large differences in seed mass among the three edge response groups that were not significant. Seed mass within a single community can vary over several orders of magnitude (Westoby 1998, Fenner and Thompson 2005). In my data, seed mass ranged from 0.03 to 9864.5 mg. Specific leaf area is broadly associated with plant growth rates (Wilson et al. 1999) and would be expected to be associated with full sun and resource rich environments that allow for rapid growth. However, the edge responses of species were not influenced by specific leaf area, perhaps due to resource heterogeneity.

Individualistic edge effects were also observed by Chen et al. (1992), who found that depth-of-edge influence (width of edge effects) varied dramatically between species.

The effect of the edge was much stronger for small western hemlock seedlings (137 m) compared to taller Douglas-fir seedlings (16 m). The unique life history characteristics of species, and how they interact with the abiotic gradients of the edge, translated into an individualistic response to the edge. Despite focusing on important structural and physiological traits, none could be used to indicate a species' edge response *a priori*. More likely, the interactive combination of multiple traits leads to a species' response to the edge environment. Gibson and Brown (1991) also observed this lack of predictability when trying to relate life history traits to succession in fields subjected to grazing. The lack of linkage of edge response with species traits suggests species' response to fragmentation are idiosyncratic. Therefore, the species colonizing the site encompassed a wide range of characteristics similar to the fields of the BSS.

Field effects were frequently observed while determining the influence of colonization and dispersal in generating the species responses to the edge (Table 2). These effects of field relate directly to factors that effect differential site availability (Cadenasso et al. 2003, Pickett and Cadenasso 2005). Some of these effects arose from the variability in initial site conditions and resources (Myster and Pickett 1990). Field effects may also be generated though spatial heterogeneity in maternal, seed-releasing plants. The greater the distance a seed source is from a field, the less likely a species will disperse to that field. For example, *Juglans nigra* (walnut) trees are restricted to one portion of the HMF old-growth forest and only successfully colonized fields close to those maternal trees. In contrast, *Cornus florida* (dogwood) trees were abundant throughout the old-growth forest (Monk 1961) and were found in all six of the fields analyzed. Field effects were not the topic of interest and therefore were accounted for

statistically in all analyses. By selecting fields that were sufficiently colonized, I controlled for landscape level issues of seed availability.

Role of Colonization and Performance in Generating Species Edge Responses

Differential colonization and performance are metrics of individual species population dynamics; the mechanistic explanation of edge responses expressed at the community scale. Both processes were important within this system. However, colonization was more likely to generate edge effects compared to performance (Figure 3). Significant edge effects for both colonization and performance were not detected for a substantial proportion of species analyzed, reflecting limitations of the data or scale effects.

The primary determinant of edge responses was colonization, a combination of seed dispersal and early establishment (Harper et al. 2005, Pickett and Cadenasso 2005). The dominance of colonization was not surprising, based on the importance of seeds and seedling ecology to plant communities (Fenner and Thompson 2005). Dispersal ability of a species can be impacted by several factors, such as dispersal adaptations and landscape connectivity. Local seed limitation affects species composition and structure in regenerating forests (McEuen and Curran 2004). The early establishment of seedlings leaves them highly susceptible to herbivory, pathogens, and other stresses (Mittelbach and Gross 1984, Fenner and Thompson 2005). However, as propagule pressure increases, environmental and biotic limitation may be exceeded, resulting in establishment (Lockwood et al. 2005).

The second most important driver of edge responses was differential performance. This process occurs once species have dispersed and established within a site and begin interacting with the local plant community (Harper et al. 2005, Pickett and Cadenasso 2005). The processes of resource availability, growth, reproduction, chemical interference, competition, and herbivory act singly, and in combination with each other, to generate dominance and spatial patterning. For example, preferential feeding by an herbivore on one species may reduce competition for neighboring plants.

There was a statistical linkage between colonization and performance that shows they may capture some of the same processes. Because of this, individual effects may not be completely separate. Colonization is an integration of the dispersal and establishment conditions of each plot. Performance describes how the established species interacts with the local plant community, impacting relative abundance. Because the conditions that allow plants to establish may also be the conditions that enhance their growth, this linkage is biologically relevant. For some species, particularly small herbaceous ones, multiple colonization events would result in more cover. Following individual plants could differentiate those processes completely.

Traits that Drive Differential Colonization and Performance

Understanding the traits that control colonization and performance would allow researchers to predict how species will respond in a fragmented landscape. Individual species traits are ultimately what determine where species will do well because not all species share the same light requirements, water use, phenology, etc. Identifying the

traits that regulate differential colonization and differential performance would therefore provide mechanistic insight into community assembly.

Despite the importance of life history traits in succession and in differentiating species, no single character was related to whether a species exhibited colonization effects (Figures 4 & 5). This is interesting because of colonization's prevalence as a determinant of spatial patterns in this system. The lack of relation to dispersal mode and seed mass is particularly surprising considering their strong connection to species' ability to colonize sites (Poschlod et al. 2005). This lack of relation might be tied to the inability to completely separate colonization and performance from the data. Alternatively, species traits may be less important in determining spatial patterns of colonization compared to species' interactions within the established plant community.

In contrast to the lack of association of colonization with species traits, differential performance was associated with clonality, dispersal mode, and peak year in succession (clonality & dispersal mode – Figure 4, peak year – Figure 5). The edge responses of non-clonal species were more likely to be driven by differential performance. The inference can be made that clonal species, which represent a classic competitive strategy (Grime 1979), were not constrained by growth or reproduction (performance) because of the ability to expand vegetatively. Non-clonal species do not have that advantage, and therefore expansion is through local dispersal and establishment of seeds.

Differential performance was associated with abiotically dispersed species. Typically, biotically dispersed species, such as those dispersed by birds, have larger seeds and colonize later in succession when plant communities are already established (Odum

1969, McDonnell 1986, McClanahan and Wolfe 1987, Debussche et al. 1996, Robinson and Handel 2000). Abiotically dispersed species, in contrast, tend to be early successional species with small seeds (Bard 1952, Bazzaz 1979, Pickett and Cadenasso 2005). These abiotically dispersed, early successional species would be much less competitive with existing vegetation compared to biotically dispersed species of later successional environments. These species disperse to the field when there is little vegetation, making establishment relatively easy. The prevalent role of performance suggests that abiotically dispersed species are much more constrained by the local environment than biotically dispersed species. Dispersal mode is also tightly connected to seed mass, therefore the lack of significant associations of performance with seed mass is interesting.

The edge responses of species that peaked late in succession were less driven by performance compared to early successional species. Species establishing later during succession, when vegetation already exists, may be more limited in finding a suitable place to establish. Subsequent growth would be restricted by the surrounding community until an opening in the canopy occurs. Despite their ease in dispersing to and establishing in sites, the edge responses of early successional species were more impacted by performance. In general, resource availability is higher in early successional communities allowing for rapid growth and direct competitive interactions. Early successional species are more connected with the environment (Bazzaz 1979, Parrish and Bazzaz 1982). This may be due to their early germination, which leaves them vulnerable to herbivory, which could strongly impact their continued growth (Bazzaz 1979).

Even though differential colonization more commonly generated edge responses, differential performance was more strongly driven by physiological and structural plant traits. Within forests, differential performance will likely generate more lasting impacts on the plant community as species disperse throughout the landscape (Harper et al. 2005).

CONCLUSIONS

This study found several important ways that edges influence successional regeneration of forests which are potentially applicable in restoration. Species' responses to the edge were individualistic with no characteristic that would allow *a priori* determination of a species' edge response. Being able to predict which species would decrease with distance from the forest edge, would allow identification of potential candidates for assisted re-establishment. In contrast, species that increase with distance from the forest edge would pose little need for management, unless invasive. The inability to predict edge responses, means that species management must be considered on a case by case basis.

Colonization effects were more prevalent than performance effects in generating species' edge responses. The importance of colonization within the system indicates that generating safe sites for dispersal could open the system for new species. Planting seeds or seedlings may be an option for reaching the desired composition because species' spatial patterns are much more constrained by dispersal. Since performance was much less linked with the forest edge, once a plant is established within a site it is likely to perform well.

Despite the prevalence of colonization in driving species' edge responses, none of the life history traits were related to colonization. In contrast, clonality, dispersal mode, and peak year were related to whether a species' edge response was driven by performance. Both clonal and biotically dispersed species grew well regardless of their location. Therefore, invasive species that are clonal or biotically dispersed may need direct remediation.

Understanding succession of plant communities on abandoned agricultural fields is important for conservation and restoration practices. Cultivation alters ecosystem processes and results in varied forest structure and species composition. In spite of this variation, succession in many old fields follows similar pathways, often moving towards the historical vegetative community. When this does not happen, then restoration efforts may be needed for succession to occur (Cramer et al. 2008). The influence of edges are likely to be critical in these efforts.

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