Tree and Shrub Seedling Colonization of Old Fields in Central New York

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TREE AND SHRUB SEEDLING COLONIZATION OF OLD FIELDS IN CENTRAL NEW YORK[1]

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Abstract. The main objective of this study was to determine the important mechanisms regulating woody plant establishment in recently abandoned agricultural fields in central New York. The study focused on the early life stages, from the dispersal of seeds to the fate of seedlings at the end of the second growing season, of common old-field invaders, primarily *Acer rubrum, Pinus strobus, Cornus racemosa,* and *Rhamnus cathartica.* We investigated patterns of survivorship and causes of mortality during each of these life stages in microsites dominated by previously established herbs and in experimental openings in the herb canopy.

Establishment of a tree or shrub seedling was much less likely from seeds landing among herbs than in openings. During the fall, seed predation by mice, especially under the cover of herbs (median of averages across all species = 6% in open, 85% under herbs), was an important process regulating the relative abundance and spatial distribution of seeds after dispersal. Seedling emergence rates were generally quite low, but for most species tended to be greater in the presence of perennial herbs (12%) and were lower under annuals and biennials (7%) and in bare soil (6%). For cohorts of seedlings followed for two growing seasons (Experiment 6A), some mortality occurred due to frost heaving (17% in open, 4% under herbs) and apparent heat stress or desiccation during the summer (5% in open, 0% under herbs); however, the largest source of mortality, especially under the herb canopy, was predation by rodents, especially meadow voles (6% in the open, 62% under herbs). Competition with herbs, especially aboveground competition, significantly reduced growth of woody seedlings. In spite of growth reduction in the presence of herbs, there was no significant relationship between seedling size and survivorship within any treatment, indicating that mortality could not be directly attributed to competition.

For different species, and at different life stages, support was found for all three of the succession models of Connell and Slatyer (1977). The tolerance model was supported in some cases of seed predation (Experiment 2), seedling emergence (Experiments 4 and 5, in part), and seedling predation (Experiment 7). The facilitation model was supported in some cases by increased seedling emergence (Experiments 4 and 5, in part) and increased seedling survivorship in the presence of herbs during periods of environmental stress (Experiments 6A and 8). The inhibition model was also supported in some cases of decreased growth (Experiment 6B) and decreased survival of seeds and seedlings (Experiments 1, 3, 6A, and 8) in the presence of herbs. The lower survivorship under herbs was largely the result of seed and seedling predation, which were the two most important processes regulating tree and shrub colonization of old fields in this study. Reduced growth of later colonists due to competition with earlier colonists is considered *direct* inhibition, while increased mortality due to predation on later colonists caused by animals whose activity is necessarily associated with the presence of earlier colonists is considered *indirect* inhibition. Seed and seedling predation are potentially important mechanisms regulating succession and should be explicitly included in studies of succession.

Key words: Acer rubrum; *central New York; competition;* Cornus racemosa; *field experiments; old-field succession;* Pinus strobus; Rhamnus cathartica; *seed predation; seedling predation; successional mechanisms.*

INTRODUCTION

Herbaceous plants dominate the early stages of succession of abandoned agricultural lands in the eastern

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United States because they are present at the time of abandonment either as buried seeds or as established plants. Woody plants eventually become established and dominant so that forests or shrublands develop on most sites (e.g., Billings 1938, Oosting 1942, Bard 1952, Bazzaz 1968, Buell et al. 1971, Keever 1979, Pickett 1982, Monk 1983). The colonization of an old field by tree and shrub seedlings is affected by several processes including seed dispersal, seed predation, seedling emer-

gence, seedling predation, and seedling competition with neighboring plants. The relative importance of these processes in regulating woody plant colonization during succession is not well understood because most studies have been observational rather than experimental (Connell and Slatyer 1977, Van Hulst 1978, Finegan 1984), and none to our knowledge has experimentally examined several of these processes throughout the early life stages of trees and shrubs invading abandoned agricultural land.

Woody plants lack a buried seed pool in agricultural soils in central New York (Gill 1987) and probably throughout the eastern United States (cf. Egler 1954), which means that the invasion of abandoned fields by woody plants is initiated by recent seed dispersal from nearby trees and shrubs. The availability of open microsites for incoming seeds decreases rapidly during the first few years of abandonment, and a major goal of this study was to investigate the subsequent success of seeds raining into open microsites vs. microsites already dominated by herbs.

Connell and Slatyer's (1977) seminal paper stimulated many experimental investigations of how well their three models described the influence of early colonists in a succession on the invasion and growth of later colonists. Connell and Slatyer's suggestion, that the three models are alternative hypotheses, has been criticized because more than one model may apply in a given sere (Pickett et al. 1987, Walker and Chapin 1987). Recently, Connell et al. (1987) emphasized that their models were intended to describe the *net* effect of an earlier species on a later one, and suggested that the net effect may be produced by the interaction of several processes. If we are to understand what regulates species colonization during succession, then we must determine the relative importance of the actual mechanisms underlying the observed net effects described by the models (e.g., Pickett et al. 1987). For instance, if later successional species have markedly less success invading under previously established herbs compared to open areas, then we would reject the facilitation and tolerance models, and accept the inhibition model (Table 1). Although the mechanistic basis of inhibition is usually assumed to be greater competition for resources under established plants (e.g., Connell and Slatyer 1977), seed and seedling predation, susceptibility to pathogens, and allelochemical suppression are additional possible mechanisms that could inhibit establishment under an intact canopy relative to openings (Grubb 1977).

In the present study we conducted a series of field experiments to determine whether the establishment of tree and shrub species that are common invaders of recently abandoned agricultural fields in central New York (Table 2) is facilitated, inhibited, or unaffected by the presence of herbaceous plants. Our study concentrated on processes affecting seeds and 1- to 2-yr-old seedlings because survival through each of these stages is necessary to permit establishment, and mortality is likely to be high. We identified those processes that significantly affected survivorship during each life stage for a given species as important mechanisms regulating tree and shrub seedling establishment in old fields.

METHODS

Sites and species

We focused on the first 2 yr of woody plant establishment in fields abandoned from agriculture in Tompkins County, New York, USA. The study sites were primarily fields with moderately well-drained soils that were abandoned from corn production. The sites were selected because they had vegetation typical of recently abandoned fields in the local area. Location, history, vegetation at the time of study, and soils at each site are described in the Appendix. The species selected for study were trees and shrubs that commonly invade recently abandoned fields (Table 2).

Preliminary investigations of woody seed dispersal into fields indicated too much variation for a systematic study based on naturally dispersed seeds. Consequently, our study concentrated on the fate of experimentally placed seeds and seedlings. The particular set of species used in a given experiment was determined by the availability of a sufficient number of seeds, or of recently germinated seedlings, at the time of initiation of that experiment.

Seed predation under herbs and in openings

The effects of the presence or absence of previously established herbs on predation rates on tree and shrub seeds were examined in the following three experiments. These experiments were conducted during October and November, during or after the main period of natural seed dispersal. Gloves were worn as seeds were set out during the late afternoon when each experiment was initiated. Because the major objective of these experiments was to test the ability of predators to detect and consume seeds under herbs compared to in openings, rather than their ability to learn that seeds were regularly available at the fixed experimental sites, these experiments were terminated after 6–7 d.

Experiment 1: Effects of herb cover on seed predation—1985.—In an area of fairly continuous herbaceous cover (75–100 cm tall) in a 2-yr-old field (Turkey Farm), nine openings 200 × 200 cm were created by cutting the herb shoots to ≈3 cm tall in nine randomly located plots. On 17 October 1985, an open, clear plastic petri dish (8.8 cm diameter, 1.3 cm deep) with five seeds each of *Acer rubrum, Pinus strobus,* and *Rhamnus cathartica* was placed in the middle of each of these openings and in a randomly located "control" under the herb canopy 200 cm away from each opening. Seed disappearance was measured the following morning, and again 3 and 6 d after setting out the seeds.

The data, even after transformation, were too highly

TABLE 1. Seeds or seedlings of later species in the sere can be transplanted and grown with and without earlier species to test the three models of plant–plant interactions (F = Facilitation, T = Tolerance, I = Inhibition) of Connell and Slatyer (1977).*

If invasion and growth after removal of earlier species are	Models rejected	Model supported and possible causal mechanisms
Decreased significantly	I and T	*Direct facilitation* Environmental amelioration
		Indirect facilitation Attracting seed dispersal agents Mycorrhizal inoculum
Increased significantly	F and T	*Direct inhibition* Competition (Resource or space monopolization) Allelopathy
		Indirect inhibition Predation Herbivory Associated pathogens
No significant difference	F and I	*Active tolerance* Physiological tolerance of low resource levels
		Passive tolerance Life history differences (growth rate, longevity)

* We have separated each model into two distinct components: facilitation and inhibition can be caused by *direct* (plant–plant) and *indirect* (early plant-associated animal–later plant) mechanisms; *active* and *passive* tolerance were distinguished by Pickett et al. (1987). We propose a set of general mechanisms that could produce effects consistent with the subcomponents of each model (see *Discussion: General models of colonization during secondary succession* for additional details).

skewed to meet the assumptions necessary for analysis of variance, so the Wilcoxon two-sample test was used to analyze for effects on seed disappearance due to treatment within each species, and the Kruskal-Wallis test was used to test for differences among species within each treatment (Sokal and Rohlf 1981).

Experiment 2: Effects of herb cover on seed predation—1986.—This experiment was designed to test if openings in the herb canopy smaller than 200 cm across could significantly reduce seed predation rates. Eight experimental blocks were randomly located in the fairly continuous herb canopy (100–150 cm tall) of an ≈10-yr-old field (Hines Road). Randomly located within each block were three experimental openings of different sizes and a "control" where herbs were left intact for at least 200 cm from an experimental opening. By cutting the herb shoots to ≈3 cm tall, experimental openings were created where the minimum distance from herb cover to the center of the openings was either 15, 30, or 45 cm. A clear plastic dish (as in Experiment 1) with five seeds each of *Fraxinus americana, Rhamnus cathartica, Cornus racemosa,* and *Viburnum dentatum* was placed in the middle of each opening and in the control under the herb canopy for each of the eight replicate blocks on 18 November 1986. A substantial snow fall (≈8–10 cm) that evening did not melt sufficiently to measure seed disappearance until 25 November.

Analysis of variance (on arcsine-transformed proportion data of seed disappearance) was performed to test for effects due to treatment, species, blocks, and interactions.

Experiment 3: Effects of herb cover and seed density on seed predation.—To test further the relation between seed disappearance and distance from herb cover, another experiment was initiated on 25 November 1986 in the same field as Experiment 2 (Hines Road).

TABLE 2. Species of trees and shrubs used in the present study. Nomenclature follows Fernald (1950). All species are native to the northeastern United States (except *Rhamnus cathartica*) and commonly invade recently abandoned fields (only rarely for *Quercus rubra*). The primary mode and time of seed dispersal are based on Fowells (1965), Schopmeyer (1974), and our own observations.

Scientific name	Common name	Primary dispersal	
		Mode	Time
Trees			
Acer rubrum	Red maple	Wind	Apr–Jun
Fraxinus americana	White ash	Wind	Sep–Oct
Pinus strobus	White pine	Wind	Sep–Oct
Populus tremuloides	Quaking aspen	Wind	May–Jun
Quercus rubra	Red oak	Squirrel, Bird	Sep–Oct
Shrubs*			
Cornus racemosa	Gray dogwood	Bird	Sep–Oct
Rhamnus cathartica	Common buckthorn	Bird	Sep–Apr
Rhus typhina	Staghorn sumac	Bird	Sep–Apr
Rubus allegheniensis	Blackberry	Bird	Aug–Sep
Viburnum dentatum	Arrow-wood	Bird	Sep–Oct

* Fruits of shrubs tend to remain attached to the plant after ripening and the time of dispersal depends largely on the rate of removal by birds. Dispersal time is therefore primarily based on fruit preference, which locally is *Rubus > Cornus > Viburnum >>> Rhamnus > Rhus.*

To set up this experiment quickly, a new design was used to avoid the time-consuming process of randomly locating plots and cutting out different size openings in the herbs as in Experiments 1 and 2. Half of the experimental area was mowed to ≈3 cm in height to create an open strip ≈4 × 25 m adjacent to an area of fairly intact herb cover. Ten transects, 200 cm apart, were run from under the herbs out into the experimental opening. Along each transect, at 200 cm into the herb cover, and at 15, 30, 45, and 100 cm out into the open, a roofing nail (head diameter ≈1.5 cm) was stuck in the ground to mark the site of seed placement. To test the effects of seed density in addition to distance from cover on rates of seed predation, half of the 10 transects were randomly selected to have one seed, and the others five seeds, of *Cornus racemosa* at each distance. In this experiment we used seeds of only one species so that testing the effects of density would not be confounded by a mixture of seeds of differing preference. Seed disappearance was measured the following morning, and again 3 and 6 d after setting out the seeds.

Analysis of variance (on arcsine-transformed proportion data of seed disappearance) was performed to test for effects due to treatment, seed density, and interactions.

Seedling emergence experiments

The effects of the presence or absence of established herbs on the emergence of tree and shrub seedlings were examined in the following two experiments. A 15-yr-old field (Teaching Farm, plot number 21) with a fairly uniform herb canopy dominated by goldenrods (*Solidago* spp.) and grasses (mostly *Phleum pratense*) was selected for these experiments. Seeds were collected locally from many individuals at several sites when possible; however, seeds of *Acer rubrum* were collected from a single felled tree for Experiment 4, and were purchased (collected in Massachusetts) for Experiment 5, and seeds of *Fraxinus americana* and *Pinus strobus* were purchased (collected in Massachusetts) for both Experiments 4 and 5. Seeds with obvious defects were excluded, and casual examination of embryos in a subsample of the seeds used suggested most were viable. In both experiments seeds were sown at "points" of known coordinates to allow relocating the same seeds over time; therefore, the seeds were planted 0.5 cm into the mineral soil to reduce the chances of their being washed away from these points.

Experiment 4: Effects of herb cover on seedling emergence—Late spring sowing.—The effects of creating openings in two types of herb canopies on the emergence of tree and shrub seedlings were examined in an experiment initiated in May and June 1983. The four treatments were designed to simulate conditions (1) under the canopy of the goldenrod–grass stage of succession (=intact 15-yr-old herbs), (2) in openings in the canopy of the goldenrod–grass stage (=15-yr-old herbs regularly clipped to 10 cm tall), (3) under the canopy

of early successional herb species arising from buried seeds (=1-yr-old herbs), and (4) in completely barren openings that tend to occur only during the first few years after abandonment (=bare soil). In the clipped 15-yr-old herb treatment, shoots of herbs were cut to only 10 cm, so emerging woody seedlings would not be cut off accidentally. In both the intact and clipped 15-yr-old herb treatments the litter layer was left intact but in the clipped herb treatment the shoots were removed after clipping. The 1-yr-old herb and bare soil treatments were imposed by spraying the perennial herbs that dominated the site with a systemic herbicide (2% solution of Roundup, active ingredient glyphosate) on 22 May 1983. Glyphosate effectively kills shoots, roots, and rhizomes of plants it contacts; however, it is rapidly detoxified in the soil and does not inhibit subsequent germination of seeds (Nomura and Hilton 1977, Torstensson and Aamisepp 1977, Marks and Mohler 1985). Most of the sprayed plants were dead by 5 June 1983 when the soil on these plots was thoroughly tilled with a rotary tiller to a depth of ≈15 cm. Half of these plots were allowed to revegetate through abundant germination of seeds of annual and short-lived perennial herbs (e.g., *Ambrosia artemisiifolia, Barbarea vulgaris, Setaria glauca, Panicum capillare, Chrysanthemum leucanthemum,* etc.) buried in the soil, and this treatment produced a vegetation similar to that on fields during the first year of abandonment from agriculture (Marks and Mohler 1985). In the other half of these plots all emerging seedlings and vegetative sprouts were regularly removed by carefully cutting their shoots at the ground level to create a bare, but minimally disturbed, soil surface.

Two replicate plots (3.5 × 1.5 m) of each treatment were randomly located within an area of 12 × 24 m on moderately well-drained soils, and another complete set of plots was located ≈25 m away, and 2 m lower in elevation, on less well-drained soils. On 9–11 June 1983, seeds of three tree species (*Acer rubrum, Fraxinus americana, Populus tremuloides*) and two shrub species (*Cornus racemosa, Viburnum dentatum*) were sown into the plots. The number of seeds per species was 60 per replicate plot ($n = 240$ seeds of each species per treatment in complete design), except for *Cornus* where available supply allowed only nine per replicate ($n = 36$ seeds of each species per treatment in complete design). Seeds of *Fraxinus, Cornus,* and *Viburnum* (with fall seed dispersal) were stratified between layers of moist, paper towels for ≈3 mo at 2°–4°C, while seeds of *Acer* and *Populus* (with spring seed dispersal) were not treated, prior to sowing.

On four occasions between 11 June 1983 and 29 July 1983 the plots were carefully checked for emerging seedlings and herb shoots were clipped to maintain the integrity of the bare soil and 15-yr-old clipped herb treatments. Every 3–4 wk during the remainder of the 1983 growing season the plots were checked for emerging seedlings and the clipping treatments were main-

tained. Regular observations for emergence and maintenance of treatments were continued in 1984 from early May to early October.

Analysis of variance (on arcsine-transformed proportion data of seedling emergence) was performed to test for effects due to treatment, soil drainage, blocks, and interactions.

Experiment 5: Effects of herb cover on seedling emergence—Fall sowing.—Since the seeds of many woody pioneer species are dispersed in the fall, Experiment 5 was designed to investigate the effects of herb cover on emergence of seeds sown in the fall. This experiment was set up adjacent to Experiment 4 and was similar to Experiment 4 in many ways. The most important differences were: only three treatments were used (intact 15-yr-old herbs, 1-yr-old herbs, and bare soil); there were six replicate plots (3.5 × 1.5 m, with random assignment of the three treatments to 0.75 × 0.50 m subplots each) within each of the two levels of soil drainage; and, five additional species (*Pinus strobus, Quercus rubra, Rhamnus cathartica, Rhus typhina,* and *Rubus alleghcniensis*) were used so that most of the common woody pioneer species in local old fields were represented. While *Quercus rubra* rarely invades recently abandoned fields, we used it to investigate possible effects of seed size on seedling emergence because it has much larger seeds than the other species. None of the seeds were cold-stratified, but half of the seeds of the shrub species, which are primarily dispersed by birds, were treated in concentrated sulfuric acid for 1 h to help scarify their seed coats. The bare soil and 1-yr-old herb treatments were imposed as in Experiment 4 by applying herbicide on 9 October 1983, and rototilling on 20 October 1983. Seeds were sown (20 seeds per species per replicate plot, except for *Quercus* where only 10 seeds were sown; *n* = 240 and 120 seeds of each species per treatment in complete design, respectively) during the last week of October and first week of November 1983. Unlike Experiment 4, some seeds (especially *Quercus* and non-acid-treated *Cornus*) were dug up by small mammals within 1–2 d of planting. These seeds were replaced and hardware cloth exclosures were then placed over each plot with their sides buried ≈10 cm into the ground. The exclosures were removed in late April 1984 and seedling emergence was monitored, and treatments were maintained, every 6–9 d until late June and every 2–3 wk until mid-August 1984.

Analysis of variance (on arcsine-transformed proportion data of seedling emergence) was performed to test for effects due to treatment, soil drainage, blocks, and interactions.

Seedling survivorship and growth under herbs and in openings

The effects of the presence and absence of previously established herbs on recently emerged seedlings transplanted into the field were examined in the following experiments. Experiment 6 tested the effects of herb cover on patterns of survivorship (6A) and growth (6B), and Experiment 7 tested the effects of sizes of openings in the herb canopy on survivorship. Survivorship patterns of seedlings transplanted under plant canopies in different fields and under different types of plant canopies within a single field were investigated in Experiment 8. To obtain seedlings for these experiments, seeds of *Acer rubrum, Pinus strobus,* and *Fraxinus americana* (all collected commercially in Massachusetts) and of *Cornus racemosa, Rhamnus cathartica,* and *Viburnum dentatum* (all collected locally) were planted into flats in early May of 1985 and again in 1986, and were kept out doors in full sunlight to germinate. Seeds were cold-stratified for ≈3 mo before sowing. Due to low germination rates (Gill 1987) only two or three of these species could be used in a given experiment. Seedlings were transplanted into treatments along with a root-ball of soilless potting mix (Promix BX) of ≈3.5 × 3.5 × 4.5 cm.

Experiment 6A: Effects of herb cover on seedling survivorship.—This experiment was designed to test the effects of already established herbs on the survivorship of recently emerged woody seedlings transplanted into a 2nd-yr field (Turkey Farm). The experiment was also used to test the effects of aboveground vs. belowground competition with herbs on the growth of the surviving woody seedlings (see *Methods: Experiment 6B* below for details). To partition the effects of herbs on woody seedlings into aboveground and belowground components, the roots and shoots of herbs were variously segregated from the roots and shoots of woody seedlings (Fig. 1). The four treatments used were intended to create conditions of no aboveground or belowground effects (A−B−), only belowground effects (A−B+), only aboveground effects (A+B−), and both aboveground and belowground effects (A+B+). The experiment was a random complete block design with each of the four treatments randomly assigned twice into eight sets of plots (1.5 × 2 m) within each of the nine replicate blocks (10 × 14 m). The soil in all experimental plots was excavated to a depth of ≈15 cm with a mattock to produce fairly uniform trenches 200 cm long × 8 cm wide × 15 cm deep running down the center of the plot. The excavated soil from the trenches within each block was pooled, and carefully sifted through a 1.27-cm mesh sieve to remove living rhizomes. Prior to refilling the trenches with the soil, the sides of plots in which belowground interactions were to be eliminated (B−) were lined with plywood partitions. To prevent roots of herbs from growing past the partitions, a machete was slid along the outside of the partitions to a depth of ≈20 cm once a month. In plots in which aboveground interactions were to be eliminated (A−), poultry wire (2.54-cm mesh) was anchored to the ground on either side of the 8 cm wide trench and extended away from it at ≈45° for a distance of ≈75 cm. The shoots of herbs growing through the wire mesh were
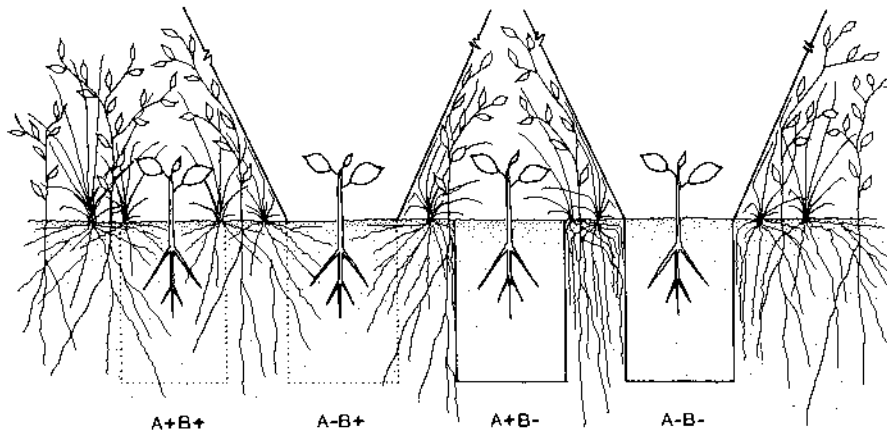
Fig. 1. Schematic cross-sectional diagram of the four treatments in Experiment 6A and B. Recently emerged seedlings of trees and shrubs (shown in bold with three leaves each) were transplanted into the center of each treatment plot: A+B+ (=both aboveground and belowground interactions with previously established herbs), A−B+ (=belowground interactions only), A+B− (=aboveground interactions only), A−B− (=no aboveground or belowground interactions). Horizontal scale is greatly compressed; the centers of adjacent plots were 1.5 m apart in the field. See *Methods: Seedling survivorship and growth under herbs and in openings: Experiment 6A* and *Experiment 6B* for more details.

gently pulled back under the mesh every 2–3 wk to maintain the integrity of the aboveground treatment. It was assumed that bending the herb shoots without breaking them would not seriously affect the root growth of the herbs so that aboveground interactions could be effectively eliminated without altering belowground interactions (i.e., for the A−B+ treatment). The effective dimensions of the opening in the herb canopy in which aboveground effects were eliminated (A−) were 200 cm long and 8 cm wide at the ground surface, but ≈150 cm wide at 75 cm above ground, due to the sloping of the poultry wire.

During the 1st wk of August 1985, three seedlings each of *Acer rubrum*, *Pinus strobus*, and *Rhamnus cathartica* were planted into randomly selected locations 15 cm apart from each other along the center of each experimental plot (n = 54 seedlings of each species per treatment in complete design). The seedlings had emerged ≈10 wk earlier, and possessed several leaves. Survivorship and probable causes of death of seedlings were recorded weekly during August, and once a month during September and October 1985. Survivorship and apparent causes of death over the winter and spring were recorded in early June 1986 soon after seedlings had leafed out, and every 3–6 wk until late October 1986.

Due to a large loss of seedlings during 1985 caused by small mammal predation (see *Results: Experiment 6A*), an exclosure was set up in late May 1986 to insure that a large enough sample of seedlings would survive until the mid-October 1986 harvest (see *Methods:* and *Results: Experiment 6B*). The entire experimental site was surrounded by the exclosure (30 cm wide aluminum flashing), which was buried ≈10 cm deep and extended ≈20 cm aboveground to prevent rodent entry. An extensive network of traps was set up to remove any rodents remaining inside the exclosure.

During the 2nd wk of June 1986, another set of two recently emerged (≈1 mo old) seedlings of *Pinus strobus*, *Rhamnus cathartica*, and *Cornus racemosa* were planted in each experimental plot into randomly selected spots previously occupied by seedlings that were lost during 1985 (n = 36 seedlings per species in each treatment in complete design). The *Cornus* seedlings were from the seeds sown during May 1985 but which did not emerge until May 1986, and were used instead of *Acer*, which had poor emergence in 1986.

The importance of different sources of mortality across treatments was tested on the number of seedlings killed using a chi-square (χ^2) test of independence (Sokal and Rohlf 1981).

Experiment 6B: Aboveground and belowground effects of herbs on woody seedling growth.—This experiment was designed to test the effects of aboveground and belowground competition with already established herbs on the growth of recently emerged woody seedlings. We planned to harvest half of the seedlings in October 1985, but did not because so many seedlings had been destroyed by rodents (see *Results: Experiment 6A*). In mid-October 1986, all 5-mo-old (≈1 mo old when planted in the field in June 1986) and all 17-mo-old (≈2 mo old when planted August 1985) seedlings were harvested. The roots were carefully excavated, and the soil was washed off. Seedlings were separated into root, stem, and leaf fractions, which were oven-dried (≈80° for 2–3 d) and then weighed.

Analysis of variance (on $\log_{10}$-transformed dry mass data) was performed to test for effects due to treatment, blocks, and interactions. A *t* test was performed on linear contrasts (Sokal and Rohlf 1981) of log-transformed dry mass data to test the hypotheses that competition suppressed growth (mean woody seedling dry mass in A−B− > in A+B+) and that aboveground competition with herbs suppressed growth more than

belowground competition (mean seedling dry mass in A+B− < in A−B+).

Various environmental measurements were taken in each treatment. During 1985 photosynthetic photon flux density (PPFD, 400–700 nm) at 10 cm was measured with a hand-held quantum sensor (LI-COR LI-190SB) and a quantum meter (LI-COR LI-185B) every 2–3 wk. From 1 August to 4 September 1986, PPFD at 10 cm was measured with four quantum sensors (one randomly located in each treatment within a single block) attached to a Campbell Scientific CR 21 datalogger. The sensors were relocated to different blocks every 3–6 d. On several occasions during both 1985 and 1986, soil temperature at 1 and 10 cm depth, air temperature at 10 cm aboveground, and temperature of leaves of *Cornus* and *Rhamnus* were measured with a Wescor TC Thermocouple Thermometer TH60. Local rainfall data were obtained from the Game Farm Road station (NOAA 1985 and 1986) ≈1.2 km from the study site. During both the 1985 and 1986 growing seasons relative soil moisture at 10 cm was measured with nine Beckman CEL-WFD gypsum blocks per treatment attached to a Soil Moisture Equipment 5091A electrical resistance meter. Predawn xylem pressure potential (XPP) for *Cornus* and *Rhamnus* was measured with a Soil Moisture Equipment Model A nitrogen-gas pressure chamber on nine seedlings per treatment on 31 August 1986. Measurements of XPP were only made once because they required destructive harvesting of seedlings. The date of measurement was selected because it was 3 d after a rain, the typical duration between rains in this area during the summer (NOAA 1985 and 1986).

Experiment 7: Effects of size of openings in herb cover on seedling survivorship.—This experiment was designed to test how the size of openings in the herb canopy affected seedling survivorship. Eight experimental blocks were randomly located in the fairly continuous herb canopy (100–150 cm tall) of an ≈10-yr-old field in the goldenrod–grass stage (Hines Road). Four treatments were randomly located within each block: a "control" where herbs were left intact for at least 200 cm from an experimental opening, and openings of three sizes created by cutting the herb shoots to ≈3 cm tall so that the minimum distance from herb cover to the center of the openings was either 15, 30, or 45 cm. On 30 June 1986, two 1-mo-old seedlings each of *Pinus strobus* and *Rhamnus cathartica* were planted in the middle of each opening and in the randomly located control within each block (*n* = 16 seedlings of each species per treatment in complete design). Seedling survivorship was recorded every 2 wk from 2 July to 14 November 1986.

The seedling survivorship data, even after transformation, were too highly skewed to meet the assumption necessary for analysis of variance, so Friedman's test for randomized blocks (Sokal and Rohlf 1981) was used to analyze for effects due to treatment and blocks within each species.
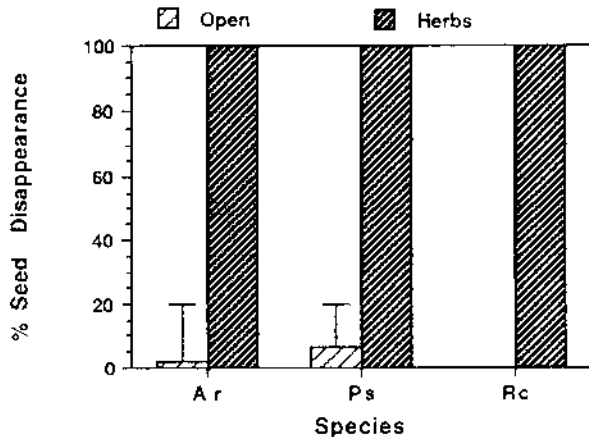

FIG. 2. Disappearance of seeds in Experiment 1 on 23 October 1985, 6 d after setting out the seeds, of *Acer rubrum* (Ar), *Pinus strobus* (Ps), and *Rhamnus cathartica* (Rc) expressed as a percentage of seeds placed (*n* = 5 seeds/species) in each of nine replicates of the following two treatments: (1) in the open, 100 cm from herb cover; (2) under herbs, 200 cm away from openings. Error bars are the maximum seed disappearance observed in any replicate in the open.

Experiment 8: Seedling survivorship under canopies of different successional ages.—The relative importance of various sources of seedling mortality under herb and shrub canopies typical of a range of early successional fields was investigated in a number of different experimental habitats (40 × 40 m each) at the Teaching Farm: two plots in active corn production (Teaching Farm plots numbers 1 and 3); two plots abandoned from corn for 1 yr (numbers 2 and 6); one plot abandoned for 2 yr (number 16); and two of the ≈15-yr-old "controls" (numbers 7 and 10). A site abandoned from corn for 3 yr in the adjacent Turkey Farm was also used (located outside the exclosure around Experiment 6A–B). Patterns of mortality in two widely separated (≈18 km) old fields (Hines Road, Snyder Road) in the goldenrod–grass stage were also investigated.

Two 1-mo-old seedlings of *Pinus strobus* and *Rhamnus cathartica* were transplanted into each of 10 randomly located replicates (*n* = 20 seedlings per species) at each site in late June 1986. Seedling survivorship and probable causes of death were recorded every 2–3 wk from early July to late November of 1986, and again in mid-May and mid-June of 1987.

No statistical analyses were performed on these data because no a priori hypothesis was proposed for testing.

RESULTS

Experiment 1: Effects of herb cover on seed predation—1985.—Seed disappearance over the first night was significantly affected by herb cover, being greater under herbs than at 100 cm into openings (Wilcoxon $U \geq 85.5$, n_1 and $n_2 = 9$, and $P < .001$ for all species). None of the seeds in openings had disappeared, whereas under herbs the mean seed disappearance rate was 84, 93, and 100%, for *Acer*, *Pinus*, and *Rhamnus*, re-
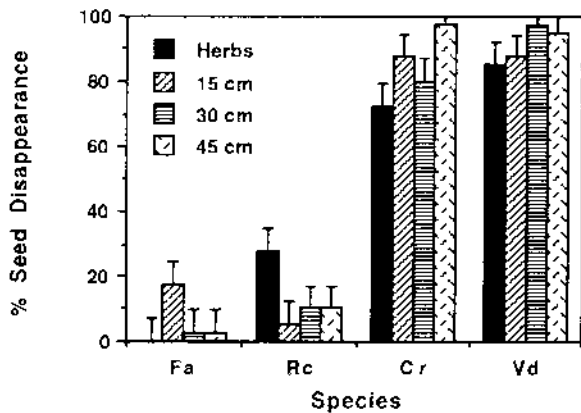
FIG. 3. Disappearance of seeds in Experiment 2 of *Fraxinus americana* (Fa), *Rhamnus cathartica* (Rc), *Cornus racemosa* (Cr), and *Viburnum dentatum* (Vd), expressed as a percentage of seed placed ($n = 5$ seeds/species) in each of eight replicates of the following four treatments: (1) under herb cover, (2) 15 cm, (3) 30 cm, and (4) 45 cm into experimental openings in the herb cover, respectively. Experiment was set out on 18 November 1986; it snowed heavily that evening, and the snow had not melted sufficiently to measure seed disappearance until 25 November 1986. Error bars are +1 SE (pooled across species and treatments, obtained from mean square for error in ANOVA).

spectively. All the remaining seeds of *Pinus* and *Acer* disappeared from under the herbs within 6 d, but only 2, 7, and 0%, of the seeds of *Acer, Pinus,* and *Rhamnus,* respectively, had disappeared from the openings after 6 d ($U \geq 81$, n_1 and $n_2 = 9$, and $P < .001$ for all species; Fig. 2). There were no significant differences among species in either treatment at any time. Based on the disappearance of seeds largely during the night, on the identity of several trapped individuals, and on urine and feces found in the seed dishes, it appeared that most seeds were consumed by small nocturnal rodents, especially deer mice (*Peromyscus* spp.).

Experiment 2: Effects of herb cover on seed predation—1986.—A substantial snowfall (8–10 cm) prevented measuring seed disappearance for 7 d. After 1 wk of being nearly completely covered by snow, there was no statistical difference in the disappearance of seeds due to distance to herb cover, but seed disappearance among species was significantly different ($F_{3,63} = 175.22, P < .001$; Fig. 3). From 72 to 98% of *Cornus* and *Viburnum* seeds disappeared, but only 0 to 28% of *Fraxinus* and *Rhamnus* seeds disappeared when averaged across treatments. In this experiment, and unless noted otherwise in other experiments, there were no significant ($P < .05$) effects due to blocks or interactions.

Experiment 3: Effects of herb cover and seed density on seed predation.—Disappearance of *Cornus* seeds during the first night was significantly ($F_{4,40} = 18.42$, $P < .001$) affected by herb cover, being greater under the herbs than in the open, but there was no significant difference due to seed density (Fig. 4A). Very few seeds were taken in the open, while 80 and 72% of the seeds,

at low and high densities, respectively, were taken from under the herbs. Seed disappearance after 6 d was still significantly ($F_{4,40} = 5.30, P < .005$) affected by herb cover, being greater under herbs (100% at low density, 92% at high density) than in the open (50% at low density, 35% at high density; Fig. 4B). Seed disappearance was significantly ($F_{1,40} = 4.61, P < .05$) affected by seed density after 6 d, being greater along low density transects than high density transects.

Experiment 4: Effects of herb cover on seedling emergence—Late spring sowing.—No tree or shrub seedlings emerged from any treatment during the 1983 season. By 7 May 1984, however, some woody seedlings had started to emerge nearly a full year after sowing. The treatments were maintained and seedling emergence was recorded every 2 wk through the end of July 1984 and monthly from August to October 1984 (no emergence occurred after mid-June). Cumulative
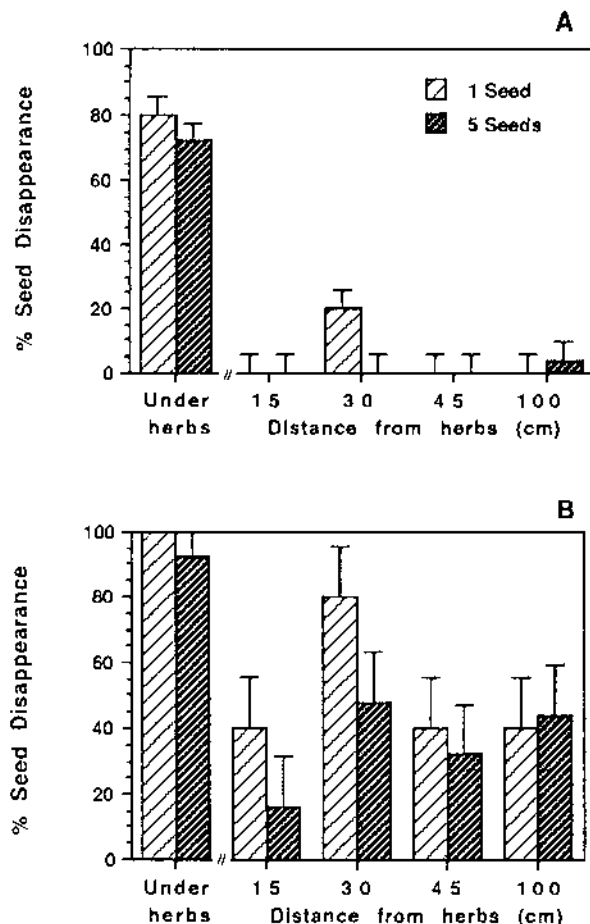
FIG. 4. Disappearance of seeds in Experiment 3 of *Cornus racemosa* expressed as a percentage of seeds placed at two densities ($n = 1$ or 5 seeds) in each of five replicates of the following five treatments: (1) under herb cover (2) 15 cm, (3) 30 cm, (4) 45 cm, and (5) 100 cm into experimental openings in the herb cover, respectively. Experiment was set out on 25 November 1986: (A) 26 November 1986, the morning after setting out seeds; and, (B) 1 December 1986, 6 d after setting out seeds. Error bars are +1 SE (pooled as in Fig. 3).

FIG 5. Cumulative emergence of seedlings in Experiment 4 by 16 June 1984 of *Acer rubrum* (Ar), *Cornus racemosa* (Cr), *Fraxinus americana* (Fa), and *Viburnum dentatum* (Vd), expressed as a percentage of the number of seeds ($n = 240$ seeds of each species per treatment in complete design, except for Cr where $n = 36$) sown during early Jun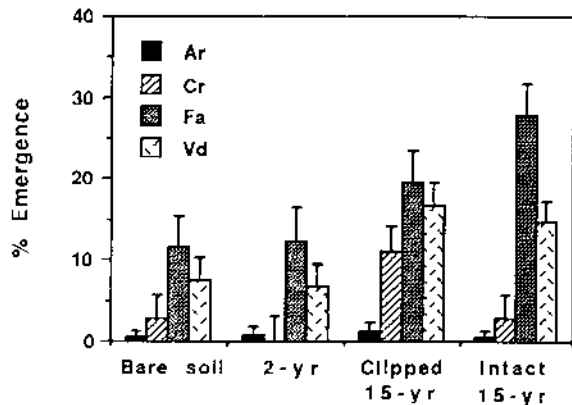e 1983. The four treatments were: (1) bare soil, (2) 1-yr-old herbs (but these were 2 yr old when woody seedlings emerged), (3) 15-yr-old herbs clipped to 10 cm tall, and (4) intact 15-yr-old herbs. Error bars are + 1 sE for each species pooled across treatments.

emergence of *Fraxinus* seedlings was significantly ($F_{3,12} = 3.68$, $P < .05$) different across treatments, being greater in the clipped and intact 15-yr-old herb plots than in the bare soil or 2-yr-old herb plots (Fig. 5). For *Acer, Cornus,* and *Viburnum,* there were no significant differences among treatments; however, emergence tended to be greater in the clipped or intact 15-yr-old goldenrod–grass plots, being $\approx 2\times$ as great as in the bare soil treatments. Seedlings of *Populus* were never observed in this experiment. There were no significant differences in seedling emergence due to soil drainage; however, *Cornus* tended to emerge better (7.9%) in the more poorly drained than in the moderately drained plots (1.4%).

Experiment 5: Effects of herb cover on seedling emer-gence—Fall sowing. —Seedling emergence during 1984 for non-acid-treated *Rhamnus cathartica* was signifi-cantly ($F_{2,10} = 16.35$, $P < .001$) different across treat-ments (Fig. 6). Average cumulative emergence from early May to late June for *Rhamnus* was 28, 7, and 23% in bare soil, the 1-yr-old herb, and the 15-yr-old herb treatments, respectively. There were also signifi-cant ($F_{1,10} = 13.28$, $P < .005$) differences in emergence of *Rhamnus* seedlings due to drainage (13 and 24% in moderately well-drained and less well-drained plots, respectively), and significant ($F_{3,10} = 3.80$, $P < .05$) differences due to interactions between blocks and drainage, and due to interactions between drainage and treatments ($F_{2,10} = 5.14$, $P < .05$). No significant dif-ferences existed for *Pinus,* but seedling emergence tend-ed to be greater under herbs than on bare soil (Fig. 6). During 1984 no seedlings of *Quercus* or acid-treated *Rhamnus* emerged, and only 1–7 seedlings emerged for the other species. Due to the difficulty of maintaining

the integrity of the bare soil treatment (total plot and treated buffer area = 22.5 m²) and the generally low levels of emergence, this experiment was terminated in mid-August 1984, so it is not known whether more seedlings would have emerged during the following spring as happened in Experiment 4, and for *Cornus racemosa* seeds sown in May 1985 for Experiment 6A, and in some greenhouse studies (data not reported).

Experiment 6A: Effects of herb cover on seedling sur-vivorship. —Survivorship from early August to late Oc-tober 1985 was much lower for seedlings growing under herbs than in the open (Fig. 7A–C). The main source of mortality during this period in all treatments was predation by rodents. While many seedlings showed signs of herbivory from rodents, snails, and slugs, we report as predation only incidents of herbivory that led to death of seedlings. Based on the presence of char-acteristic runways through the litter, regular sightings during the day, and the identity of several trapped individuals, most seedling predation was apparently caused by meadow voles (*Microtus pennsylvanicus*). The stem of *Pinus* seedlings was frequently cut diag-onally below the cotyledons, and the intact shoot was often left lying on the ground. For both *Rhamnus* and *Acer,* it was more common to find the root system completely dug up, with a diagonal cut across the root collar just above the ground surface and the shoot often missing. The next largest cause of mortality was the disappearance of seedlings, with no sign of digging or of any plant remains. The presence on the ground of intact roots and shoots of many dead seedlings during the first growing season and into the following June indicated that missing seedlings did not decompose between sample visits. It was assumed, therefore, that missing seedlings had been consumed or removed by predators. Subsequent discussion of predation rates re-fers to the sum of losses from predation and disap-pearance (="Aspred" in Table 3–5). The proportion

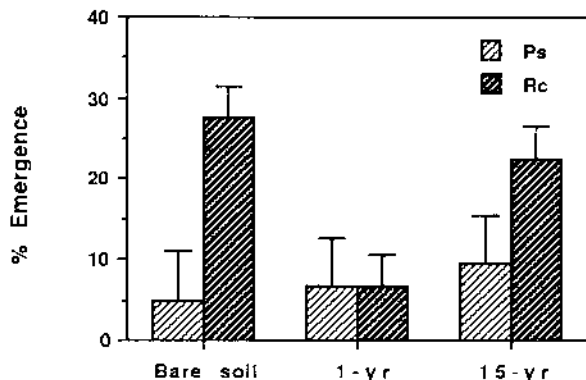FIG. 6. Cumulative emergence of seedlings in Experiment 5 by 24 June 1984 of *Pinus strobus* (Ps) and *Rhamnus ca-thartica* (Rc), expressed as a percentage of the number of seeds ($n = 240$ seeds of each species per treatment in complete design) sown in mid-November 1983 in six replicates each of the following three treatments: (1) bare soil, (2) 1-yr-old herbs, (3) 15-yr-old herbs. Error bars as in Fig. 5.
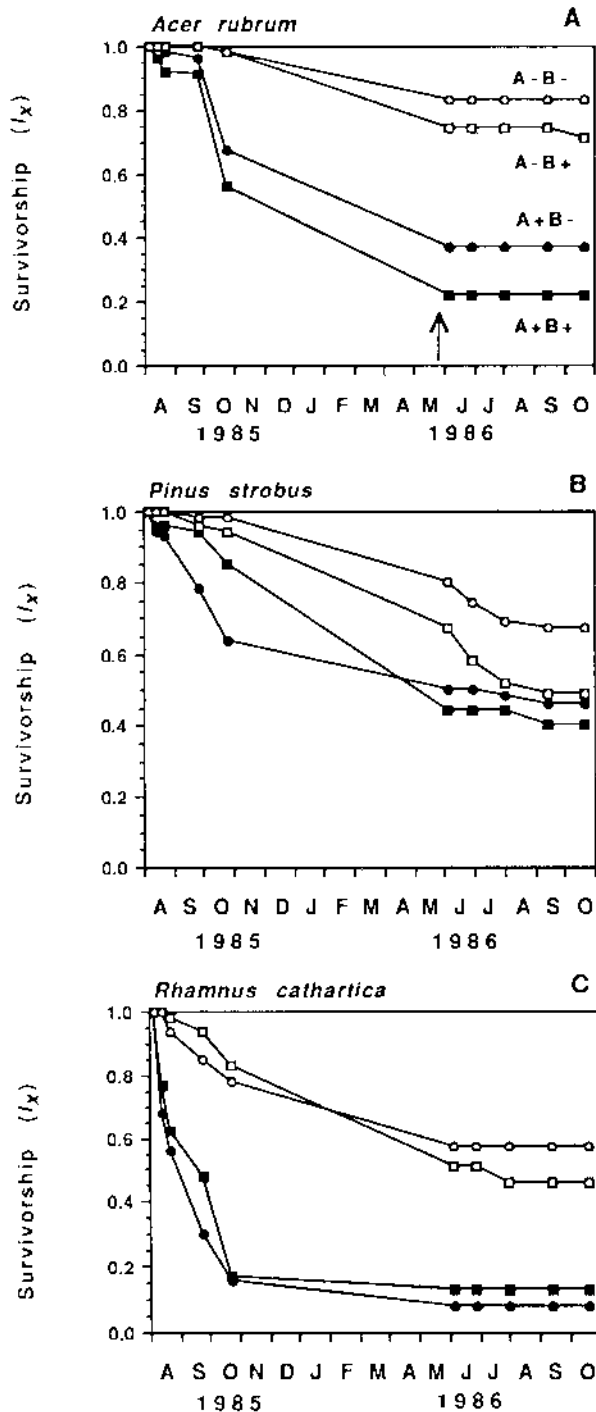
Acer rubrum A

Pinus strobus B

Rhamnus cathartica C

FIG. 7. Survivorship (l_x) of cohorts of 54 seedlings each of *Acer rubrum*, *Pinus strobus*, and *Rhamnus cathartica* in Experiment 6A planted into each of the four treatments (as illustrated in Fig. 1) in early August 1985. A−B− (=no aboveground or belowground interactions with herbs), A−B+ (=belowground only), A+B− (=aboveground only), A+B+ (=both aboveground and belowground). The arrow indicates when the small mammal exclosure was established. No error bars given as there was no replication within treatments, but analyses of specific sources of mortality among treatments at the end of the first growing season (24 October 1985), begin-

of seedlings assumed killed by predators was significantly $(P < .001)$ different across treatments, being ≈20, 9, and 5× as great, on average, under herbs (A+B+ and A+B−) as in the open (A−B+ and A−B−) for *Acer*, *Pinus*, and *Rhamnus*, respectively. (Mortality data and χ^2 values are given in Tables 3–5.)

Mortality rates from October 1985 to June 1986 decreased for all species especially for *Rhamnus* seedlings under herbs (Fig. 7A–C). The major cause of the over-winter mortality in the open (A−B+ and A−B−) was due to frost heaving, causing ≈79, 80, and 62% of seedling mortality during this period for *Acer*, *Pinus*, and *Rhamnus*; frost heaving under herbs (A+B+ and A+B−), in contrast, caused on average only 13, 28, and 40% of seedling mortality in those treatments for *Acer*, *Pinus*, and *Rhamnus*, respectively (Tables 3–5). Also, mortality from frost heaving tended to be greater in the more poorly drained blocks. Predation remained the major source of mortality under herbs, causing ≈78, 54, and 60% of the deaths of *Acer*, *Pinus*, and *Rhamnus* seedlings (Tables 3–5).

Survivorship from June to October 1986 remained essentially constant under herbs (Fig. 7A–C) after the small mammal exclosure was established. Most mortality for all species across treatments occurred to seedlings that had been partially frost heaved during the winter of 1985 and that subsequently desiccated and died during the summer of 1986. This phenomenon occurred to the greatest extent in A−B+, and was most severe for *Pinus* (Tables 3–5).

Survivorship during the study was greatest in the open (Fig. 7A–C). Average survivorship for all species was 70% (range = 54–85%) in the open (A−B+ and A−B−) and 31% (range = 9–54%) under herbs (A+B− and A+B+) through the beginning of the second growing season. Average survivorship was 64% (range = 48–83%) in the open and 30% (range = 9–50%) under herbs by the end of the second growing season.

Survivorship of seedlings planted in 1986 was generally ≈90% or greater (Fig. 8), after the exclosure had effectively eliminated loss by predation. While there were no significant differences across treatments in survivorship of seedlings of *Cornus* and *Rhamnus*, there were significant ($\chi^2 = 10.29$, df = 3, $P < .025$) differences for *Pinus* seedlings, with average survivorship of 92, 92, 64, and 75% in A+B+, A+B−, A−B+, and A−B−, respectively. Mortality of pine seedlings in these open plots appeared to be from heat and/or desiccation stress.

Experiment 6B: Aboveground and belowground effects of herbs on woody seedling growth.—1. Environmental conditions.—Environmental conditions are reported only for 1986 because the relative

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ning of the second growing season (6 June 1986), and the end of the second growing season (21 October 1986) are given in Tables 3–5.

TABLE 3. Proportion of *Acer rubrum* seedlings dying from different sources of mortality in Experiment 6A during the first growing season (6 August 1985–24 October 1985), the first dormant season (25 October 1985–6 June 1986), and the second growing season (7 June 1986–21 October 1986) for cohorts of 54 *A. rubrum* seedlings planted into each of the four treatments in early August 1985.

Source of mortality*	Treatments†				Testing‡	
	A+B+	A+B−	A−B+	A−B−	χ^2	P
			6 August 1985–24 October 1985			
N	54	54	54	54		
Pred	.407	.296	0	.019	41.97	.001
Gone	.019	.037	.019	0	NA	···
AsPred	.426	.333	.019	.019	46.62	.001
Heav	0	0	0	0	NA	···
Unkn	0	0	0	0	NT	···
Total	.426	.333	.019	.019	46.62	.001
			25 October 1985–6 June 1986			
N	31	36	53	53		
Pred	.129	.083	0	.038	7.68	.100
Gone	.290	.278	.038	0	26.95	.001
AsPred	.419	.361	.038	.038	35.59	.001
Heav	.097	.028	.189	.094	6.12	.250
Unkn	.065	.028	0	0	NT	···
Total	.581	.417	.227	.132	22.45	.001
			7 June 1986–21 October 1986			
N	13	21	41	46		
Pred	0	0	0	0	NA	···
Gone	0	0	0	0	NA	···
AsPred	0	0	0	0	NA	···
Heav	0	0	0	0	NA	···
Unkn	0	0	.024	0	NT	···
Total	0	0	.024	0	NA	···

* Pred = proportion of N clearly killed by predators; Gone = proportion of N that disappeared, but were apparently consumed by predators as explained in text (*Results: Experiment 6A: effects of herb cover on seedling establishment*); AsPred = proportion of N assumed killed by predators (equals Pred + Gone) (the small-mammal exclosure was erected in late May 1986, and effectively eliminated predation as a source of mortality after that time); Heav = proportion of N killed by frost heaving during the winter, or heaved during the winter but not dead until the next growing season; Unkn = proportion of N killed by unknown causes, seedlings slowly died standing apparently due to heat and desiccation stress or to pathogens.

† Treatments (as illustrated in Fig. 1): A+B+ = seedling in presence of aboveground and belowground interactions with herbs, A+B− = aboveground only, A−B+ = belowground only, A−B− = herbs not present. N = number of seedlings alive at the beginning of a time interval.

‡ A chi-square (χ^2) test of independence on the number of seedlings killed (= $N \times$ proportion) was used to determine if mortality sources varied significantly (P = probability of a greater χ^2 statistic by chance) across treatments. NT = not tested because cause of death was unknown; NA = not appropriate to test data because at least one of the calculated expected values was ≤1.0 (Snedecor and Cochran 1967).
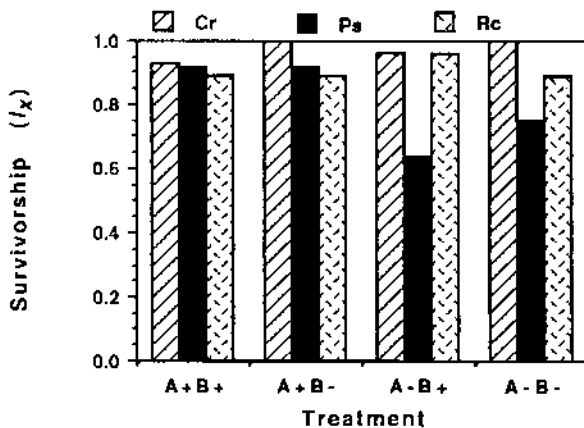

FIG. 8. Cumulative survivorship (l_x) of cohorts of 36 seedlings each of *Cornus racemosa* (Cr), *Pinus strobus* (Ps), and *Rhamnus cathartica* (Rc) in each of the four treatments of Experiment 6A during June 1986-October 1986. Seedlings were planted during June 1986, after the small-mammal ex-

patterns of photosynthetic photon flux density (PPFD), temperature, and soil moisture across the four treatments were similar in the two years. During August and early September 1986, integrated PPFD at 10 cm was ≈10× as great in the open (A−B+ and A−B−, combined) as under herbs (A+B− and A+B+, combined) (Fig. 9A). Average (± 1 SE) integrated daily total PPFD was 26.4 ± 1.8 mol·m⁻²·d⁻¹ in the open treatments and 2.6 ± 0.4 mol·m⁻²·d⁻¹ under herbs. Peak levels of instantaneous PPFD on a typical day were ≈1800 μmol·m⁻²·s⁻¹ in open treatments and ≈260 μmol·m⁻²·s⁻¹ under herbs (Fig. 9B). Levels of PPFD in the open treatments were ≈75–90% of "full sun"

closure was established. Treatments as illustrated in Fig. 1. Error bars not given as there was no replication within treatments, but survivorship of *Pinus* was significantly different among treatments ($\chi^2 = 10.29$, df = 3, $P < .025$).

TABLE 4. Proportion of *Pinus strobus* seedlings dying from different sources of mortality in Experiment 6A during the first growing season, the first dormant season, and the second growing season for cohorts of 54 *P. strobus* seedlings planted into each of the four treatments in early August 1985. See Table 3 for details and abbreviations.

Source of mortality	Treatments				Testing	
	A+B+	A+B−	A−B+	A−B−	χ^2	P
	6 August 1985–24 October 1985					
N	54	54	54	54		
Pred	.148	.185	.056	0	13.14	.005
Gone	0	.167	0	0	27.59	.001
AsPred	.148	.352	.056	0	32.67	.001
Heav	0	0	0	0	NA	⋯
Unkn	0	0	0	.019	NT	⋯
Total	.148	.352	.056	.019	29.19	.001
	25 October 1985–6 June 1986					
N	46	35	51	53		
Pred	.065	.057	.020	0	4.37	.250
Gone	.130	.086	.039	0	8.45	.050
AsPred	.196	.143	.059	0	13.23	.005
Heav	.174	0	.235	.151	9.25	.050
Unkn	.087	.029	0	.038	NT	⋯
Total	.457	.172	.294	.189	11.39	.010
	7 June 1986–21 October 1986					
N	25	29	36	43		
Pred	0	0	0	0	NA	⋯
Gone	0	0	0	0	NA	⋯
AsPred	0	0	0	0	NA	⋯
Heav	.040	.069	.250	.093	8.36	.050
Unkn	.040	0	0	.023	NT	⋯
Total	.080	.069	.250	.116	5.84	.250

TABLE 5. Proportion of *Rhamnus cathartica* seedlings dying from different sources of mortality in Experiment 6A during the first growing season, the first dormant season, and the second growing season for cohorts of 54 *R. cathartica* seedlings planted into each of the four treatments in early August 1985. See Table 3 for details and abbreviations.

Source of mortality	Treatments				Testing	
	A+B+	A+B−	A−B+	A−B−	χ^2	P
	6 August 1985–24 October 1985					
N	54	54	54	54		
Pred	.426	.389	.130	.148	19.80	.001
Gone	.407	.444	.019	.037	48.93	.001
AsPred	.833	.833	.148	.185	96.14	.001
Heav	0	0	0	0	NA	⋯
Unkn	0	0	.019	.037	NT	⋯
Total	.833	.833	.167	.222	88.57	.001
	25 October 1985–6 June 1986					
N	9	9	45	42		
Pred	0	0	0	0	NA	⋯
Gone	0	.333	.156	.071	6.45	.100
AsPred	0	.333	.156	.071	6.45	.100
Heav	.111	.111	.200	.167	0.78	.900
Unkn	0	0	0	0	NT	⋯
Total	.111	.444	.356	.238	3.86	.500
	7 June 1986–21 October 1986					
N	8	5	29	32		
Pred	0	0	0	0	NA	⋯
Gone	0	0	0	0	NA	⋯
AsPred	0	0	0	0	NA	⋯
Heav	0	0	.069	0	NA	⋯
Unkn	0	0	.034	0	NT	⋯
Total	0	0	.103	0	NA	⋯

During May–October 1986 ≈ 562 mm of rain were recorded ≈ 1.2 km from the study site (Fig. 10A, for June–September), 50 mm more than the long-term average (NOAA 1986). Soil moisture was usually lowest in A+B+ and usually highest in A−B− (Fig. 10B). Predawn xylem pressure potential (XPP) on 31 August 1986 was significantly different across treatments for both *Cornus* ($F_{3,32} = 7.29$, $P < .001$) and *Rhamnus* ($F_{3,32} = 10.11$, $P < .001$) (Fig. 11). Average (± 1 SE, pooled across treatments) predawn XPP for *Cornus* and *Rhamnus* in A+B+ was -0.52 ± 0.05 and -0.61 ± 0.04 MPa, while the average value across the other three treatments was -0.27 and -0.35 MPa, respectively. The same pattern of lower moisture status in
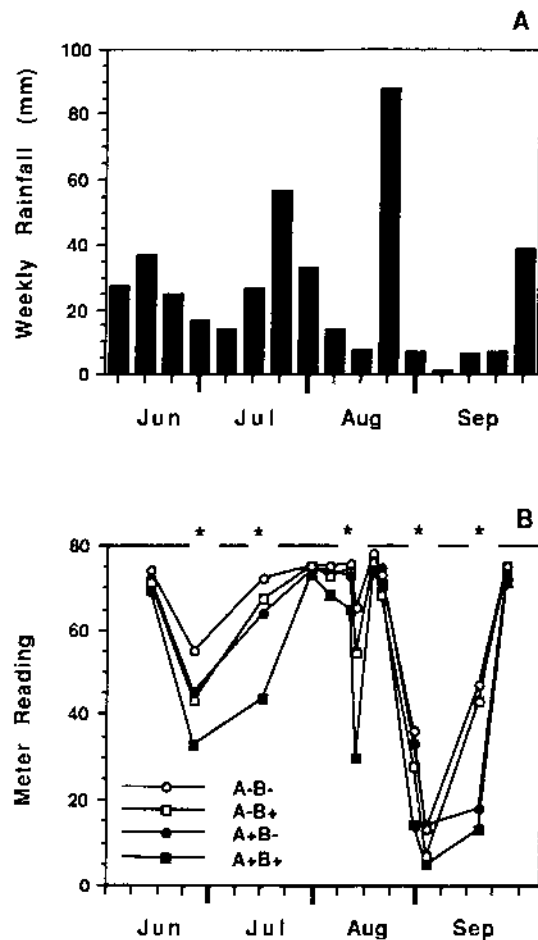

Fig. 9. Average photosynthetic (400–700 nm) photon flux density (PPFD) at 10 cm above the ground surface under herbs (A+B+ and A+B−, combined) and in the open treatments (A−B+ and A−B−, combined). Treatments as illustrated in Fig. 1. (A) Integrated daily total PPFD for 21 complete days during the period from 1 August to 4 September 1986 (equipment failure prevented complete diurnal data collection on 12–17 and 23–30 August). (B) Instantaneous PPFD averaged every 10 min during 4 August 1986. This date was selected to represent a typical diurnal course of PPFD in the treatments because the daily totals (2.6 and 31.0 mol·m⁻¹· d⁻¹, in herb-covered and open treatments, respectively) were the closest to the 21-d averages. The decrease in photon irradiance near solar noon (1300 EDT) was due to clouds. EDT = Eastern Daylight Time.

measurements taken ≈ 1 m above the herb canopy (data not presented).

During the middle of the day (1100–1500 Eastern Daylight Time) on four occasions during the 1986 growing season soil temperature at 1 and 10 cm, air temperature at 10 cm, and temperature of *Rhamnus* and *Cornus* leaves tended to be 2°–5°C warmer in the open than under herbs, and the highest leaf temperature recorded was 29.0° in A−B− (data not presented). So, while PPFD was nearly an order of magnitude greater in the open, the temperature of the soil, air, and leaves was only ≈ 10–15% greater than under herbs.

Fig. 10. Rainfall and soil moisture during June–September 1986. (A) Weekly total rainfall at the Game Farm Road weather station (NOAA 1986), ≈ 1.2 km from the study site, shown by vertical bars. (B) Average relative soil moisture at 10 cm depth from 14 June to 27 September 1986. Treatments as illustrated in Fig. 1. Gravimetric soil moisture and the gypsum block readings showed a nonlinear relationship typical of such measurements (e.g., Goltz et al. 1981), but soil moisture was very highly correlated (Spearman $r_s = 0.97$, $n = 62$, $P < .001$) with the rank of meter readings, so higher meter readings indicate relatively greater soil moisture (Gill 1987). Statistically significant ($P < .05$) differences among treatments are denoted by asterisks in top border of graph.
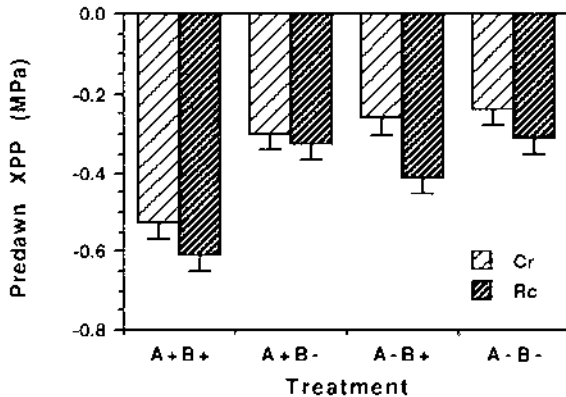
FIG. 11. Predawn xylem pressure potential (XPP) on 31 August 1986 for nine (one per block) 3-mo-old seedlings of *Cornus racemosa* (Cr) and *Rhamnus cathartica* (Rc) in each of the four treatments (as illustrated in Fig. 1). The most recent rainfall was 25 mm on 27 August, and prior to that 55 mm fell on 24 August. Error bars are −1 SE for each species, pooled across treatments.

A+B+ at that time was also observed in the gypsum block readings (Fig. 10B). Measurements on *Pinus* seedlings were not made because mortality had already decreased the potential size of the harvest sample, especially in the A−B+ treatment (Fig. 8).

2. Growth of 5-mo-old and 17-mo-old seedlings.— Total dry mass of 5-mo-old seedlings of *Cornus racemosa, Pinus strobus,* and *Rhamnus cathartica,* all showed significant differences across the treatments ($F_{3,24} = 111.65, 51.32$, and 52.02, respectively; $P < .001$ for all species; Fig. 12). Linear contrasts indicated that seedlings of all three species had significantly greater dry mass in A−B− than in A+B+ (t values for linear contrasts of 16.05, 10.42, and 10.91; for *Cornus, Pinus,* and *Rhamnus,* respectively; $P < .001$ for all species). Linear contrasts also indicated that seedlings of all species had significantly greater dry mass in A−B+ than in A+B− ($t = 8.65, 6.70, 5.99$; for *Cornus, Pinus,* and *Rhamnus; P < .001* for all species).

Total dry mass of 17-mo-old seedlings of *Acer rubrum, Pinus strobus,* and *Rhamnus cathartica* all showed significant differences across treatments ($F_{3,85} = 36.63, F_{3,82} = 54.60,$ and $F_{3,48} = 16.77$, respectively; $P < .001$ for all species; Fig. 13). Linear contrasts indicated that seedlings of all three species had significantly greater dry mass in A−B− than in A+B+ ($t = 8.99, 11.93,$ and 5.54; for *Acer, Pinus,* and *Rhamnus; P < .001* for all species). Linear contrasts also showed that seedlings of all three species had significantly ($P < .001$ for *Acer* and *Pinus,* and $P < .025$ for *Rhamnus*) greater mass in A−B+ than in A+B− ($t = 3.71, 3.87,$ and 2.14 for *Acer, Pinus,* and *Rhamnus,* respectively).

For both 5-mo- and 17-mo-old seedlings, shoot height and rooting depth (rooting depth was estimated, after careful excavation, as the vertical distance from the soil surface to the tip of the deepest extractable root) of all species tended to show patterns similar to those
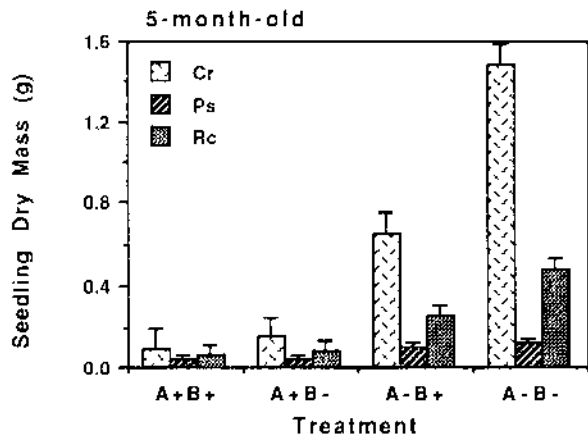

FIG. 12. Average total dry mass of 5-mo-old *Cornus racemosa* (Cr), *Pinus strobus* (Ps), and *Rhamnus cathartica* (Rc) in Experiment 6B that had emerged in mid-May 1986, were planted in mid-June 1986, and were harvested in mid-October 1986. Treatments as illustrated in Fig. 1. There were 24, 27, 26, and 27 *Cornus* seedlings, 32, 33, 23, and 27 *Pinus* seedlings, and 23, 24, 26, and 24 *Rhamnus* seedlings, harvested from A+B+, A+B−, A−B+, and A−B−, respectively. Average (±1 SE) dry mass of a random sample of 18 of the 1-mo-old seedlings in mid-June 1986 was 0.041 ± 0.009, 0.015 ± 0.002, and 0.010 ± 0.001 g, for *Cornus, Pinus,* and *Rhamnus,* respectively. Error bars are +1 SE for each species, pooled across treatments.

of total dry mass across treatments; for instance, seedlings in the absence of herbs (A−B−) tended to be taller and to have deeper roots than in A+B+ (Gill 1987). Also, root/shoot ratios and allocation of biomass to roots, stems, and leaves showed some statis-
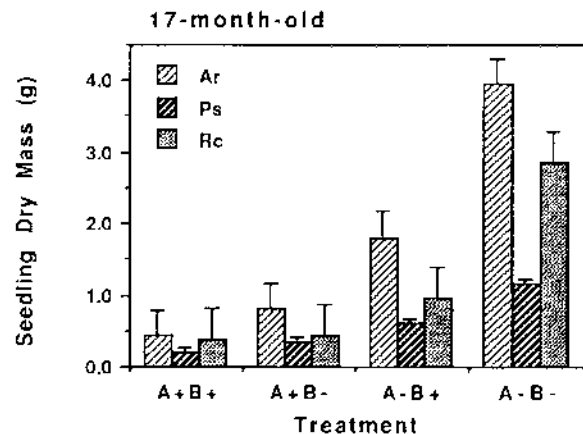

FIG. 13. Average total dry mass of 17-mo-old seedlings of *Acer rubrum* (Ar), *Pinus strobus* (Ps), and *Rhamnus cathartica* (Rc) in Experiment 6B that had emerged in May 1985, were planted into treatments in early August 1985, and were harvested in mid-October 1986. Treatments as illustrated in Fig. 1. There were 10, 15, 30, and 34 *Acer* seedlings, 18, 19, 21, and 28 *Pinus* seedlings, and 6, 6, 18, and 22 *Rhamnus* seedlings, harvested from A+B+, A+B−, A−B+, and A−B−, respectively. Average (±1 SE) total dry mass of a random sample of 18 seedlings in early August 1985 was 0.267 ± 0.020, 0.102 ± 0.009, 0.040 ± 0.003 g, for *Acer, Pinus,* and *Rhamnus,* respectively. Error bars as in Fig. 12.
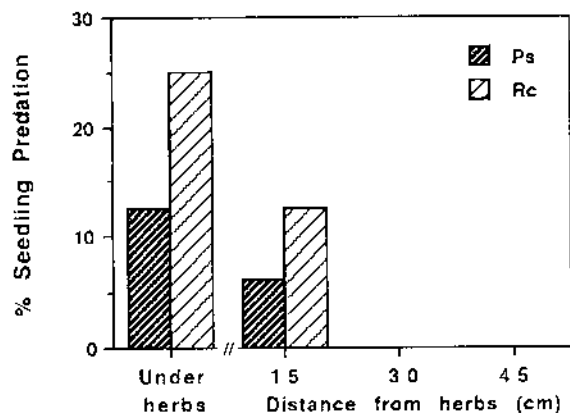
FIG. 14. Cumulative mean predation of *Pinus strobus* (Ps) and *Rhamnus cathartica* (Rc) seedlings in Experiment 7 during June–November 1986 under an herb canopy and 15, 30, and 45 cm out into experimental openings replicated in eight blocks. There was a total of 16 seedlings of each species per treatment in complete design. Predation rates under herbs and at 15 cm into the open ranged from 0 to 50% for *Pinus* and 0 to 100% for *Rhamnus*.

tical differences, but the differences among means were small; however, specific leaf mass was always significantly greater where herb shoots were excluded (Gill 1987).

Experiment 7: Effects of size of openings in herb cover on seedling survivorship.—From June to November 1986, no seedlings of *Pinus* or *Rhamnus* located at least 30 cm into experimental openings in the herb canopy were killed; however, there were no significant differences among treatments due to the large amount of variation in predation among replicates under the canopy and at 15 cm into openings (Fig. 14).

Experiment 8: Seedling survivorship under canopies of different successional ages.—Seedling mortality due to frost heaving occurred only in the two corn field plots (Fig. 15A–B), which had very little vegetative or litter cover during the winter. Essentially all of the mortality, 30–45% for *Pinus* and 45–65% for *Rhamnus*, in the corn plots was due to frost heaving, with no mortality clearly due to predation. The few *Rhamnus* seedlings (5%) that disappeared in each of the two active corn plots were in areas that experienced substantial water and soil movement during the spring runoff period and the seedlings were apparently washed away or buried, rather than taken by predators. Seedlings that disappeared in all the older plots and fields, however, were apparently killed by predators. Predation (=clearly killed by predators plus those missing) at sites ≥ 1 yr old was the only source of mortality for *Rhamnus*, and was often the major source of mortality for *Pinus* (Fig. 15A). Most predation occurred during the summer and fall, rather than during the winter or spring. Some *Pinus* seedlings died from unknown causes, particularly in the 2- and 3-yr-old plots. Most of these seedlings were apparently healthy at the end of

the growing season, but were dead by the following spring.

DISCUSSION

General models of colonization during secondary succession

In our study the probability of tree and shrub seedling establishment was generally lower under herbs than in openings, consistent with the inhibition model of Connell and Slatyer (1977); in spite of this net inhibition, however, cases of facilitation and tolerance occurred as well. The few studies on woody seedling
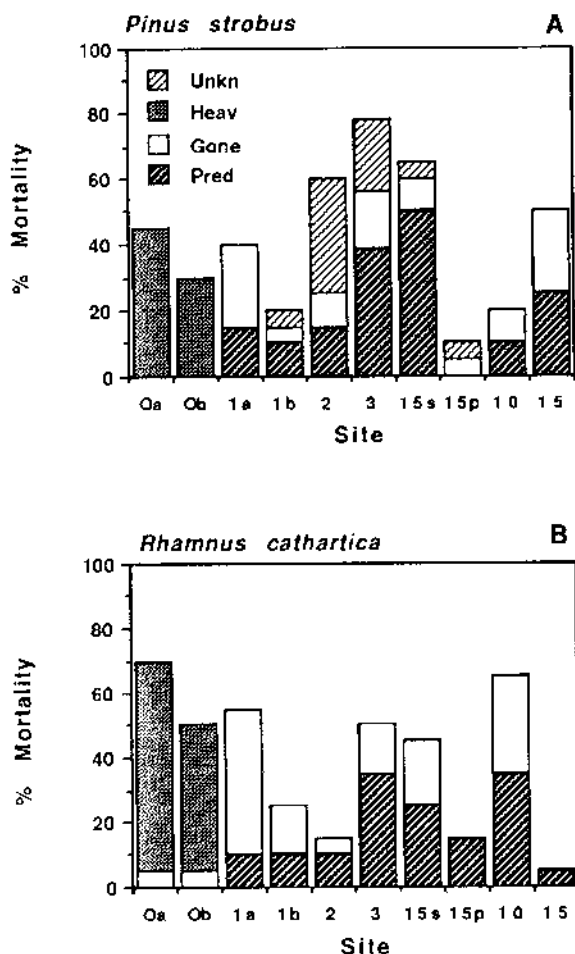

FIG. 15. Cumulative percentage of seedlings dying from different sources of mortality in 10 replicate plots (*n* = 20 per species per site) in each site from June 1986 to June 1987 in Experiment 8. The first eight sites were in the Teaching Farm: 0a and 0b were in active corn production; 1a and 1b had been abandoned for 1 yr; 2 and 3, for 2 and 3 yr, respectively; 15s and 15p for ≈15 yr, but were dominated by shrubs and pine saplings, respectively. The last two sites were in widely separated fields in the goldenrod–grass stage that had been abandoned for ≈10 and 15 yr, respectively: 10 was Hines Road; 15 was Snyder Road. (See *Methods: Experiment 8* and Appendix for more details.) Pred = clearly killed by predators; Gone = disappeared, but assumed eaten by predators; Heav = frost heaved; Unkn = unknown cause of death.

growth under herbs, although not designed specifically to test the Connell and Slatyer models, also show some support for each of the models (e.g., Bormann 1953, vonAlthen 1970, Webb 1974, Harrison and Werner 1984, Zutter et al. 1986). The few explicit experimental tests of Connell and Slatyer's models have investigated interactions between early and later successional herbs (e.g., Abul-Fatih and Bazzaz 1979, Hils and Vankat 1982, Armesto and Pickett 1986), and these studies have also shown support for each of the models depending on the successional age of the field and the structural and life history characteristics of the species assemblages involved (Armesto and Pickett 1986).

Since the Connell-Slatyer models describe the net outcomes (Connell et al. 1987) of interactions among species in succession (beneficial, detrimental, or neutral), it is not surprising that studies of succession involving more than one life stage or one species should produce results consistent with more than one model (e.g., Finegan 1984, Walker and Chapin 1987, Morris and Wood 1989). Also, each of the Connell-Slatyer models can be subdivided into two components caused by very different types of mechanisms. Facilitation and inhibition can be either *direct* or *indirect*: direct effects on later colonists act through changes caused in the physical environment by earlier colonists, while indirect effects act on later colonists through the activity of animals or microbes necessarily associated with the presence of earlier plant colonists. Pickett et al. (1987) distinguished *active* from *passive* tolerance: active tolerance is due to physiological tolerance of low levels of resource, while passive tolerance is due to different life history traits, particularly slower growth and greater longevity. These important distinctions should be incorporated into an elaborated Connell and Slatyer framework (see Table 1).

Facilitation. — We found increased seedling emergence, especially of *Fraxinus*, in the presence of long-lived herbs (Fig. 5), and we found decreased seedling mortality due to environmental extremes in the presence of herbs during both the winter and the summer (Tables 3–5, Figs. 7, 8, and 15). Decreased mortality from heat/desiccation stress during the summer and frost heaving during the winter are probably caused by environmental amelioration induced by earlier plants (e.g., direct facilitation), but, it is unclear if increased emergence is due to direct facilitation, or from indirect facilitation mediated by beneficial microbes associated with earlier colonists. Survival of *Liquidambar styraciflua* seedlings in North Carolina old fields has been shown to be facilitated by herbs (Bormann 1953). Also, survival and growth of *Quercus velutina* and *Q. alba* in Michigan old fields appeared to be facilitated by the presence of herbs (Harrison and Werner 1984).

Inhibition. — Survivorship of seeds (Figs. 2 and 4) and seedlings (Tables 3–5, Fig. 7) was often much lower under herbs, and growth of surviving seedlings (Figs. 12 and 13) was lower under herbs. We are aware of no other studies in which survivorship of seeds or seed-lings of woody plants was reduced by the presence of herbs in old fields, but studies from forest plantations have shown tree seedling growth is reduced by herbs (vonAlthen 1970, Webb 1974, Zutter et al. 1986). Competition and allelopathy are mechanisms of direct inhibition on growth of later colonists caused by earlier colonists, but reduced survivorship due to higher rates of predation occurring among earlier herbs is indirect inhibition, and details of this novel mechanism of inhibition are discussed later (see *Seed and seedling predation as novel mechanisms of the inhibition model*).

Tolerance. — Herbs had no statistically significant effect on certain colonization events: seed predation under snow (Fig. 3); seedling emergence of *Acer, Cornus,* and *Viburnum* (Fig. 5) and *Pinus* (Fig. 6); and, predation on *Pinus* and *Rhamnus* seedlings (Fig. 14). Failure to find significant effects of herbs on these colonization events causes us to reject inhibition and facilitation and to conclude that for these species at these life stages our results are consistent with the tolerance model. Survival of seedlings of *Pinus taeda* was not significantly different in bare soil compared to under herbs in North Carolina old fields (Bormann 1953).

Pickett et al. (1987) suggest that failure to show significant differences in establishment of later successional species following experimental removal of earlier species only weakly supports the tolerance model. While we agree with Pickett et al. (1987) that it is difficult to distinguish between active and passive tolerance in a field experiment, we suggest that a third type of tolerance (e.g., noninteractive tolerance) may occur when early species have no statistical effect on colonization during some life stages of later species.

Mechanisms regulating colonization during early life stages of woody plants

The net inhibitory effect of herbs on woody seedling invasion of old fields in our study was caused by a variety of mechanisms that usually resulted in increased mortality of woody seedlings in the presence of herbs. Seeds dispersed into a field faced several potential sources of mortality (i.e., failure of seedlings to emerge, competition, predation, pathogens, and environmental extremes) and the relative importance of mechanisms regulating colonization often differed among life stages and species. Recent field experiments using a similar life stage approach have also revealed that several different mechanisms are important at different life stages in regulating tree and shrub seedling establishment during primary succession on floodplains in Alaska (Walker and Chapin 1986, Walker et al. 1986) and during postfire succession in semiarid woodlands in Australia (Wellington and Noble 1985a, b). The important mechanisms regulating colonization of old fields by woody seedlings in our study are summarized below.

Seed dispersal. — Seed dispersal is the initial event regulating woody plant colonization of old fields, and is equally important in driving succession in other ar-

eas where no viable pool of buried seeds or vegetative fragments exists (e.g., Wood and del Moral 1987). The species composition, abundance, and spatial distribution of seeds dispersed into a field were determined primarily by the proximity, fecundity, and mode of dispersal of trees and shrubs of different species that happened to be adjacent to the field (Gill 1987). This dependence on the proximity and fecundity of seed sources introduces an important stochastic element to woody plant colonization of old fields. It further suggests that it will be difficult to predict specific successional "pathways" (Pickett et al. 1987) with much precision for any given field.

Postdispersal seed predation. — Seed predation was a major mechanism regulating woody plant invasion of old fields in the present study; both the spatial distribution and relative abundance of seeds dispersed into a field could be significantly altered by seed predators. While the fate of seeds that disappeared was not certain, we assumed that most seeds that disappeared in these experiments were destroyed by small, nocturnal mammals, especially *Peromyscus* spp. (Klein 1960). In forests, fields, and laboratory experiments *Peromyscus* spp. have been shown to consume large quantities of seed, including the endocarp and embryo in most cases (Hamilton 1941, Abbott 1961, Whitaker 1963, Wolff et al. 1985). Also, most of the *Pinus strobus* seeds cached by rodents in coniferous forests during the fall were relocated and consumed during the winter and spring (Abbott and Quink 1970).

For all species there was greater predation of seeds located under herbs than in openings (Figs. 2 and 4). When the ground was covered by several centimetres of snow, however, seeds faced equal predation risk regardless of location (Fig. 3). Mice were presumably active under the snow (e.g., Getz 1959), and were locating and consuming the seeds, as has been reported by Radvanyi (1970) in a temperate coniferous forest. The behavior of seed predators could also alter the relative abundance of seeds of different species. The relative abundance of *Cornus* and *Viburnum* seeds was significantly reduced compared to *Fraxinus* and *Rhamnus* seeds both in openings and under herbs (Fig. 3). While the preference by small mammals for seeds of *Pseudotsuga* over *Tsuga* influenced species composition during natural revegetation in coniferous forests of the Pacific Northwest following clearcuts (Gashwiler 1967), the importance of seed predation in regulating woody plant colonization during old-field succession has not been previously reported.

Seedling emergence. — The species-specific requirements for successful emergence were additional important processes affecting woody plant colonization, but the specific mechanisms responsible for differences in emergence are unknown. Tree and shrub seedling emergence rates were generally quite low and emergence often did not occur for a full year after sowing. Possible causes for the delayed and low rates, or the complete failure, of emergence deserve further study.

For most species, however, emergence rates were somewhat greater in the presence of goldenrods and grasses than bare soil (except *Rhamnus*) or short-lived herbs (Figs. 5 and 6). Slightly higher rates of seedling emergence under the goldenrod–grass canopy could be due to higher surface soil moisture occurring because of less evaporation from the soil surface under the thicker cover than in either bare ground or 1- and 2-yr-old herb plots (data not presented). Also infiltration of precipitation into the soil under the goldenrod–grass canopy may have been more effective due to better surface soil structure in those plots, which were not herbicided or rotary tilled. Seeds of *Pinus strobus* have been shown to germinate better under partial shade cast by herbs or trees than on bare, dry soil (Smith 1940, Smith 1951).

Another possible reason for greater emergence in the goldenrod–grass plots was that heaving of the soil surface during freeze–thaw cycles during the winter was less than in the bare soil and short-lived herb plots. Fifty-five percent of the bamboo plot stakes ($\approx$0.5–1.0 cm diameter, pushed $\approx$10–15 cm into the ground) were heaved out of the ground in the bare soil and short-lived herb plots, while only 1% of the stakes was heaved in the goldenrod–grass plots. In New Jersey, Buell et al. (1971) found the most severe frost heaving occurred the first winter after abandonment because the relatively thin herb cover and litter layer could not effectively insulate the soil surface. Seeds in the bare soil and short-lived herb plots were therefore more likely to be heaved out of the ground. The fate of heaved seeds is unknown; some may subsequently desiccate on the surface, and others may be washed away and germinate elsewhere.

The higher rates of emergence of non-acid-treated *Rhamnus* seeds in both the bare soil and goldenrod–grass treatments, compared to the short-lived herb treatment, suggest that early successional herbs may have inhibited *Rhamnus* emergence. Water-soluble leachates of certain old-field herbs can significantly reduce the germination rates of *Prunus serotina* seedlings (Horsely 1977). Also, *Ambrosia artemisiifolia*, an important dominant (48% of total cover) in the 1-yr-old herb plots of Experiment 5, has been reported to be allelopathic and inhibit the germination of herbaceous plants (Jackson and Willemsen 1976).

Seedling survivorship during the first growing season. — The major source of mortality during the first growing season was predation by small mammals, especially *Microtus pennsylvanicus*. Seedling predation was thus an important mechanism regulating woody plant colonization of old fields in this study, and this has not been emphasized in reviews of processes regulating succession in Temperate Zone communities (e.g., Drury and Nisbet 1973, Connell and Slatyer 1977, Finegan 1984, Huston and Smith 1987). Buell et al. (1971) suggest, but offer no data, that herbivores can retard woody plant invasion onto former agricultural fields. A recent study, conducted in the same area as

Buell et al. (1971), indicated that predation of *Acer rubrum* seedlings by small mammals can have a potentially important impact during old-field succession (Rankin and Pickett 1989). Mills (1986) also found that seedling predation can be an important factor regulating postfire succession in chaparral.

Survivorship was much lower for woody seedlings growing among old-field herbs than in the open, primarily due to greater rates of seedling predation under herbs. Predation was an important source of mortality during different years and in widely separated fields (Tables 3–5, Figs. 7, 14, and 15). It is curious that in many instances very little of the seedling was actually consumed even though the stem was cut off below the cotyledons, or the seedling was completely dug up. However, McAuliffe (1986) has reported jackrabbits cutting off the stem of *Cercidium* seedlings ≈1 cm above the ground surface, and not consuming much of the seedling. Small mammals have also been reported to dig up and kill young seedlings, possibly in search of a cache of seeds (Abbott and Quink 1970, Sork 1987). Voles (*Microtus* and *Clethrionomys*) in particular, have been observed to cut off stems of herbs and to leave cut segments on the ground (Summerhayes 1941, Getz 1985), to cut down plants emerging into their runways (Summerhayes 1941), to dig up and eat roots (Getz 1985), and to sever shoots of woody seedlings at the hypocotyl above or below the ground surface (Pigott 1985). The evolution and ecological consequences of the behavior by voles of killing but not consuming woody seedlings deserve further study.

Some of the *Pinus* and *Rhamnus* seedlings dying of unknown causes in the open treatments were observed to desiccate slowly and develop lesions on their stems, particularly in the higher light and lower soil moisture conditions of the A−B+ treatments (Figs. 7 and 8). Similar symptoms observed on *Pinus strobus* seedlings in open, dry sites were diagnosed as heat stress by Smith (1940), but pathogens may be responsible for some of these unexplained deaths.

Seedling survivorship during the first winter. —Both predation and frost heaving (except for *Rhamnus* seedlings under herbs) were important sources of mortality over the first winter (Figs. 7 and 15). With the exception of Buell et al. (1971), the importance of frost heaving in regulating woody plant establishment during succession has been overlooked. Its importance is probably restricted, however, to more open and wetter sites in regions where freezing temperatures occur while little or no snow is on the ground. Seedling mortality due to frost heaving was greater in the open than under herbs (Tables 3–5, Fig. 15). Buell et al. (1971) reported that mortality of woody seedlings due to frost heaving was greatest in 1st-yr old fields in New Jersey, because the largely exposed soil surface was poorly insulated.

Seedling growth during the first two growing seasons. —Competition with herbs clearly reduced woody seedling growth, and aboveground competition was more severe than belowground competition (Figs. 12 and 13). Herbs reduce growth of tree seedlings in forest plantations (vonAlthen 1970, Webb 1974, Zutter et al. 1986). None of these studies partitioned aboveground from belowground effects, however, so the relative importance of aboveground vs. belowground competition was not determined.

The relative importance of aboveground vs. belowground competition will probably differ depending on the species and the environment under study. The greater importance of aboveground competition in this study was probably due to greater depletion of light than of water (and nutrients?) by the herbs. Herb shoots decreased daily total PPFD at woody seedling height by ≈90% (Fig. 9A), and average instantaneous PPFD was ≈500 and 50 $\mu mol \cdot m^{-2} \cdot s^{-1}$ in the open vs. under herbs (Fig. 9B), which is near the photosynthetic light saturation and compensation points, respectively, for *Pinus strobus* and *Acer rubrum* (Hicks and Chabot 1985). In contrast, the predawn XPP of woody seedlings after several days without rain was only ≈50% lower in the presence of competition from herb roots (Fig. 11). The average XPP during this relatively dry period of the summer was only ≈−0.6 MPa for seedlings faced with belowground competition, and water stress in most temperate woody species does not occur until potentials are below −1.0 MPa (Hsiao 1973). Also, the summer of 1986 was wetter than average, and the Turkey Farm is a fairly mesic site due to its low topographic position and moderate soil drainage; therefore, belowground competition might have been more important in drier years or at drier sites.

Some tests of Connell and Slatyer's models have used changes in aboveground biomass (grams per square metre) or aerial coverage as an index of performance (e.g., Abul-Fatih and Bazzaz 1979, Hils and Vankat 1982, Armesto and Pickett 1986). If survivorship rather than growth is used as an index of the probability of colonization, then a different picture may emerge since competition (or allelopathy) had little clear inhibitory effect on woody seedling survivorship in our study. While seedlings were smaller and had lower survivorship under herbs than in the open (Tables 3–5, Figs. 7, 12 and 13), there was no statistical relationship between survivorship and seedling size within a treatment. For instance, larger seedlings were just as likely as smaller seedlings to be killed by predators under herbs or by frost heaving in the open. Since there was little evidence of size-dependent (i.e., competition-mediated) mortality over the course of this study, competition was a relatively unimportant mechanism regulating woody seedling colonization.

Seed and seedling predation as novel mechanisms of the inhibition model

An unexpected and important result of our study was that predation of seeds and seedlings was greater under herbs. The greater predation of seeds (Figs. 2

and 4) and seedlings (Tables 3–5, Figs. 7, 14, and 15) under herbs, and the fairly high predation of seeds under the snow (Fig. 3), may be due to rodents avoiding exposure to carnivores (e.g., Kotler 1984, Pearson 1985, Klatt and Getz 1987). The generally greater rate of disappearance of *Cornus racemosa* seeds occurring singly as opposed to in groups of five, particularly in openings (Fig. 4B), may also be due to carnivore-avoidance behavior by rodents apparently reluctant to remain exposed long enough to consume all five seeds. Predation of seeds of woody plants can be important in the North Carolina Piedmont, especially during wet springs (D. De Steven, *personal communication*). In the New Jersey Piedmont, Rankin and Pickett (1989) indicate that herbivory may influence *Acer rubrum* establishment, and rabbit herbivory on seedlings of several species of woody plants may be especially heavy in open microsites (M. Meadows, *personal communication*). In our study rabbits were only rarely observed but may have a greater impact if more abundant. While deer were regularly observed at several of our study sites, they did not browse on the small woody seedlings.

Predation of seeds and seedlings of woody plants in microsites occupied by herbs is a novel mechanism producing results consistent with the inhibition model. Because the increased risk of mortality for species arriving later is necessarily, but indirectly, associated with the presence of prior colonists, this type of mechanism should be considered indirect inhibition. While herbivory or predation may be greater among earlier colonists (indirect inhibition), indirect facilitation could also occur if survivorship of seeds or seedlings of later species is increased because they are less conspicuous, or if consumers avoid foraging among early colonists. Plant–animal interactions should be explicitly included as potential regulation mechanisms in models of succession.

The relationships among woody seedling establishment, openings in the herb canopy, and the behavior of seed and seedling predators may be size dependent. If the woody plants were larger, bouts with consumers would less likely be fatal. Or, if the plant consumers were larger, rabbit or deer for instance, then woody seedlings in openings might be more conspicuous and thus less likely to escape. Also, the potential importance of seed and seedling predation by rodents is probably proportional to their local population densities, which are notable for fluctuating between very high and low levels (Hamilton 1937, Elton 1942, Krebs and Myers 1974).

A life stage probability model of seedling establishment under herbs and in the open

An estimate of the probability of seedling establishment from the time a seed lands in a field until the beginning of the second growing season can be estimated by the sum of the products of the transition
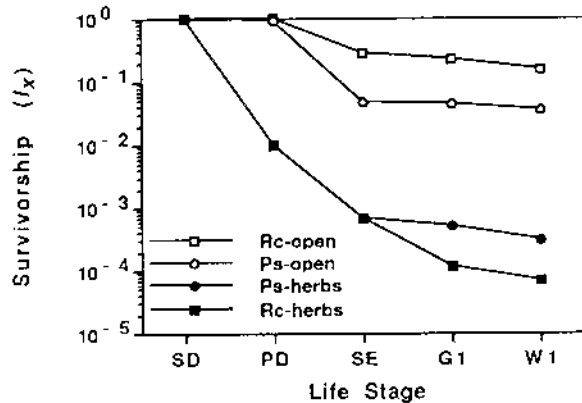

FIG. 16. Synthesis of survivorship (log scale) through the end of each early life stage from seed dispersal to the end of the first winter (i.e., beginning of the second growing season) for *Pinus strobus* (Ps) and *Rhamnus cathartica* (Rc) colonizing open microsites or microsites occupied by herbs. When the probability of transition through a life stage in a given experiment was zero (as for escape from predation under herbs in Fig. 2), the transition probability was set to 0.01. Data on post-dispersal survivorship of seeds are from Fig. 2, on seedling emergence from Fig. 6, and on seedling survivorship during the first growing season and winter from Fig. 7B–C. SD = seed dispersal, arbitrarily defined as 1.0; PD = post-dispersal; SE = seedling emergence; G1 = first growing season; W1 = first winter.

probabilities through each life stage (assuming probabilities are independent). This demographic model integrates the results of important regulating mechanisms during each of the early life stages and identifies the key factors controlling seedling establishment during the 1st yr of life. Establishment probabilities for both *Pinus* and *Rhamnus*, the two species for which data are available through all life stages, were estimated for seeds falling in the open vs. those falling among herbs.

Seeds of both species falling in the open were highly likely to escape predation (Figs. 2 and 16). The probability of survival from dispersal through successful emergence of seeds of *Rhamnus* landing in the open was much greater (0.28) than *Pinus* seeds falling in the open (0.05) (Fig. 16), because of the relatively greater rates of seedling emergence by *Rhamnus* in the open than under 1-yr-old herb canopies (Fig. 6). The probability that seeds of *Rhamnus* and *Pinus* landing in the open would produce seedlings that survived until the end of the first growing season (0.23 and 0.04, respectively) and until the beginning of the second growing season (0.15 and 0.03) were not much lower than their respective probabilities of emergence (Fig. 16), suggesting that for these species the major factor regulating establishment for seeds falling in the open was successful seedling emergence.

Seeds of *Pinus* and *Rhamnus* falling among herbs were all consumed within 6 d (Fig. 2), and establishment under herbs could be inhibited completely at this early life stage unless enough seeds were present to

TABLE 6. The probability that seedlings of wind-dispersed woody species beginning their second growing season could arise from seeds landing in open microsites compared to under herbs based on the year of seed input (0 = year of field abandonment).*

| | Probability of seed rain, survivorship, and seeding establishment | | | | | | | |
| | Into open | | | | Under herbs | | | |
Year of seed input	SR	×	L_x	=	PE	SR	×	L_x	=	PE
0	0.70		0.05		0.0350	0.30		0.008		0.0024
1	0.15		0.05		0.0075	0.85		0.008		0.0068
2	0.05		0.05		0.0025	0.95		0.008		0.0076
Cumulative probability					0.0450					0.0168

* Probability of seed rain (SR) into each type of microsite was estimated as the average relative frequency of each type during each year after abandonment (Gill 1987). Survivorship (L_x) from the time of seed dispersal to the beginning of the second growing season in openings (= 0.050) and under herbs (= 0.008) was assumed constant each year. Survivorship estimates based on averages for all species in experiments 1-6A. Probability of establishment (PE) of seedlings entering their second growing season was estimated as the product of probability of seed rain and survivorship in each microsite each year, and cumulative probability was the sum of annual establishment probabilities and does not account for attrition of seedlings after the beginning of the second growing season.

satiate consumers; however, we arbitrarily set this zero transition probability to 0.01 to continue to estimate survivorship through subsequent seedling life stages under herbs. While seedling emergence under herbs was often greater than in the open, the much greater seed predation reduced the probability of survival from dispersal through successful emergence for seeds of either species falling among herbs to 0.0007 (Fig. 16). The probability that seeds under herbs would produce seedlings that survived to the end of the first growing season (0.00012 and 0.0005, of *Rhamnus* and *Pinus*, respectively) and until the beginning of the second growing season (0.00007 and 0.00031) was much lower than in the open, due primarily to the tremendous loss of seeds and seedlings to predation (Tables 4 and 5, Figs. 7B–C and 16); predation, therefore, was the primary factor determining the establishment probability for seeds falling among herbs.

This demographic model highlights not only the overall lower probability of successful seedling colonization of early old fields by seeds falling among herbs, it also suggests important species–microsite interactions. In open microsites, seeds of *Rhamnus* were more likely to become established than seeds of *Pinus*; in contrast, under herbs, seeds of *Pinus* were more likely to become established seedlings than seeds of *Rhamnus* (Fig. 16). This suggests that the initial species composition of woody invaders of old fields will be influenced by the species composition of the seed rain and the abundance and distribution of open microsites in the field when seeds are dispersing. For instance, seedling establishment (when pooled over all species) was about an order of magnitude more likely for seeds that landed in the open than under herbs, but open microsites were only common during the 1st yr after field abandonment. During the autumnal seed dispersal period of many of the woody invaders (Table 2), herbs occupied 6–23% of the ground area just after corn was harvested from intensively managed fields, and over

90% in a poorly managed field; furthermore, during the autumn 1 and 2 yr after abandonment, herbs covered from 75 to 100%, and 86 to 100%, of the ground area, respectively (Gill 1987). The average amount of bare ground was ≈70, 15, and 5%, for corn, 1-yr-, and 2-yr-old fields, respectively; however, the frequency of bare patches of different sizes within fields was not measured. While it appears that bare patches need be only ≈30 cm across to affect seed and seedling predation (Figs. 4 and 14), the patch-size distribution and patch-size dependence of woody plant establishment in old fields need further study.

In the following analysis we assumed that the likelihood of landing in the open or under herbs for wind-dispersed seeds was proportional to the percentage of bare or herb-covered area within a field (probably a good assumption), that openings had the same effect regardless of size, and that all species of woody invaders behaved similarly in either microsite type (both somewhat weak assumptions). The year following abandonment there would be ≈14.6× as many seedlings of wind-dispersed species arising from seeds falling into openings as under herbs; in subsequent years, however, established seedlings were equally or more likely to arise from seeds landing among herbs, because the greater probability of establishment in openings was counterbalanced by the unlikelihood of seeds falling into open microsites (Table 6). For the first 3 yr after abandonment the cumulative probability of seedlings of wind-dispersed species arising from seeds falling in openings was ≈2.7× as likely as from those falling under herbs, primarily because of the increased probability of establishment in openings and the relative abundance of openings during the 1st yr (Table 6). This suggests that the composition of the first wave of woody species invading a given field depends heavily on which species adjacent to the field have large seed crops during the year of field abandonment, as has also been suggested by Bormann (1953), when many open

microsites exist. This increased success of early woody pioneers in open sites and the rapid decrease of openings early during succession may explain the fairly even age structure of populations of early woody invaders (Werner and Harbeck 1982, Rankin and Pickett 1989).

Seedlings of bird-dispersed species may be less likely to arise in openings, however, because input of seeds is largely restricted to areas under vegetation that is stout enough to serve as a perch (e.g., McDonnell and Stiles 1983, McDonnell 1986). This may explain in part the earlier colonization of many old fields by wind-dispersed woody species (Beckwith 1954, Buell et al. 1971, McDonnell 1986) and the more frequent occurrence of seedlings of bird-dispersed species under larger woody individuals, often of wind-dispersed species that arrived earlier (Beckwith 1954, Werner and Harbeck 1982, McDonnell 1986). Since seeds of bird-dispersed species are less likely to land in open microsites, one could hypothesize that bird-dispersed species might survive better than wind-dispersed species under prior colonists; however, our results for *Pinus* and *Rhamnus* (Fig. 16) were inconsistent with this hypothesis. Clearly, much additional field experimentation on species with different life histories, focused on particular life stages and in fields of varying characteristics, will be necessary to understand better the rich variety of mechanisms that regulate the colonization of old fields by woody species.

CONCLUSIONS

In summary, the establishment of an individual shrub or tree seedling during old-field succession is a very low probability event, and is less likely for seeds landing among herbs than in an opening. The succession of abandoned farmland to forest in the northeastern United States occurs only when sufficient seed input overcomes all of the forces that mitigate against woody plant establishment. The rate of invasion, the spatial distribution, and relative abundance of woody species colonizing a field depend initially on the proximity, fecundity, and mode of dispersal of the woody species that happen to be in adjacent hedgerows or forests. The spatial pattern of potential colonization initially imposed by seed rain into a recently abandoned field can be subsequently altered due to the patchy nature of herb cover, interactions among seed and seedling predators and their carnivores, and environmental conditions necessary for successful emergence. Seed and seedling predation were the two most important mechanisms regulating tree and shrub colonization, especially under herbs; the significantly greater rates of predation among herbs is a case of indirect inhibition. Increased seedling emergence, and increased seedling survivorship during periods of environmental stress, which occurred for some species in the presence of herbs, were consistent with the facilitation model; however, the increased risk of seed and seedling predation

under herbs more than offsets any advantages of association with herbs.

LITERATURE CITED

Abbott, H. G. 1961. White pine seed consumption by small mammals. Journal of Forestry 59:197–201.

Abbott, H. G., and T. F. Quink. 1970. Ecology of eastern white pine seed caches made by small forest mammals. Ecology 51:271–278.

Abul-Fatih, H. A., and F. A. Bazzaz. 1979. The biology of *Ambrosia trifida* L. Influence of species removal on the organization of the plant community. New Phytologist 83: 813–816.

Armesto, J. J., and S. T. A. Pickett. 1986. Removal experiments to test mechanisms of plant succession in old fields. Vegetatio 66:85–93.

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

Bazzaz, F. A. 1968. Succession on abandoned fields in the Shawnee Hills, southern Illinois. Ecology 49:924–936.

Beckwith, S. L. 1954. Ecological succession on abandoned farm lands and its relation to wildlife management. Ecological Monographs 24:349–375.

Billings, D. W. 1938. The structure and development of old field shortleaf pine stands and certain associated physical properties of the soil. Ecological Monographs 8:437–499.

Bormann, F. H. 1953. Factors determining the role of loblolly pine and sweetgum in early old-field succession in the Piedmont of North Carolina. Ecological Monographs 23: 339–358.

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.

Connell, J. H., I. R. Noble, and R. O. Slatyer. 1987. On the mechanisms producing successional change. Oikos 50:136–137.

Connell, J. H., and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. American Naturalist 111: 1119–1144.

Drury, W. H., and I. C. T. Nisbet. 1973. Succession. Journal of the Arnold Arboretum 54:331–368.

Egler, F. E. 1954. Vegetation science concepts. I. Initial floristic composition, a factor in old-field vegetation development. Vegetatio 4:412–417.

Elton, C. 1942. Voles, mice and lemmings. Problems in population dynamics. Clarendon, Oxford, England.

Fernald, M. L. 1950. Gray's manual of botany. American Book, New York, New York, USA.

Finegan, B. 1984. Forest succession. Nature 312:109–114.

Fowells, H. A. 1965. Silvics of forest trees of the United States. United States Department of Agriculture Forest Service Agriculture Handbook Number 271.

Gashwiler, J. S. 1967. Conifer seed survival in a western Oregon clearcut. Ecology 48:431–438.

Getz, L. L. 1959. Activity of *Peromyscus leucopus*. Journal of Mammalogy 40:449–450.

———. 1985. Habitats. Pages 286–309 *in* R. H. Tamarin, editor. Biology of new world *Microtus*. Special publication number 8. American Society of Mammalogists, Shippensburg, Pennsylvania, USA.

Gill, D. S. 1987. Woody plant colonization of old fields in central New York. Dissertation. Cornell University, Ithaca, New York, USA.

Goltz, S. M., G. Benoit, and H. Schimmelpfennig. 1981. New circuitry for measuring soil water matric potential with moisture blocks. Agricultural Meteorology 24:75–82.

Grubb, P. J. 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. Biological Reviews of the Cambridge Philosophical Society 52:107–145.

Hamilton, W. J. 1937. The biology of microtine cycles. Journal of Agricultural Research 54:779–790.

———. 1941. The food of small forest mammals in the eastern United States. Journal of Mammalogy 22:250–263.

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

Hicks, D. J., and B. F. Chabot. 1985. Deciduous forests. Pages 262–277 *in* B. F. Chabot and H. A. Mooney, editors. Physiological ecology of North American plant communities. Chapman and Hall, New York, New York, USA.

Hils, M. H., and J. L. Vankat. 1982. Species removals from a first-year old-field plant community. Ecology 63:705–711.

Horsely, S. B. 1977. Allelopathic inhibition of black cherry by fern, grasses, goldenrods and asters. Canadian Journal of Forest Research 7:205–216.

Hsiao, T. C. 1973. Plant responses to water stress. Annual Review of Plant Physiology 24:519–570.

Huston, M., and T. Smith. 1987. Plant succession: life history and competition. American Naturalist 130:168–198.

Jackson, J. R., and R. M. Willemsen. 1976. Allelopathy in the first stages of secondary succession on the Piedmont of New Jersey. American Journal of Botany 63:1015–1023.

Keever, C. 1979. Mechanisms of plant succession on old fields of Lancaster County, Pennsylvania. Bulletin of the Torrey Botanical Club 106:299–308.

Klatt, B. J., and L. L. Getz. 1987. Vegetation characteristics of *Microtus ochrogaster* and *M. pennsylvanicus* habitats in east-central Illinois. Journal of Mammalogy 68:569–577.

Klein, H. G. 1960. Ecological relations of *Peromyscus leucopus noveboracensis* and *P. maniculatus gracilis* in central New York. Ecological Monographs 30:387–407.

Kotler, B. P. 1984. Risk of predation and structure of desert rodent communities. Ecology 65:689–701.

Krebs, C. J., and J. H. Myers. 1974. Population cycles in small mammals. Advances in Ecological Research 8:267–399.

Marks, P. L., and C. L. Mohler. 1985. Succession after elimination of buried seeds from a recently plowed field. Bulletin of the Torrey Botanical Club 112:376–382.

McAuliffe, J. R. 1986. Herbivore limited establishment of a Sonoran desert tree, *Cercidium microphyllum*. Ecology 67:276–280.

McDonnell, M. J. 1986. Old field vegetation height and the dispersal pattern of bird-disseminated woody plants. Bulletin of the Torrey Botanical Club 113:6–11.

McDonnell, M. J., and E. W. Stiles. 1983. The structural complexity of old field vegetation and the recruitment of bird-dispersed plant species. Oecologia (Berlin) 56:109–116.

Mills, J. N. 1986. Herbivores and early postfire succession in southern California chaparral. Ecology 67:1637–1649.

Monk, C. D. 1983. Relationship of life forms and diversity in old-field succession. Bulletin of the Torrey Botanical Club 110:449–453.

Morris, W. F., and D. M. Wood. 1989. The role of lupine

in succession on Mount St. Helens: facilitation or inhibition? Ecology 70:697–703.

Neeley, J. A. 1965. Soil survey. Tompkins County, New York. United States Department of Agriculture, Washington, D.C., USA.

NOAA. 1985. National Oceanic and Atmospheric Administration, Climatological data, New York. Volume 97. National Climatic Data Center, Asheville, North Carolina, USA.

———. 1986. National Oceanic and Atmospheric Administration, Climatological data, New York. Volume 98. National Climatic Data Center, Asheville, North Carolina, USA.

Nomura, N. S., and W. H. Hilton. 1977. The adsorption and degradation of glyphosate in five Hawaiian sugarcane soils. Weed Research 17:113–121.

Oosting, H. J. 1942. An ecological analysis of the plant communities of Piedmont, North Carolina. American Midland Naturalist. 28:1–126.

Pearson, O. P. 1985. Predation. Pages 535–566 *in* R. H. Tamarin, editor. Biology of new world *Microtus*. Special publication number 8. American Society of Mammalogists, Shippensburg, Pennsylvania, USA.

Pickett, S. T. A. 1982. Population patterns through twenty years of oldfield succession. Vegetatio 49:45–59.

Pickett, S. T. A., S. L. Collins, and J. J. Armesto. 1987. Models, mechanisms and pathways of succession. Botanical Review 53:335–371.

Pigott, C. D. 1985. Selective damage to tree-seedlings by bank voles (*Clethrionomys glareolus*). Oecologia (Berlin) 67:367–371.

Radvanyi, A. 1970. Small mammals and revegetation of white spruce forests in western Alberta. Ecology 51:1102–1105.

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.

Schopmeyer, C. S. (Technical Coordinator). 1974. Seeds of woody plants in the United States. United States Department of Agriculture Forest Service Agriculture Handbook Number 450.

Smith, D. M. 1951. The influence of seed bed conditions on the regeneration of eastern white pine. Connecticut Agricultural Experiment Station Bulletin 545.

Smith, L. F. 1940. Factors controlling the early development and survival of eastern white pine in central New England. Ecological Monographs 10:373–420.

Snedecor, G. W., and W. G. Cochran. 1967. Statistical methods. Sixth edition. Iowa State University, Ames, Iowa, USA.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. Second edition. W. H. Freeman, New York, New York, USA.

Sork, V. L. 1987. Effects of predation and light on seedling establishment in *Gustavia superba*. Ecology 68:1341–1350.

Summerhayes, V. S. 1941. The effect of voles (*Microtus agrestis*) on vegetation. Journal of Ecology 29:14–48.

Torstensson, N. T. L., and A. Aamisepp. 1977. Detoxification of glyphosate in soil. Weed Research 17:209–212.

Van Hulst, R. 1978. On the dynamics of vegetation: patterns of environmental and vegetational change. Vegetatio 38:65–75.

vonAlthen, F. W. 1970. Methods of successful afforestation of a weed infested clay soil. Forest Chronicle 46:139–143.

Walker, L. R., and F. S. Chapin, III. 1986. Physiological controls over seedling growth in primary succession on an Alaskan floodplain. Ecology 67:1508–1523.

Walker, L. R., and F. S. Chapin, III. 1987. Interactions among processes controlling successional changes. Oikos 50:131–135.

Walker, L. R., J. C. Zasada, and F. S. Chapin, III. 1986.

The role of life history processes in primary succession on an Alaskan floodplain. Ecology 67:1243–1253.

Webb, D. P. 1974. Effects of competition on microclimate and survival of planted sugar maple (*Acer saccharum* Marsh) seedlings in southern Ontario. Great Lakes Forest Research Centre, Canadian Forestry Service, Department of the Environment, Report O-X-209, Sault Ste. Marie, Ontario, Canada.

Wellington, A. B., and I. R. Nobel. 1985a. Seed dynamics and factors limiting recruitment of the mallee *Eucalyptus incrassata* in semi-arid, south-eastern Australia. Journal of Ecology 73:657–666.

Wellington, A. B., and I. R. Nobel. 1985b. Post-fire recruitment and mortality in a population of the mallee *Eucalyptus incrassata* in semi-arid, south-eastern Australia. Journal of Ecology 73:645–656.

Werner, P. A., and A. L. Harbeck. 1982. The pattern of tree seedling establishment relative to staghorn sumac cover in Michigan old fields. American Midland Naturalist 108:124–132.

Whitaker, J. O. 1963. Food of 120 *Peromyscus leucopus* from Ithaca, New York. Journal of Mammalogy 44:418–419.

Wolff, J. O., R. D. Dueser, and K. S. Berry. 1985. Food habits of sympatric *Peromyscus leucopus* and *Peromyscus maniculatus*. Journal of Mammalogy 66:795–798.

Wood, D. M., and R. del Moral. 1987. Mechanisms of early primary succession in subalpine habitats on Mount St. Helens. Ecology 68:780–790.

Zutter, B. R., G. R. Glover, and D. H. Gjerstad. 1986. Effects of herbaceous weed control on a young loblolly pine plantation. Forest Science 32:882–899.

APPENDIX

Primary Study Sites

Hines Road.—The Hines Road site was in the middle of a 1.5-ha field ($\approx$440 m elevation) located 0.1 km northeast of the intersection of Trumbull Corners Road with Hines Road (42°23′ N, 76°38′ W). The field was abandoned from corn production for $\approx$20 yr, was occasionally mowed and grazed by horses for $\approx$10 yr, but was undisturbed for the last $\approx$10 yr. The vegetation in the field during 1986 was strongly dominated by *Solidago* spp., though a number of other forbs and grasses were present. A number of shrubs (mostly *Cornus racemosa* and *Viburnum dentatum*) and saplings (mostly *Fraxinus americana* and *Pinus strobus*) were present, particularly along the eastern edge of the field, but few woody species were present in the middle of the field where the experiments were performed. The southern edge of the field faces Hines Road and the other three sides are bounded by hedgerows dominated primarily by *Acer saccharum, Fraxinus americana,* and *Prunus serotina.*

The moderately to somewhat poorly drained channery silt loam (Langford series) at the site was derived from acidic (pH < 5.5) glacial till, and overlayed a largely impermeable fragipan (Neeley 1965).

Snyder Road.—The Snyder road site ($\approx$340 m elevation) was located 0.5 km east-northeast of the intersection of Warren Road with Snyder Road (42°30′ N, 76°27′ W). The study site was in the northwest corner of a field ($\approx$10 ha) that was abandoned from row crop agriculture for $\approx$15 yr. In 1986 the vegetation was strongly dominated by *Solidago* spp. with a mixture of other forbs and grasses. The site was bounded on the north and west by hedgerows (dominated by *Acer saccharum, Populus tremuloides, Fraxinus americana,* and *Carya* spp.), and on the east by woods (dominated by *Acer saccharum, Fagus grandifolia,* and *Quercus rubra*). The field was bounded on the south by Snyder Road and the northern edge of the Tompkins County Airport.

The moderately drained channery silt loam (Erie series) at the site was derived from acidic (pH 5–6) glacial till (Neeley 1965).

Teaching Farm.—The Teaching Farm ($\approx$300 m elevation, 42°26′ N, 76°26′ W) is $\approx$10 ha and is managed by the Section of Ecology and Systematics at Cornell University for instruction and demonstration of patterns and processes during secondary succession. The eastern edge of the farm abuts Turkey Hill Road, $\approx$0.3 km south of the intersection of Ellis Hollow Creek Road. The farm was planted with hay-field grasses and legumes, and for many years was grazed by domestic turkeys. Turkey production was abandoned in $\approx$1970. The site was largely undisturbed until 1982 when a number of 40 × 40 m plots were established. Buffer strips ($\approx$10 m wide) between the plots were mowed once a year, usually in midsummer. Most of the newly established experimental plots were mowed, herbicided (Roundup, active ingredient glyphosate), plowed, disked, and planted with corn. Corn was grown on these plots for 2 yr, and then several plots were abandoned each year (these were the abandoned corn plots of Experiment 8). Several plots remained untreated as "controls," which were dominated mostly by shrubs, primarily *Cornus racemosa, Viburnum dentatum,* and *V. lentago,* but one also had a number of individuals of *Pinus strobus* emerging above the shrubs (these were 15s and 15p "control" plots in Experiment 8). Several other plots were mowed, but not herbicided or plowed, to set back the shrubs and favor the perennial herbs, mostly goldenrods and grasses (one of these was used in Experiments 4 and 5).

A mosaic of several moderately to somewhat poorly drained silt loams across the site was derived primarily from acidic (pH < 5.5) glacial till, and in most places overlayed a largely impermeable fragipan (Neeley 1965).

Turkey Farm.—The Turkey Farm field ($\approx$3 ha), managed by Cornell University Farm Services, had been in a rotation of corn and oats for at least 15 yr. The study site ($\approx$70 m east-west × 50 m north-south) was located in the western end of the field and was abandoned from agriculture in the fall of 1983. The site ($\approx$290 m elevation) was $\approx$0.4 km west-southwest of the intersection of Ellis Hollow Creek Road with Turkey Hill Road (42°26′ N, 76°26′ W). During 1985 the field was in its 2nd yr after abandonment, and was densely covered with herbs (primarily *Phleum pratense, Barbarea vulgaris, Erigeron* spp., *Trifolium* spp., and *Solidago* spp.). The site was bounded on the north by woods dominated by large *Pinus strobus,* with a vigorous subcanopy of *Acer saccharum, Fagus grandifolia,* and a few other hardwood species. A shrub thicket on the west was similar to that described for the Teaching Farm "control" plots. Corn and oats were still being grown in the field to the east of the site.

The soil at the site was derived from acidic (pH 5–6) glacial outwash, with a well-drained gravelly silt loam (Chenango series) along the northern edge of the site grading into a moderately well-drained gravelly silt loam (Braceville series) toward the south (Neeley 1965).

The Turkey Farm site and the Teaching Farm site are only $\approx$200 m from each other; however, it should be noted that they had different histories, soils, and somewhat different vegetation. Both sites were formerly part of the Reed Farm.