Patterns and Causes of Resistance to Tree Invasion in Rights-of-Way

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PATTERNS AND CAUSES OF RESISTANCE TO TREE INVASION IN RIGHTS-OF-WAY[1]

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Abstract. This study was designed to identify the critical life-history stages and ecological processes responsible for variation in rates of tree invasion in utility rights-of-way in the Hudson Valley of New York. We used repeated censuses to estimate natural rates of tree seedling establishment, growth, and survival in the 12 major plant communities found along rights-of-way in the region. An individual-based model was used to integrate our field data and calculate measures of the rate of tree invasion in each plant community. The most common tree invaders were species with large, wind-dispersed seeds (i.e., *Acer rubrum* and *Fraxinus americana*) although these were rarely the most common tree species in the forests bordering the corridors. In narrow (≈30–50 m wide) rights-of-way there was little relationship between seedling density and distance to the nearest seed sources; however, in wide corridors, seed dispersal clearly limited tree invasion. Annual variation in seed production in adjacent forests was also a major factor in the high spatial and temporal variability in tree seedling establishment. Growth rates of newly established seedlings did not vary significantly among the different communities; however, seedling growth rates increased dramatically once the seedlings emerged above shrub or herb-dominated canopy. Thus, the duration of competition (i.e., the number of years required by a seedling to emerge above the shrub or herbaceous canopy) appears to have been more important than the initial intensity of competition in determining variation among communities in resistance to tree invasion. As a result, shrub communities generally had high resistance to invasion. Among herbaceous communities, the highest resistance to invasion occurred in communities dominated by the grass *Schizachyrium scoparium* (little bluestem) on poor soils.

Key words: competition; dispersal limitation; disturbance; herbivory; Hudson River Valley, New York; individual-based models; old fields; tree invasion; utility rights-of-way.

INTRODUCTION

There is considerable interest in the use of communities of native shrubs and herbs to arrest succession along utility rights-of-way, thereby reducing both the costs and the environmental consequences of more intensive management using mowing or non-selective herbicide application (Niering and Egler 1955, Niering and Goodwin 1974, Bramble and Byrnes 1976, Niering et al. 1986). In many parts of the eastern United States rights-of-way represent a major component of the regional landscape, maintaining early successional communities in networks of long, narrow corridors. Successful tree invasion requires a sequence of events from tree seed dispersal to eventual emergence of a sapling above the shrub and herb-dominated vegetation. Resistance to tree invasion will thus depend on the net effects of a wide range of processes affecting seeds, seedlings, and saplings. There have been a number of recent experimental studies that examine the effects of seed predation, competition, and herbivory on invasion of abandoned agricultural lands by woody plants (e.g., Burton and Bazzaz 1991, DeSteven 1991*a, b,* Gill and Marks 1991). There is also a large literature describing temporal patterns of tree establishment within old fields (e.g., Bard 1952, Buell et al. 1971, Rankin and Pickett 1989). There have been relatively few studies, however, of the effects of variation in biotic and abiotic factors across a range of communities or environments on either the rate or direction of woody plant invasion in early-successional communities.

The general objective of this study was to understand the patterns and causes of variation in rates of tree invasion among right-of-way communities in the Hudson Valley of New York. We used repeated censuses to estimate natural rates of tree seedling establishment, growth, and survival in 12 right-of-way community types distributed across a broad range of environments. Our field data were then incorporated into a simple demographic model to predict the net rates of invasion for different tree species and communities. Our analyses document the specific demographic processes (e.g., establishment, growth, survival) that have the greatest effect on variation in tree invasion, and help identify the critical mechanisms (e.g., competition, disturbance, or herbivory) underlying resistance to invasion.

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TABLE 1. The 12 community types commonly found along utility rights-of-way in southeastern New York. Detailed descriptions of the communities are given in Canham and Wood (1993).

Abbreviation	Dominant species (common name)
Grass dominated:	
SCSC	*Schizachyrium scoparium* (Little bluestem grass meadows)
SCMO	*Schizachyrium scoparium–Polytricum* spp. (Little bluestem meadows with moss cover)
Grass–shrub dominated:	
RUSC	*Rubus flagellaris–Schizachyrium scoparius* (Creeping raspberry and little bluestem)
GRCO	Grass species–*Cornus racemosa* (Grasses with interspersed gray dogwood shrubs)
Herb dominated:	
DEPU	*Dennstaedtia punctilobula* (Hayscented fern on rocky sites)
LYSA	*Lythrum salicaria* (Purple loosestrife)
Herb–shrub dominated:	
DEKA	*Dennstaedtia punctilobula–Kalmia latifolia* (Hayscented fern and mountain laurel)
SORU	*Solidago* species–*Rubus flagellaris* (Goldenrod species and dewberry)
Shrub dominated:	
CORA	*Cornus racemosa* (Gray dogwood thickets)
KAVA	*Kalmia latifolia–Vaccinium angustifolium* (Mountain laurel and low-bush blueberry thickets)
RUAL	*Rubus allegheniensis* (Blackberry thickets)
VAKA	*Vaccinium corymbosum–Kalmia angustifolia* (Highbush blueberry and sheep laurel thickets)

METHODS

We selected 16 study sites along utility rights-of-way in the mid-Hudson Valley of New York (latitude 41°30′–42°30′ N, longitude 73°30′–74°30′ W, elevation 40–550 m above mean sea level). The study sites were stratified along a gradient of soil moisture, fertility, and elevation, and screened for environmental homogeneity within a site and freedom from recent human disturbance or management. All sites had been managed in the past using selective herbicides and/or cutting, but had not been treated for at least 3 yr prior to this study, and were protected from management or human disturbance during the course of this study. All of the rights-of-way were established prior to 1960. The majority of the study sites were located on land that had been abandoned from agriculture either before or soon after the establishment of the right-of-way.

Sampling design and seedling censuses

At each site we established a plot 60 m in length spanning the entire width of the right-of-way (25–60 m). Within each plot, 30 2-m^2 quadrats were randomly placed with a 1-m minimum spacing between adjacent quadrats. Quadrat positions were mapped and permanently marked, and the distance to the nearest forest edge was measured. For our purposes, tree seedlings were defined as stems of seed origin and <2 m tall. The 480 quadrats were searched for existing tree seedlings at the start of the study (1987), and then recensused (including identification of newly established seedlings) at the beginning and end of the 1988 and 1989 growing seasons. All seedlings were marked with aluminum tags. In each census we recorded status (live, dead, or dead due to animal predation), seedling age class (first year vs. older seedlings) and evidence of woody browse and dieback (i.e., loss of the terminal leader from stress or physical damage). Height, extension growth of the terminal leader, and the presence of shrubs or herbs overtopping individual seedlings were recorded at the end of each growing season.

At the eight sites bordered by closed forest, the species and the diameter at breast height (dbh) of all trees >10 cm dbh were recorded in a 20 × 80 m plot parallel to and just inside the forest on each side of the corridor. In addition, the location and size of any reproductively mature trees located within the right-of-way were recorded. We used these data to compare the tree composition in the adjacent forests to tree seedling composition within the rights-of-way (using *G* tests).

Right-of-way community types

Vegetation in the 480 quadrats was classified into 12 communities using TWINSPAN analysis (Hill 1979) of cover for all shrub and herb species (Canham and Wood

1993; Table 1). Individual sites contained mosaics of from 1 to 5 different communities. Sites in the Catskill Mountains were characterized by dry, sandy soils and were dominated by ericaceous shrubs (e.g., *Kalmia, Vaccinium*) or ferns (*Dennstaedtia punctilobula*) (Table 1). Sites at lower elevations in the Hudson Valley presented a wider range of environmental conditions. The overwhelmingly dominant shrub at these lower elevations was *Cornus racemosa.* It occurred across a wide range of moisture conditions but was most abundant on mesic to wet sites. Herbaceous communities on mesic to wet sites were dominated by species of *Solidago* (primarily *S. rugosa*), and often had a creeping shrub (dewberry [*Rubus flagellaris*]) in the understory. Sites on coarse-textured and thin soils in the region were dominated by the grass *Schizachyrium scoparium* (little bluestem). There were two distinct variants of this community: one with an understory of moss (*Polytrichum* spp.), the other with an understory of dewberry (*R. flagellaris*). Taxonomic nomenclature follows Gleason and Cronquist (1963) unless other authorities are listed.

Analysis of seedling demography

We used our census data to calculate annual rates of seedling establishment, growth, and survival for these different communities and sites. Rates of seedling establishment were regressed on shrub cover and distance to the nearest forest edge using least-squares regression. Relative growth rates were used to compensate for size dependencies. Relative growth rates for the major tree species were compared across community types, sites, and community types within site using analysis of variance (ANOVA), with both community types and sites treated as fixed effects. Mean relative growth rates of seedlings suffering physical dieback were compared to mean relative growth rates of seedlings without dieback using *t* tests. The likelihood of repeated dieback over two successive years was tested with a *G* test. χ^2 statistics were used to test (1) the effects of the presence of overtopping shrub or herb cover on browse rates and (2) the likelihood that a seedling browsed in the first year of the study would also be browsed in the second year. The χ^2 statistics were computed using weighted least-squares estimation of one-way categorical linear models using the CATMOD procedure (SAS Institute 1987). The categorical linear models provide an analysis for a categorical response (browsed vs. unbrowsed) that is analagous to a traditional analysis of variance for a continuous dependent variable. The relationship of mean relative growth to survivorship was assessed by comparing the growth rates of those seedlings surviving to 1989 with those seedlings that did not survive (*t* test), as well as by maximum likelihood analysis of the relation between the probability of mortality and size and growth rate. All analyses other than the maximum likelihood estimates were done using SAS (SAS Institute 1987).

Microsite characteristics

We examined the distribution of seedlings within a subset of the quadrats to test whether seedlings occurred preferentially in small-scale openings. We selected seven community types that had (1) reasonable numbers of newly established tree seedlings and (2) adequate representation within a single site, and ran two or three 1-m-long transects through the 7–20 quadrats containing that community type (n = 21–40 transects per site). We recorded the percentage of each transect without litter or vegetation cover in 10-cm intervals. We also characterized the microsites around each seedling in the target quadrat with respect to the presence of bare soil or vegetation openings. *G* tests were used to compare the observed distributions of seedling microsites to the expected distributions assuming seedlings were randomly distributed with respect to bare-soil patches and vegetation openings.

An individual-based model of tree invasion

We used a simple demographic model of tree seedling growth and survival, parameterized using our field data, to calculate rates of tree seedling invasion in different community types. This model allows us to evaluate the cumulative impact of both biotic and abiotic conditions within a community on the fate of tree seedlings, once they become established in a quadrat. Our field data do not allow us to estimate seed input and losses prior to seedling establishment, and observed rates of seedling establishment were extremely variable among sites, communities, and years. Much of this variation was clearly due to variation in seed production in adjacent forests, and reflects spatial and temporal variation in invasion pressure, rather than variation in the resistance to invasion by right-of-way communities. Thus, our model is restricted to analysis of processes acting after seedling establishment. Specifically, the model predicts two different aspects of tree seedling invasion. The first is the ratio of the number of seedlings established in a given year (for any specified area) to the number of those seedlings that will ultimately survive to reach 2 m in height (Establishment/Emergence Ratio, E/E). The second parameter is the time it takes for the fastest seedling in a cohort to reach 2 m in height (Time to First Emergence above shrub cover, TFE).

The model begins with a fixed number of newly established seedlings. The model then tracks the fate of each seedling individually until it either dies or becomes taller than 2 m. When a seedling becomes taller than 2 m it is considered to have "emerged" as a sapling above the surrounding vegetation (since none of the dominant species in the 12 community types normally exceed 2 m in height). Seedling height is incremented each year as a function of seedling height class

(0–50 cm, 50–100 cm, and 100–200 cm), since our data show that even relative growth rates tend to increase with seedling height over the range of heights from 0 to 1 m.

Our field results document a pervasive pattern of herbivory and physical dieback of the terminal leaders of tree seedlings. These processes, lumped together as "annual damage", reduce seedling growth, and may actually result in a decline in seedling height. We used our field data to calculate the annual probability that a seedling in any of the three height classes would be damaged in a given community. In the model, this probability of damage is applied randomly to seedlings. If a seedling experiences damage in a given year, its height growth is incremented by the much smaller estimated height growth of damaged seedlings.

In the model, seedling mortality is assumed to be a simple function of age. Specifically, our field data show a high mortality rate for seedlings during their 1st yr. After that, annual mortality rates are relatively low (<5% of the seedlings per year), and the model assumes that mortality is independent of size or age after the 1st yr. Our field data often show a negative relationship between growth rate and probability of mortality. However, the model is conservative in this regard, and treats growth and mortality as independent.

RESULTS

Effects of adjacent forests and corridor width on tree invasion

Tree seedling composition within the right-of-way corridors was significantly different from the composition of the adjacent forests for all eight sites in which forest edge communities were sampled (Table 2) (G tests, $P < 0.001$). Red maple (*Acer rubrum*) was by far the most abundant tree seedling within the corridors (50% of all seedlings), but accounted for only 17% of the basal area in adjacent forests. The next two most abundant seedling species within the corridors at the eight sites—white ash (*Fraxinus americana,* 14%) and quaking aspen (*Populus tremuloides,* 6%)—were also both overrepresented in the corridors relative to adjacent forests (Table 2). Species such as oaks (*Quercus* spp.) that have large, animal-dispersed seeds, were generally much more common in adjacent forests than in the corridors (Table 2). The major exception was black oak (*Q. velutina*), which had comparable relative abundances in both the corridors and adjacent forests. Black oak is the dominant oak species in forests that have become reestablished on abandoned agricultural lands in the region (Glitzenstein et al. 1990).

Tree seedling densities in the right-of-way corridors declined sharply with increasing distance from the nearest forest edge (Fig. 1). Species found at distances >70 m from a forest edge were primarily bird-dispersed (i.e., *Juniperus virginiana* and *Prunus serotina*) (Fig. 1). Seedlings of wind-dispersed species accounted for 89.4% of all tree seedlings within the 16 sites. Species with large, wind-dispersed seeds—i.e, red maple, sugar maple (*Acer saccharum*), striped maple (*A. pennsylvanicum*), and white ash—comprised 76.4% of the wind-dispersed seedlings. Species with small, wind-dispersed seeds—yellow birch (*Betula lutea*), black birch (*B. lenta*), gray birch (*B. populifolia*), and quaking aspen—accounted for only 4.8% of the wind-dispersed seedlings (and thus only 4.3% of the total number of seedlings). The remainder of the wind-dispersed seedlings were of species with intermediate seed sizes. Species with primarily animal-dispersed seeds (10.5% of all seedlings) were evenly divided among large-seeded species dispersed primarily by mammals (48%; *Quercus* spp., *Carya* spp.) and small-seeded species dispersed primarily by birds (52%; *Juniperus virginiana, Prunus* spp., *Sassafras albidum*).

TABLE 2. Relative abundance of species among tree seedlings within utility rights-of-way (corridors), and among adult trees in forests bordering the rights-of-way (corridor edges). Numbers shown for adult trees (relative basal area) and tree seedlings (relative densities) are based on data from 8 of the 16 sites studied in the Hudson Valley (New York, USA).

Species	Edge composition: relative basal area of trees (%)	Corridor composition: relative density of tree seedlings (%)
Acer rubrum	17.07	50.15
Acer saccharum	2.37	0.35
Betula lenta	0.27	1.79
Betula populifolia	2.38	0.40
Fraxinus americana	2.13	13.61
Juniperus virginiana	9.91	3.19
Magnolia acuminata	1.25	0.00
Populus tremuloides	0.43	5.68
Pinus strobus	15.09	5.58
Populus grandidentata	1.11	0.00
Prunus serotina	1.63	2.76
Quercus alba	3.82	0.54
Quercus rubra	9.47	1.85
Quercus coccinea	9.27	5.14
Quercus velutina	3.74	3.44
Quercus prinus	8.14	0.83
Tsuga canadensis	8.89	0.29
Sassafras albidum	0.28	1.93
Other species	2.75	2.47

Demography of tree seedling invasion

Establishment.—Tree seedling establishment was extremely variable, and ranged from 0–7.8 seedlings/m^2/yr. In 1988, 76% of all newly established seedlings were white pines, and 99% of these white pine seedlings occurred at a single site. In 1989, 77% of all new germinants were red maple seedlings, and 76% of those were found at a single site. In both years there was a significant negative relationship between establishment and distance to the nearest forest edge (1988, $r = -0.145$, $P = 0.003$; 1989, $r = -0.103$, $P = 0.032$). Studies of rates of predation on tree seeds in this region

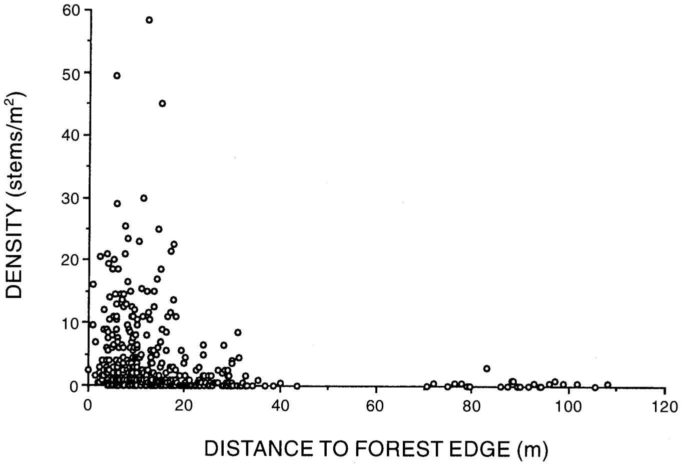

FIG. 1. Densities of tree seedlings (<2 m tall) in rights-of-way (25–60 m wide) as a function of the distance from an adjacent forest edge at 16 sites in the Hudson Valley, New York. Densities were determined by summing seedling abundance for all tree species in each of 472 plots. Distances were measured from each of the plots to the nearest forest edge (i.e., the canopy drip line).

have suggested that there are higher rates of seed predation in shrub communities than in herbaceous communities (McDonnell et al. 1993). However, our data showed no relationships between tree seedling establishment and shrub cover.

Height growth and dieback.—Seedling relative growth rates varied significantly among tree species ($F = 5.45$, df = 6, 1280, $P < 0.0001$, for the seven major tree species). White pine and black oak are both frequent components of forests that develop on abandoned agricultural land in the region (Glitzenstein et al. 1990). While both species occurred at low densities within our sites, they had the highest relative height growth rates of any of the major tree species (25.6%/yr, and 21.1%/yr, for white pine and black oak, respectively, in 1989, averaged across all sites). Red maple—the most abundant species of seedling invader—had the lowest growth rate of the major species (7.2%/yr), while the next most common species, white ash, had an intermediate growth rate of 15.4%/yr in 1989.

A competition experiment using many of the same communities revealed that growth rates of experimentally planted tree seedlings beneath intact vegetation were uniformly low across a wide range of communities and environments (Berkowitz et al. 1993). In our study there were significant differences in height growth rates among community types for the smallest seedling size class (0–25 cm height) for both red maple ($F = 2.06$, $P = 0.021$) and white pine ($F = 3.66$, $P = 0.0036$) but not for white ash ($F = 0.38$, $P > 0.05$) or for all species combined (0–25 cm height class, $F = 1.29$, $P > 0.05$) (see also Tables 4 and 5).

TABLE 3. Probability of survival to the end of each time period for seedlings in the 1988 and 1989 cohorts.

	1988 cohort			1989 cohort		
Time period	Red maple	White pine	All species	Red maple	White pine	All species
Spring 1988 to Fall 1988	0.733	0.200	0.325			
Fall 1988 to Spring 1989	0.775	0.649	0.719			
Spring 1989 to Fall 1989	1.000	0.934	0.959	0.869	0.960	0.890

Rates of dieback of the terminal leader ranged from 16% in 1987–1988 to 24% of all seedlings in 1988–1989. White pine had distinctively low rates of dieback (1 and 3% for 1988 and 1989, respectively), while gray birch and the two most common oak species had high rates of dieback (ranging from 24–52% for individual years). The growth rates of seedlings suffering dieback in 1988–1989 were significantly lower than for seedlings not experiencing dieback (18.1%/yr vs. 25.5%/yr, respectively, $t = 2.44$, $P < 0.015$). Moreover, seedlings suffering dieback in 1987–1988 were more than twice as likely to experience dieback the next winter compared to seedlings that had been undamaged in 1987–1988 (probability of dieback in 1988–1989 = 0.54 vs. 0.23, $G = 51.19$, $P < 0.0001$).

Survivorship.—Seedling survivorship was very low for 1st-yr seedlings during 1988, presumably because of an early summer drought (Table 3). For older seedlings, and for 1st-yr seedlings in 1989, survivorship varied a great deal among individual community types (Table 4).

Models for the probability of mortality as a function of relative growth rate and size, fit using maximum likelihood methods (see *Methods*), indicate that seedling mortality declined with both increasing relative growth rate and increasing size, and that the relationships between mortality, growth rate, and size varied in the different community types (Fig. 2). When averaged across all community types, the probability of seedling mortality declined modestly with increasing

TABLE 4. Major seedling parameters used to compute invasibility for seven representative community types. Community type codes are defined in Table 1.

	Community type						
	RUAL	CORA	DEKA	SCSC	SORU	DEPU	GRCO
Mortality							
1st-yr	0.99*	0.99*	0.50	0.99*	0.87	0.27	0.00
Older	0.308	0.169	0.176	0.114	0.071	0.123	0.144
Growth rate							
(0–50 cm)	0.275	0.244	0.138	0.338	0.270	0.248	0.358
(50–100 cm)	0.366	0.246	0.138	0.173	0.360	0.250	0.285
Damage†							
(0–50 cm)	0.125	0.255	0.250	0.556	0.200	0.140	0.178
(50–100 cm)	0.000	0.333	0.250	0.333	0.491	0.375	0.417
Damaged growth‡							
(0–50 cm)	0.087	0.337	0.005	0.022	0.064	0.005	−0.273
(50–100 cm)	0.000	−0.284	−0.005	0.208	0.228	0.043	0.040
E/E ratio§	20 000	3333	2222	1333	29	19	18
TFE‖ (yr)	27	21	37	20	15	17	14

* Set to 0.99 because no new seedlings survived the first summer during 1988–1989.

† Fraction of seedlings in the size class experiencing either dieback or browsing.

‡ Relative growth rate of seedlings that experienced dieback or browsing.

§ Establishment/Emergence ratio = ratio of no. of seedlings established in a given year to the no. of those seedlings that will ultimately survive to reach 2 m in height.

‖ Time to First Emergence = time it takes the fastest growing seedling in a cohort to emerge above the shrub/herb canopy (i.e., growth to 2 m height).

relative growth rate (Fig. 2). Annual mortality rates dropped by roughly an order of magnitude as seedlings increased in size from 10 to 100 cm height (Fig. 2).

Browsing of tree seedlings by herbivores.—Rates of browsing in the two years of the study ranged from 22–27%/yr for all tree species combined. In both 1988 and 1989, gray birch had the highest percentage of stems browsed (50–53%), while white pine had the lowest (5–19%). There was also significant variation in rates of browsing among different community types (1989 data, $\chi^2 = 50.64$, $P < 0.0001$), ranging from 12.1% in hayscented fern communities (DEPU) to 38.3% in little bluestem–moss communities. Tree seedlings overtopped by shrubs or herbs were much less likely to be browsed than were exposed seedlings (Fig. 3; $\chi^2 = 72.67$, $P < 0.0001$). Seedlings were much more likely to be browsed in the 2nd yr of the study if they had also been browsed in the previous year (50% chance of browsing vs. 20% for seedlings not browsed the previous year; $G = 99.385$, $P < 0.000$). However, browsing had no significant influence on the likelihood of mortality in the following year ($G = 3.057$, $P > 0.05$).

Distribution and importance of small-scale openings.—Bare ground was rare in all of the community types (Fig. 4), and the vast majority of tree seedlings occurred in locations with both litter and vegetation cover. While relatively few seedlings were found in small-scale openings, they did occur with 2–6 times higher frequencies than expected at random for all of the community types except mountain laurel–blueberry (KAVA) (Fig. 4). Seedlings also occurred more commonly than expected in litter-free patches in three of the seven communities (Fig. 4). Seedling growth rates in vegetation openings were greater than growth rates beneath intact vegetation for all of the community types except highbush blueberry–sheep laurel thickets (VAKA). However, the differences were significant in only the goldenrod–dewberry (SORU) communities ($t = -2.45$, $P = 0.0173$). Thus, our results suggest that seedlings did exploit small-scale openings, but that the openings were relatively rare and not required for successful invasion.

Individual-based model of tree seedling invasion

Our individual-based model of tree seedling invasion integrates our data on growth, mortality, browsing, and dieback to compute an index of the invasibility of the different communities. It should be noted that the predictions for a given community represent the average of the effects of the range of physical sites on which that community occurred. In effect the model predicts the trajectory of tree invasion given the current composition, structure, and environment of the community. Actual, long-term rates of tree invasion will obviously be strongly influenced by successional changes in the composition and structure of the community, and by future disturbances and management practices.

Our results indicate that the invasibility of different communities varies by over 3 orders of magnitude (Fig. 5) from blackberry thickets in which the establishment/emergence ratio (E/E) = 20 000 to mixed grass–gray dogwood communities in which E/E = 18. Our results suggest that a significant component of the generally slow rate of tree invasion in this region is simply due to the long time lag between seedling establishment

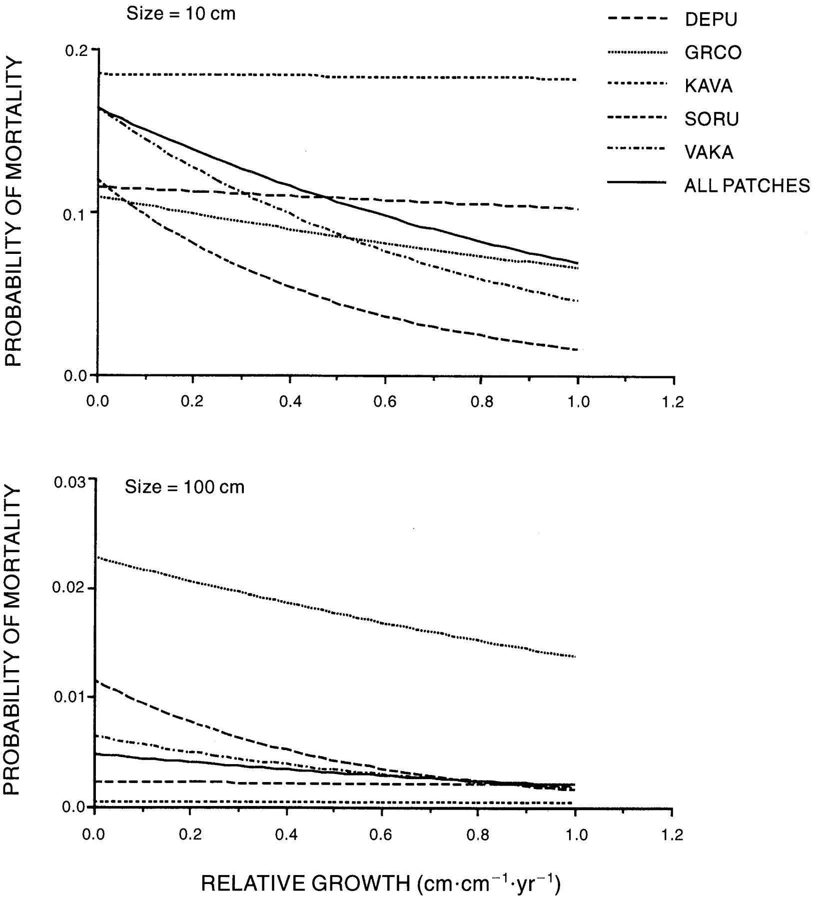

FIG. 2. Probabilities of tree seedling mortality as a function of seedling relative rate of height growth. Functions were estimated using binomial regression in a maximum likelihood estimator. Probabilities for two seedling height classes are presented for those five community types with sufficient numbers of seedlings to estimate the model parameters, and for all community types combined. Community type codes are defined in Table 1.

and sapling emergence, with emergence times ranging from 14 to 37 yr following establishment (Fig. 6).

While there is considerable variation in invasibility within different structural types, the shrub communities in general had high resistance to invasion. Our two grass-dominated communities occur on extremely dry sites, and had higher resistance to invasion than our two herb-dominated communities, which occur on more mesic sites. The three communities with the lowest resistance to invasion (GRCO, DEPU, and SORU; Fig. 5) are all dominated by low-statured species that occur on productive sites (grasses, ferns, and herbaceous perennials, respectively).

Variation in resistance to invasion among the communities was due to a variety of factors (Table 4). High resistance to invasion in blackberry thickets (RUAL, E/E = 20 000) was due to extremely high seedling mortality. However, growth rates of seedlings that did survive were relatively high (Table 4). Gray dogwood thickets (CORA)—with the second highest resistance to invasion, (E/E = 3333)—also had relatively high mortality rates. However the dogwood thickets also had moderate levels of damage (browsing and dieback), and damaged seedlings had severely reduced growth rates. Even without considering the effects of slow growth rates on the probability of mortality in a given year, the slow growth rates of the damaged seedlings lead to a longer compounding of the high annual mortality of older seedlings, and thus significantly reduce the probability of survival of seedlings to emergence.

The community with the third highest overall resistance to invasion was dominated by hayscented fern and mountain laurel (DEKA, E/E = 2 222). This community had much lower 1st-yr mortality than CORA or RUAL, but still had relatively high rates of mortality in older seedlings (Table 4). Damage rates were moderate, and, as in the dogwood thickets, growth rates of damaged seedlings were severely reduced.

Little bluestem meadows had the fourth highest resistance to invasion (E/E = 1 333). These communities occur on sites with thin, coarse-textured soils, and have a relatively sparse canopy that allows high light penetration. Undamaged seedlings that survive their 1st yr have relatively high growth rates. However, 1st-yr sur-

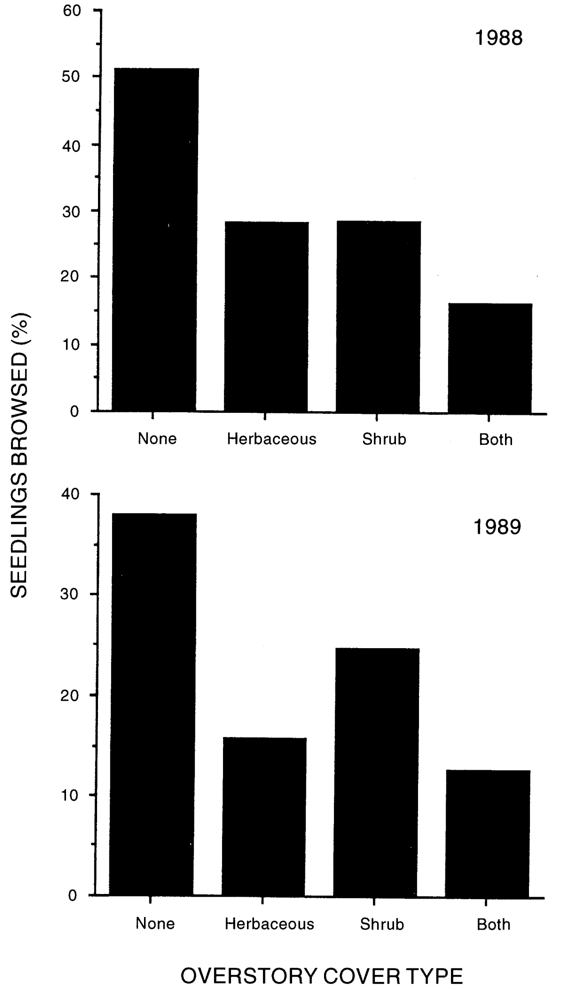

FIG. 3. Percentages of tree seedlings browsed in 1988 and 1989 in relation to the presence or absence of shrub or herbaceous cover directly above a seedling.

vival was very low, and the frequency of browsing on the relatively exposed tree seedlings is high.

The three communities with the lowest resistance to invasion (SORU, E/E = 29; DEPU, E/E = 19; GRCO, E/E = 18) had a wide range of variation in 1st-yr mortality and rates of browsing and dieback. However, all three had relatively high survival and growth rates for older seedlings (Table 4).

Only two species—red maple and white ash—occurred in high enough densities to allow us to estimate model parameters for individual tree species/community pairs (Table 5). Gray dogwood thickets (CORA) had relatively high resistance to invasion by both tree species because of high initial mortality rates (Table 5). Hayscented fern communities (DEPU) had relatively low resistance to invasion by either species because of relatively low mortality rates. Goldenrod-dewberry communities (SORU) had very low resistance to invasion by white ash because of extremely low seedling mortality. However, these communities had relatively high resistance to invasion by red maple due to the extremely high rates of red maple seedling mortality (Table 5).

DISCUSSION

Our results document an extremely wide range of variation in resistance to tree invasion among different communities. The communities with the lowest resistance to invasion were dominated by herbaceous species on productive sites. We found high resistance to tree invasion in communities with a wide range of species compositions and community structures, as well as in a wide range of physical environments. However, the demographic parameters responsible for resistance to tree invasion differed widely among the different communities.

Dispersal vs. recruitment limitation of tree invasion

Two distinct sets of forest tree species are conspicuously underrepresented in rights-of-way: the light-seeded, wind-dispersed species (e.g., *Betula* spp.), and the heavy-seeded, animal-dispersed species (e.g.,

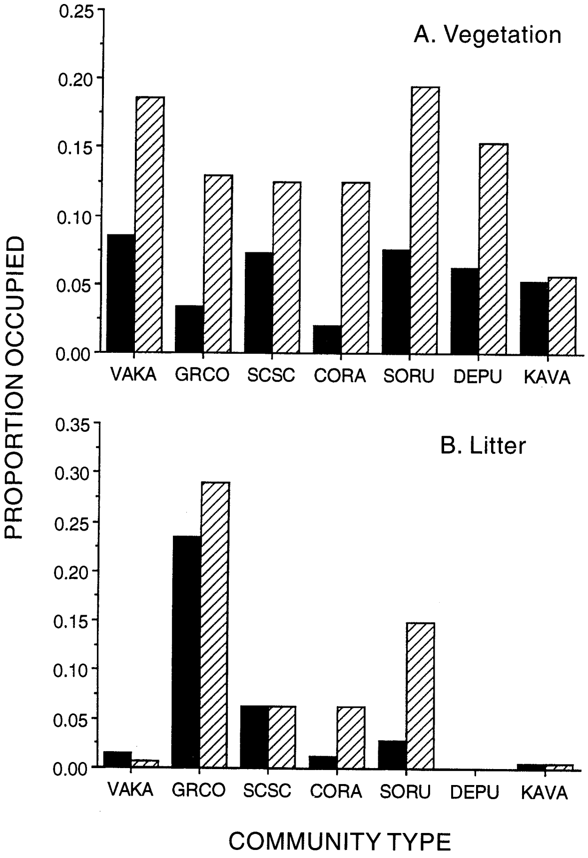

FIG. 4. Proportions of quadrat area occupied by patches >10 cm in diameter without vegetation cover (A) or litter (B) (solid bars), and the proportions of tree seedlings within the quadrats that occurred in those microsites (hatched bars). Community types are defined in Table 1.

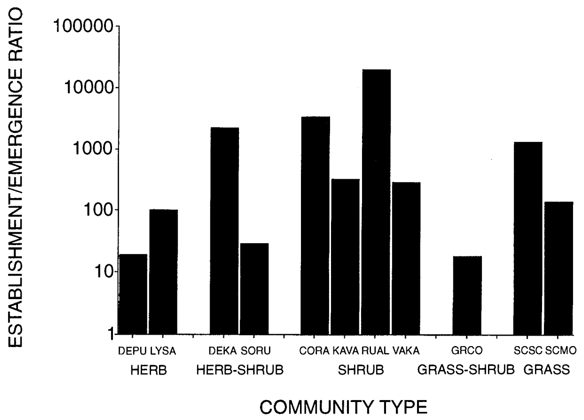

FIG. 5. Establishment to emergence ratios (E/E) for 11 of the 12 community types listed in Table 1. E/E was defined as the number of seedlings that must become established before one sapling emerges through the vegetation (reaches 2 m in height). The community types are divided into five structural types based on dominant species: herbaceous, shrub, grass, and communities that are mixtures of herbs and shrubs or grasses and shrubs.

Quercus spp.). We feel that the low densities of heavy-seeded, animal dispersed species reflect limitation due to very low rates of dispersal into the corridors, rather than active inhibition of seedling establishment by right-of-way communities. Rapid growth rates and high survival of the few oak seedlings that do become established in corridors support this interpretation.

The decline in tree seedling density with increasing distance from the nearest forest edge suggests that there is also dispersal limitation of seedling densities for the large-seeded, wind-dispersed species (e.g., red maple and white ash) that dominate the tree seedling layer within the rights-of-way. However, the wide range of variation in seedling density even close to a forest edge indicates that dispersal limitation only sets an upper bound on the densities of these species.

Dispersal limitation is not an adequate explanation for the low densities of light-seeded, wind-dispersed pioneer tree species (i.e., *Betula* spp., *Populus* spp.). Given their relatively high rates of dispersal into corridors (McDonnell and Koch 1993), and their widely documented success at colonizing disturbances in which competing vegetation is absent or sparse, we feel that their low densities reflect extremely effective resistance to invasion by essentially all intact communities, regardless of whether the low rates of seedling establishment are due to competition (e.g., Gill and Marks 1991), herbivory (e.g., DeSteven 1991*a*), or physical inhibition by litter (Facelli and Pickett 1991).

Our results highlight extremely large variation in rates of establishment of new tree seedlings in both time and space. A significant fraction of this variation was clearly due to spatial and temporal variation in seed production by canopy trees in the adjacent forests. The vast majority of new seedlings established in 1988 were white pine seedlings that emerged following a large seed crop at one site. Variation in seed predator populations may provide an additional, important source of spatial and temporal variation in rates of tree seedling establishment within rights-of-way. The predominant woody seed predator in both old fields and utility rights-of-way in this region is *Peromyscus leucopus* (McDonnell et al. 1993). *Peromyscus* densities can fluctuate significantly from year to year (Adler and Tamarin 1984, Ostfeld 1988). While we did not examine seed predation, recent research has highlighted the importance of this process for tree invasion in old fields (DeSteven 1991*a,* Gill and Marks 1991).

Patterns and mechanisms of resistance to tree invasion

Tree seedling growth and survival.—Seedling growth rates obviously have a direct effect on the time it takes for saplings to emerge above a shrub and herb canopy. However, the more significant effects of variation in seedling growth rates on invasion of a right-of-way are in the compounding of annual mortality rates over the time it takes for a seedling to reach a size at which the negative effects of neighboring shrubs and herbs become negligible. A number of studies have documented high mortality rates for 1st-yr tree seedlings in old fields (DeSteven 1991*b,* Gill and Marks 1991). Our results show similar patterns. However, our model demonstrates that resistance of rights-of-way to tree invasion is also highly sensitive to slight changes in the relatively low annual mortality rates of older seedlings.

Disturbance.—Naturally ocurring canopy openings (>10 cm in diameter) were relatively rare (<8% of area), although the frequency of openings was higher

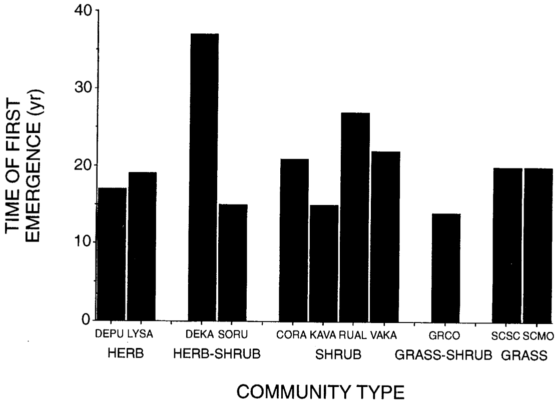

FIG. 6. Times of first emergence for 11 of the 12 community types listed in Table 1. Time of first emergence was defined as the number of years between the establishment of a cohort of tree seedlings and the time that the first sapling emerged through the vegetation (i.e., reached 2 m in height). The community types are divided into five structural types based on dominant species: herbaceous, shrub, grass, and communities that are mixtures of herbs and shrubs or grasses and shrubs.

TABLE 5. Major parameters used to compute invasibility for red maple and white ash seedlings in three community types. Community type codes are defined in Table 1.

	CORA		DEPU		SORU	
	Red maple	White ash	Red maple	White ash	Red maple	White ash
Mortality						
1st-yr	0.360	0.99*	0.333	0.111	0.99	0.10
Older	0.360	0.167	0.176	0.021	0.088	0.036
Growth rate						
(0–50 cm)	0.280	0.198	0.251	0.212	0.191	0.216
(50–100 cm)	0.280	0.198	0.251	0.212	0.191	0.090
Damage†						
(0–50 cm)	0.042	0.617	0.146	0.100	0.465	0.044
(50–100 cm)	0.040	0.617	0.143	0.250	0.750	0.200
Damaged growth‡						
(0–50 cm)	−0.048	0.376	−0.039	0.103	0.011	0.239
(50–100 cm)	−0.048	−0.264	−0.265	0.103	−0.169	0.239
E/E ratio§	909	2000	59	2	20 000	2
TFE‖ (yr)	16	22	18	20	44	19

* Set to 0.99 because no new seedlings survived the first summer during 1988–1989.

† Fraction of seedlings in the size class experiencing either dieback or browsing.

‡ Relative growth rate of seedlings that experienced dieback or browsing.

§ Establishment/Emergence ratio = ratio of no. of seedlings established in a given year to the no. of those seedlings that will ultimately survive to reach 2 m in height.

‖ Time to First Emergence = time it takes the fastest growing seedling in a cohort to emerge above the shrub/herb canopy (i.e., growth to 2 m height).

than observed in a study by Goldberg and Gross (1988) on mid-successional old fields dominated by herbaceous perennials, and lower than the frequency of openings in a 30-yr old field on a poor site studied by Harrison and Werner (1984). In our sites, tree seedlings did occur more frequently in openings than expected at random, and while their growth rates were generally higher in openings, the patterns were significant in only one community (goldenrod–dewberry). It is notable that these goldenrod–dewberry communities occur on mesic, productive sites, where release from competition in an opening would be expected to have a strong effect on seedling growth. On a highly eroded, sandy site in Michigan, Harrison and Werner (1984) found that oak seedling colonization occurred primarily in small openings, but that subsequent growth rates and survival were higher if the openings closed.

Herbivory.—Our results document a pervasive pattern of browsing by vertebrates (primarily white-tailed deer) on tree seedlings. We have not examined the effects of invertebrate herbivores, either aboveground (e.g., Fox and Morrow 1986) or belowground (e.g., Brown and Gange 1989). The current literature indicates that the impacts of insect herbivores on plant community dynamics vary widely (Brown 1985, Huntly 1991). Our model demonstrates that vertebrate browsing can significantly reduce tree invasion in rights-of-way, particularly in communities such as little bluestem meadows where seedlings are highly exposed even when relatively small. The greatest uncertainty concerns the long-term consequences of browsing. Our results show that seedlings browsed in a given year have a high probability of being browsed in the next year; however we did not detect short-term effects of browsing on seedling survival. We expect that browsing repeated over the course of 5–10 yr will have significant effects on seedling survival (Krefting et al. 1966).

We observed very little outright predation on tree seedlings (i.e., death due to clipping of a seedling near its base). In contrast, Gill and Marks (1991) and Ostfeld and Canham (1993) found predation by meadow voles (*Microtus pennsylvanicus*) to be one of the major sources of seedling mortality in herbaceous communities. Our current methods could have easily missed this form of mortality, since experiments show that predation by meadow voles can occur extremely quickly after seedlings germinate (Ostfeld and Canham 1993), and the censuses for the present study took place in early June, several months after seedling emergence. Many of our communities are dominated by shrubs, and would not have been expected to have high populations of meadow voles (Rose and Birney 1985). Our results suggest that seedlings in openings should be at a greater risk of browsing by deer (Fig. 3). However, the risk of outright predation on tree seedlings by voles can be much lower in small openings (i.e., as small as 8 cm wide) than beneath intact vegetation (Gill and Marks 1991, Ostfeld and Canham 1993).

Duration vs. intensity of competition.—Our results indicate that the growth of small seedlings is relatively low across a wide range of sites and community types. A large field-competition experiment using a subset of eight of our community types confirms this result, and demonstrates that the uniformly low growth rates are due to an inverse relationship between the intensities of competition and physical stress along a site quality gradient (Berkowitz et al. 1993). However, seedling growth rates remain low only until they emerge above the surrounding low-growing species. In shrub communities, seedling emergence is significantly delayed by the tall canopy, and the rate of invasion is significantly reduced by the compounding of annual mortality rates over much longer periods of time. Thus, variation in resistance to tree invasion is more closely related to variation in the duration of competition (as measured by the number of years that it takes for a seedling to emerge above its neighbors) than to variation among sites in the intensity of competition in any given growing season.

MANAGEMENT IMPLICATIONS

Our results indicate that vegetation managers responsible for controlling tree invasion in rights-of-way will observe a great deal of variation in net rates of tree invasion because of both site-to-site differences in invasion pressure (largely governed by the proximity and composition of neighboring forests) and both site and community-level variation in resistance to tree invasion. Early-successional communities on productive sites had the lowest resistance to tree invasion. However, a related study indicates that rates of colonization and spread of shrubs are very high in these communities (Boeken and Canham 1993) if the sites are managed using highly selective herbicide application (Dreyer and Niering 1986) rather than mowing or broadcast herbicide applications. Thus, resistance to tree invasion should increase over time on these sites under a selective management regime. In general, our results reinforce the conclusions of other studies of the development of ecologically based right-of-way management that the most important management principle is to minimize disturbance to right-of-way vegetation through highly selective herbicide applications or cutting of individual saplings after they emerge above the surrounding shrub and herb canopy (Pound and Egler 1953, Niering and Goodwin 1974, Bramble and Byrnes 1976, Dreyer and Niering 1986).

One goal of traditional right-of-way management has been to minimize long-term costs by increasing the length of the rotation cycle (years between successive management), combined with methods such as less selective, foliar application of herbicides to treat both high densities and a wide range of seedling and sapling sizes. In contrast, the highly selective removal of individual saplings following emergence above the shrub and herb community represents a harvesting of smaller numbers of the largest individuals from a relatively continuous distribution of seedling and sapling sizes. One of the unique limitations of right-of-way management is the need to guarantee that not even a single individual sapling reaches the wire security zone. Thus, under highly selective management, the maximum management rotation cycle is effectively determined by the time it takes for the fastest sapling of any species to grow from the point at which it emerges above the low-growing canopy to the height of the wire security zone. While the growth rates of these emergent saplings may be reduced by both belowground competition and herbivory, the major effects of low-growing communities are to reduce the densities of smaller seedlings prior to emergence. In addition, the optimal management rotation cycle may need to be much shorter than the maximum described above to prevent large, emergent saplings from displacing shade-intolerant shrub and herb species, and leaving large openings for future tree invasion when the saplings are ultimately removed. Thus, it seems likely that highly selective, ecologically based management will require relatively short rotation times, regardless of the degree of resistance of right-of-way communities to tree invasion.

Long-term selective management also has the potential for creating novel communities (Bramble and Byrnes 1983, Dreyer and Niering 1986), as shrubs displace shade-intolerant species and eventually develop understories of more shade-tolerant grasses and herbaceous species. We suspect that resistance to tree invasion may be even further enhanced by the development of these novel assemblages of species. However, we propose that the long-term dynamics of right-of-way communities should also be examined for their importance in the maintenance of overall landscape diversity. As abandoned agricultural lands in this region progressively develop into forests, rights-of-way may represent an increasingly important reservoir of early successional species and habitats in the landscape (Marks 1983).

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LITERATURE CITED

Adler, G. H., and R. H. Tamarin. 1984. Demography and reproduction in island and mainland white-footed mice (*Peromyscus leucopus*) in southeastern Massachusetts. Canadian Journal of Zoology **62**:58–64.

Bard, G. E. 1952. Secondary succession on the Piedmont of New Jersey. Ecological Monographs **22**:195–215.

Berkowitz, A. R., C. D. Canham, and V. R. Kelly. 1993. Net effects of right-of-way communities on tree seedling growth and survival. Pages 271–298 *in* C. D. Canham, editor. Vegetation dynamics along utility rights-of-way: factors affecting the ability of shrub and herbaceous communities to resist invasion by trees. Final Technical Report. Empire State Electric Energy Research Corporation, Altamont, New York, USA.

Boeken, B., and C. D. Canham. 1993. Dynamics of gray dogwood (*Cornus racemosa*) thickets. Pages 47–72 *in* C. D. Canham, editor. Vegetation dynamics along utility rights-of-way: factors affecting the ability of shrub and herbaceous communities to resist invasion by trees. Final Technical Report. Empire State Electric Energy Research Corporation, Altamont, New York, USA.

Bramble, W. C., and W. R. Brynes. 1976. Development of a stable, low plant cover on a utility right-of-way. Pages 167–176 *in* R. Tillman, editor. Proceedings of the first national symposium on environmental concerns in rights-of-way management. Mississippi State University, Starkville, Mississippi, USA.

Bramble, W. C., and W. R. Brynes. 1983. Thirty years of research on development of plant cover on an electric transmission right-of-way. Journal of Arboriculture **9**:67–74.

Brown, V. K. 1985. Insect herbivores and plant succession. Oikos **44**:17–22.

Brown, V. K., and A. C. Gange. 1989. Differential effects of above- and below-ground insect herbivory during early plant succession. Oikos **54**:67–76.

Buell, M. F., H. F. Buell, J. A. Small, and T. G. Siccama. 1971. Invasion of trees in secondary succession on the New Jersey Piedmont. Bulletin of the Torrey Botanical Club **98**: 67–74

Burton, P. J., and F. A. Bazzaz. 1991. Tree seedling emergence on interactive temperature and moisture gradients and in patches of old-field vegetation. American Journal of Botany **78**:131–149.

Canham, C. D., and D. M. Wood. 1993. The component communities of vegetation mosaics along rights-of-way. Pages 31–46 in C. D. Canham, editor. Vegetation dynamics along utility rights-of-way: factors affecting the ability of shrub and herbaceous communities to resist invasion by trees. Final Technical Report. Empire State Electric Energy Research Corporation, Altamont, New York, USA.

DeSteven, D. 1991*a*. Experiments on mechanisms of tree establishment in old-field succession: seedling emergence. Ecology **72**:1066–1075.

———. 1991*b*. Experiments on mechanisms of tree establishment in old-field succession: seedling survival and growth. Ecology **72**:1076–1088.

Dreyer, G. D., and W. A. Niering. 1986. Evaluation of two herbicide techniques on electric transmission rights-of-way: development of relatively stable shrublands. Environmental Management **10**:113–118.

Facelli, J. M., and S. T. A. Pickett. 1991. Plant litter: its dynamics and effects on plant community structure. Botanical Review **57**:1–32.

Fox, L. R., and P. A. Morrow. 1986. On comparing herbivore damage in Australian and north temperate systems. Australian Journal of Ecology **11**:387–393.

Gill, D. S., and P. L. Marks. 1991. Tree and shrub seedling colonization of old fields in central New York. Ecological Monographs **61**:183–206.

Gleason, H. A., and A. Cronquist. 1963. Manual of vascular plants of Northeastern United States and adjacent Canada. Van Nostrand, New York, New York, USA.

Glitzenstein, J. S., C. D. Canham, M. J. McDonnell, and D. R. Streng. 1990. Effects of environment and land-use history on upland forests of the Cary Arboretum, Hudson Valley, New York. Bulletin of the Torrey Botanical Club **117**:106–122.

Goldberg, D. E., and K. L. Gross. 1988. Disturbance regimes of midsuccessional old fields. Ecology **69**:1677–1688.

Harrison, J. S., and P. S. Werner. 1984. Colonization by oak seedlings into a heterogeneous successional habitat. Canadian Journal of Botany **62**:559–563.

Hill, M. O. 1979. TWINSPAN: a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Cornell University, Section of Ecology and Systematics, Ithaca, New York, USA.

Huntly, N. 1991. Herbivores and the dynamics of communities and ecosystems. Annual Review of Ecology and Systematics **22**:477–503.

Krefting, L. W., M. H. Stenlund, and R. K. Seemel. 1966. Effect of simulated and natural deer browsing on mountain maple. Journal of Wildlife Management **30**:481–488.

Marks, P. L. 1983. On the origin of the field plants of the Northeastern United States. American Naturalist **122**:210–228

McDonnell, M. J., and J. M. Koch. 1993. Woody plant seed dynamics in powerline corridors located in southern New York. Pages 87–128 *in* C. D. Canham, editor. Vegetation dynamics along utility rights-of-way: factors affecting the ability of shrub and herbaceous communities to resist invasion by trees. Final Technical Report. Empire State Electric Energy Research Corporation, Altamont, New York, USA.

McDonnell, M. J., D. Van Dorp, and J. M. Koch. 1993. Influence of vegetation structure and landscape configuration on woody seed predation along powerline corridors. Pages 128–142 *in* C. D. Canham, editor. Vegetation dynamics along utility rights-of-way: factors affecting the ability of shrub and herbaceous communities to resist invasion by trees. Final Technical Report. Empire State Electric Energy Research Corporation, Altamont, New York, USA.

Niering, W. A., G. D. Dreyer, F. E. Egler, and J. P. Anderson, Jr. 1986. Stability of a *Virburnum lentago* shrub community after 30 years. Bulletin of the Torrey Botanical Club **113**:23–27.

Niering, W. A., and F. E. Egler. 1955. A shrub community of *Virburnum lentago,* stable for twenty-five years. Ecology **36**:356–360.

Niering, W. A., and R. H. Goodwin. 1974. Creation of relatively stable shrublands with herbicides: arresting "succession" on rights-of-way and pasturelands. Ecology **55**: 784–795.

Ostfeld, R. S. 1988. Fluctuations and constancy in populations of small rodents. American Naturalist **131**:445–452.

Ostfeld, R. S., and C. D. Canham. 1993. Effects of meadow vole population density on tree seedling survival in old fields. Ecology **74**:1792–1801.

Pound, C. E., and F. E. Egler. 1953. Brush control in southeastern New York: fifteen years of stable tree-less communities. Ecology **34**:63–73.

Rankin, W. T., and S. T. A. Pickett. 1989. Time of establishment of red maple (*Acer rubrum*) in early oldfield succession. Bulletin of the Torrey Botanical Club **116**:182–186.

Rose, R. K., and E. C. Birney. 1985. Community ecology. Pages 310–339 *in* R. H. Tamarin, editor. Biology of New World *Microtus*. American Society of Mammalogy Special Publication **8**.

SAS Institute. 1987. SAS/STAT guide for personal computers. Version 6 edition. SAS Institute, Cary, North Carolina, USA.