Experimental Studies of Hickory Recruitment in a Wooded Hedgerow and Forest

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McCARTHY, B. C. (Department of Environmental and Plant Biology, Ohio University, Athens, OH 45701). Experimental studies of hickory recruitment in a wooded hedgerow and forest. Bull. Torrey Bot. Club 121: 240–250. 1994. — An examination of the vegetation in and around an old-growth oak-hickory forest in Central New Jersey suggested that hickories (*Carya* spp., Juglandaceae) were not regenerating in the forest at the same rate as in adjacent wooded hedgerows (5–7 m wide corridors dominated by trees and shrubs). The goal of this study was to experimentally examine how factors affecting seed and seedling survival might account for these differential recruitment patterns in contrasting landscape elements. To determine seed discovery efficiency by small vertebrates, I planted seeds of mockernut hickory (*C. tomentosa* (Poir.) Nutt.) with and without their aromatic husk in both forest and hedgerow. Regardless of diaspore type or habitat, seed discovery by herbivores was found to be 85–100% after only 5 days. Gray squirrels (*Sciurus carolinensis*), the principal predator–disperser, were determined to be equally abundant in both landscape elements. To assess the effects of diffuse competition and predation on seedling establishment and survival, I constructed split-plot shade/exclosure cages into which 576 seedlings were explanted and subsequently monitored (survival and mortality agent) for three years. Browsing by deer and rabbits resulted in considerable mortality after one year, particularly in the forest (64% mortality) compared to the hedgerow (21% mortality). During the second year, the major source of mortality switched to physiological stress resulting from drought. Mortality due to drought stress was more noticeable in the hedgerow. By the end of the third year few seedlings remained alive (ca. 1% in forest, 10% in hedgerow). Over the 3-yr period, a small percentage of seedlings were lost due to other factors such as root grubbing, whole plant removal, and litterfall. Shading (50%), to emulate diffuse competition by overstory, was not found to affect survival to any significant extent in either habitat. Phytophagous insects did not result in any observable mortality but did remove 1–10% of the leaf area of the majority of seedlings in both habitats in each field season. I conclude that certain stages of recruitment may be significantly influenced by the presiding landscape element.

Key words: *Carya tomentosa*, hedgerow, herbivory, landscape ecology, New Jersey, oak-hickory vegetation, population dynamics, seed predation, seedlings.

Hickories (*Carya* spp., Juglandaceae) are an important component of many forest associations in the eastern United States (Braun 1950; Burns and Honkala 1990). They typically co-occur with oaks (*Quercus* spp., Fagaceae) and share many life history attributes (e.g., anemophilous pollination, monoecious breeding system, masting habit, seed predation and dispersal by small mammals, intermediate to in-tolerant shade tolerance, etc.). The importance of hickory in pre-settlement forests of the mid-Atlantic region has been well documented (Braun 1950; Spurr 1951; Russell 1980; Delcourt and Delcourt 1987; Webb 1988). In recent years, numerous investigators have examined overstory-understory relations in eastern deciduous forests and concluded that many late successional species such as hickories and oaks are failing to re-place themselves and are likely on a regional decline (Buell et al. 1966; Good 1968; Keever 1973; Christensen 1977; Sork 1983b; Parker et al. 1985; McCarthy et al. 1987; Nowacki and Abrams 1991; Abrams 1992). Understories in mixed oak and oak hickory forests are typically domianted by shade tolerant maple species (*Acer rubrum* and *A. saccharum*) (Lorimer 1984). Even where intermediate and intolerant species can be found in the understory, little recruitment is expected into larger size classes (Adams and Anderson 1980; Lorimer 1984; Fralish 1988).

Much of the failure to perpetuate forests of intermediate and intolerant species composition is believed to be associated with changing disturbance regimes and land use patterns accom-

panying European settlement (Russell 1980; Crow 1988). Natural and anthropogenic fire by native Americans was common in the mid-Atlantic states region during precolonial times (Buell et al. 1954; Russell 1983; Abrams 1992). Following European settlement, fire and logging continued to perpetuate vegetation composed primarily of shade intolerant species. In addition to fire and logging, European settlement also resulted in a dramatic change in the physical configuration of the forested landscape. What was a relatively homogeneous cover of forest vegetation in various successional stages became an increasingly fragmented landscape of woodlots, hedgerows, and agricultural fields (Perlin 1989). Thus, present day landscapes in the mid-Atlantic region are extremely heterogeneous and comprised of many types and sizes of patches (e.g., forests, woodlots, hedgerows, utility corridors, old-fields, agricultural fields, development).

The recognition of the importance of landscape composition and dynamics has provided the foundations of landscape ecology (Forman and Godron 1981, 1986; Naveh and Lieberman 1984; Turner 1989). Landscape ecology has been instrumental in highlighting the need to consider the spatial context of ecological processes and interactions; i.e., patch type is ecologically important. For example, we know that there are considerable differences in the biotic and abiotic structure of certain landscape elements, such as wooded hedgerows and intact forests (Forman 1983; Forman and Baudry 1984; Forman and Godron 1986); however, few studies have utilized an experimental approach towards elucidating the ecological consequences of patch type on the regeneration of intermediate and/or intolerant hardwoods (however, see Sork 1983b).

Observations in and around an old-growth oak-hickory forest in central New Jersey suggested that hickories were not regenerating (i.e., low abundance of seedlings and saplings) in the intact forest, but, were more abundant in adjacent hedgerows (3-storied, 5–7 m wide corridors dominated by trees and shrubs). This prompted me to address the general question of how patch type (landscape element) may be influencing the regeneration of mid- and intolerant tree species in the current landscape configuration. Since the two patch types have markedly different abiotic environments and therefore presumably different biotic interactions, I hypothesized that tree regeneration patterns would be markedly different and that intolerant species might maintain their dominance in certain patch types. More

specifically, the objectives of this study were to determine if (1) seed predation patterns differed between hedgerow and forest, (2) seedling establishment and survival patterns differed between the two landscape elements.

Methods. STUDY SITE. Fieldwork was conducted at the Hutcheson Memorial Forest (HMF), formerly Mettlar's Woods, located in Somerset County, New Jersey (40°30'N, 74°34'W). HMF is a 25 ha tract of old-growth forest surrounded by a matrix of old fields, agricultural lands, wooded hedgerows, and rural/suburban development. Somerset County experiences a subcontinental temperate climate with 112 cm mean annual precipitation and a mean annual temperature of 11.7 C (Robichaud and Buell 1973). Forests of the region are considered either as oak-hickory or mixed oak (Robichaud and Buell 1973; Forman and Elfstrom 1975) and were included in the oak-chestnut region of Braun (1950). The forest exists on soils derived from the Triassic red shales of the Piedmont (Wolfe 1977). The soils are generally classified as Penn Shaly Silt Loams (Kirkham 1976).

All studies were conducted at the southern end of the forest and in an adjacent hedgerow. Further details regarding the vegetation and a photograph of the hedgerow can be found in Forman and Godron (1986: fig. 4.8) and Forman and Baudry (1984). Oddly, mature hickories (*Carya* spp.) were not described as being present in these hedgerows by Forman and Godron (1986); however, trees of 35–55 yr were fairly common (see study trees listed in McCarthy and Quinn 1989, 1990). Voucher specimens of *Carya* collected at HMF are on file at the Chrysler herbarium of Rutgers University.

MICROENVIRONMENTS OF HEDGEROW AND FOREST. Hedgerows have markedly different microenvironments than interior forest (Forman and Godron 1986). Light and soil moisture are two factors that are likely to influence the recruitment of tree species. To assess the microenvironment of the hedgerow and forest, I placed a 50 m transect in the vicinity of my study plots and collected data on light and soil moisture at 1 m intervals. Fifty photosynthetic photon flux density (PPFD) measurements were recorded at a height of 0.5 m using an analog LiCor light meter and reported as $\mu mol \cdot m^{-2} \cdot sec^{-1}$ in both the hedgerow and forest. Light was characterized on one clear day in July 1988 between 11:00 and 13:00 hr. Soil moisture was determined gravi-

metrically at the same 50 points. Soil moisture was determined once in May (spring) and again in July (summer) of 1988. Likewise, soil moisture was sampled at four random points within shaded and unshaded portions of the experimental cage units.

SEED PREDATOR-DISPERSER ABUNDANCE. The primary seed dispersal agent (and seed predator) for hickory at HMF is the gray squirrel. Because squirrels have been shown to have a marked effect on seed germination success (Barnett 1977) and seedling recruitment (Sork 1983b), and because the behavior of gray squirrels has been shown to be very sensitive to vegetative cover and habitat configuration (Lima et al. 1985; Lima and Valone 1986; Newman and Caraco 1987; Newman et al. 1988), I also examined their distribution and abundance patterns in the two patch types. To determine the usage frequency of hedgerow and forest by gray squirrels, I live-trapped squirrels using ten Hav-a-heart® traps placed at 10 m intervals along a 100 m transect in each habitat. Each trap line was run for a period of 5 days in three separate trapping periods (spring, summer, autumn) for 3 consecutive years (1987, 1988, 1989). Squirrels were aged using tail-pelage characteristics (Sharp 1958) and categorized as either juvenile, sub-adult, or adult. Sub-adults and juveniles were later merged into one category (juvenile) because of the small number of sub-adults trapped. In addition, each squirrel was sexed, weighed (g), and ear-tagged. Ear-tagging provided an identity label from which I was later able to determine what proportion of squirrels were residents vs. transients. Data were analyzed using the G-test of Sokal and Rohlf (1981).

SEED DISCOVERY EXPERIMENT. To determine what proportion of seeds are actually discovered by predator-dispersers in each patch type, I conducted a seed predation experiment. Technically, the diaspores of Carya are 1-seeded nuts; however, for convenience I will refer to them henceforth as seeds. Seeds were collected from one particularly fecund mockernut hickory (Carya tomentosa (Poir.) Nutt.) tree at HMF during the late summer and autumn of 1987. Seeds were collected at two dates, once in late August when the nuts still had an intact, green, aromatic husk, and again in late September when many of the husks had dried and dehisced from the nut. The importance of the aromatic husk (juglone, 5-hydroxy-1,4-naphthoquinone; Gilbert et al. 1967) in seed discovery by squirrels has never

been investigated (Stapanian and Smith 1984) so was included in the design of this experiment. Thus, nuts were designated as either "with husk" or "without husk." In mid-October, three paired seed plots (5 × 5 m) were established in both the hedgerow and forest. Each plot received twenty-five seeds placed on the 1 m intersecting grid points. Seeds were placed under the leaf litter in a small depression (similar to nut-caching behavior of squirrels). Rubber gloves and a disposable EPA hazardous waste suit were worn to decrease possible human scent cues. No flagging or any other type of marking was used to indicate plot locations, thus reducing visual cues to seed predator-dispersers. The number of undiscovered nuts remaining after five days and fourteen days was recorded. Data were analyzed using the G-test (Sokal and Rohlf 1981).

SEEDLING EXPERIMENTS. The same half-sib seeds collected from HMF in 1987 (above) were used to generate seedlings in the Rutgers University greenhouse. Approximately 1000 seeds were placed in flats containing potting mix, watered, and placed in a cold room for stratification at 5°C for 120 days. In February, flats were transferred to the greenhouse where seeds were allowed to germinate. After 30 d, germinated seeds (ca. 90%) were removed from the flats and placed in 10 cm plastic pots. Seedlings were grown for 90 d, during which time they were watered daily and fertilized (20:20:20 NPK, Peters Soluble Fertilizer) twice (at 30 d and 60 d). In early May, 576 seedlings were selected for uniformity in height, number of leaves, and leaf quality, and subsequently used for field experiments.

Both biotic and abiotic pressures may differ greatly between forest and hedgerow habitats. Regular periods of observation at HMF indicated that rabbits and deer were more abundant in the forest than in the hedgerow. Additionally, measurements and observations in 1987 and other published studies (e.g., Forman and Godron 1986) indicate that the microenvironment of the hedgerow was significantly different from that of the forest. From these data, I hypothesized that both solar radiation and browsers were probably influencing early recruitment patterns in the hedgerow and forest. Therefore, I designed paired plots to examine the effects of shading ("diffuse competition") and herbivores ("predation"). The experimental units were constructed of standard 2 × 4 inch (5 × 10 cm) lumber and roughly measured 2 × 2 × 4 m (H × W × L) in size; each unit was split in half along the

long dimension and received protection from herbivores using 2.5 cm mesh "chicken wire" to a height of 1 m. One unit of each pair was randomly selected to receive a covering of 50% shade cloth (Fig. 1). Three replicate experimental units were placed in both the forest and hedgerow. Forty-eight seedlings were planted in each unit such that 24 were protected from herbivores (caged) and 24 were exposed (uncaged).

At seven sample periods over a 3-yr period, each of the 576 seedlings was visited to score survival and seedling quality. If a seedling was damaged or killed, the mode of disturbance was recorded. Leaf damage due to phytophagous insects was visually evaluated and scored by categories of leaf area removal: <10%, 10–50%, >50%. Mortality was assessed and categorized into five groups: rooting (seedling dug up by squirrel and germinating nut removed), browsing (whole shoot removal), drought (seedling intact but brown and dry), pulling (fully removed from planted position), litter (falling tree branch). Even though individual plants were followed over time, "survival" and "mortality" must still be loosely interpreted because *Carya* seedlings are vigorous resprouters after browsing. In this study, a browsed seedling was scored as dead when no aboveground plant parts were discernible; however, this same seedling could potentially resprout at an undetermined time in the future. Several seedlings in this study were observed to resprout after being browsed. However, the vast majority (>98%) were truly dead when all aboveground parts were missing.

Survival and mode of mortality frequency data were analyzed using log-linear models (Hintze 1987). Full models were analyzed for all four terms: date (seven sample periods), location (hedgerow or forest), shade (with or without shade cloth), and exclosure (caged or open). Partial association probabilities were estimated for terms individually and all possible combinations to test for interactions.

Results. MICROENVIRONMENT OF HEDGEROW AND FOREST. The light environment of the hedgerow was considerably more heterogeneous than that of the forest. Light values in the hedgerow ranged from 5 to 1200 $\mu mol \cdot m^{-2}sec \cdot^{-1}$ while those in the forest ranged from 3 to 160 $\mu mol \cdot m^{-2} \cdot sec^{-1}$ (Fig. 2). Average light intensity was greater in the hedgerow compared to the forest ($P < 0.001$, Mann-Whitney U-test).

Soil moisture was not as variable between the two landscape elements. The spring of 1988 re-
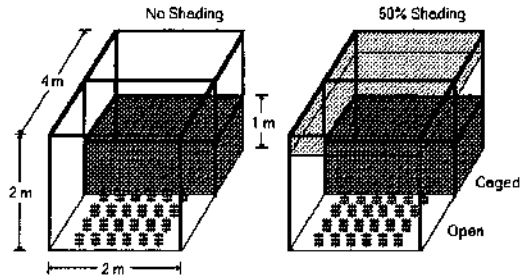

Fig. 1. Paired experimental units used in seedling experiments. Each unit is constructed of standard 2 × 4 inch (5 × 10 cm) lumber. N = 48 seedlings per single unit (24 exposed to herbivores, 24 protected from herbivores). One unit was randomly selected to receive 50% shade cloth. Three replicate pairs were erected in each landscape element.

ceived average rainfall (NOAA 1988) and soil moisture was found to be generally high (40–50%) in both habitats. No significant difference in soil moisture was observed between habitats in the spring ($P > 0.05$, Mann-Whitney U-test). Regional rainfall during the summer of 1988 was well below normal (NOAA 1988). At this sampling period, hedgerows were observed to have considerably drier soils ($P < 0.01$, Mann-Whitney U-test). Soil moisture beneath shade cloth plots never differed significantly from unshaded plots within the same landscape element at any sample date (all $P > 0.10$).

SQUIRREL DISTRIBUTION AND ABUNDANCE. A total of 39 squirrels were trapped over the nine sample periods (Fig. 3). Recaptures within a sample period were common; recaptures between sample periods were uncommon. Ear tags were occasionally ripped out but all animals could still be re-identified based on pelage characteristics, sex, and weight. Adults were 3–5 times more abundant than juveniles/sub-adults (Fig. 3). There were no differences in the total number of squirrels in the hedgerow compared to the forest ($P > 0.10$, G-test). Sex ratios were roughly equal within age categories and habitats except for the forest where a male bias was evident ($P < 0.05$, G-test). The small number of captures prevented further statistical testing within sample periods.

SEED DISCOVERY EXPERIMENT. Of the 300 nuts used in this experiment, 285 (95%) were discovered and removed within 5 days. Within the hedgerow, 72 of 75 (96%) nuts with husks were discovered compared to 75 of 75 (100%) without husks. Within the forest, 66 of 75 (88%) nuts with husks were discovered compared to 72 of 75 (96%) nuts without husks. Apparently, naive
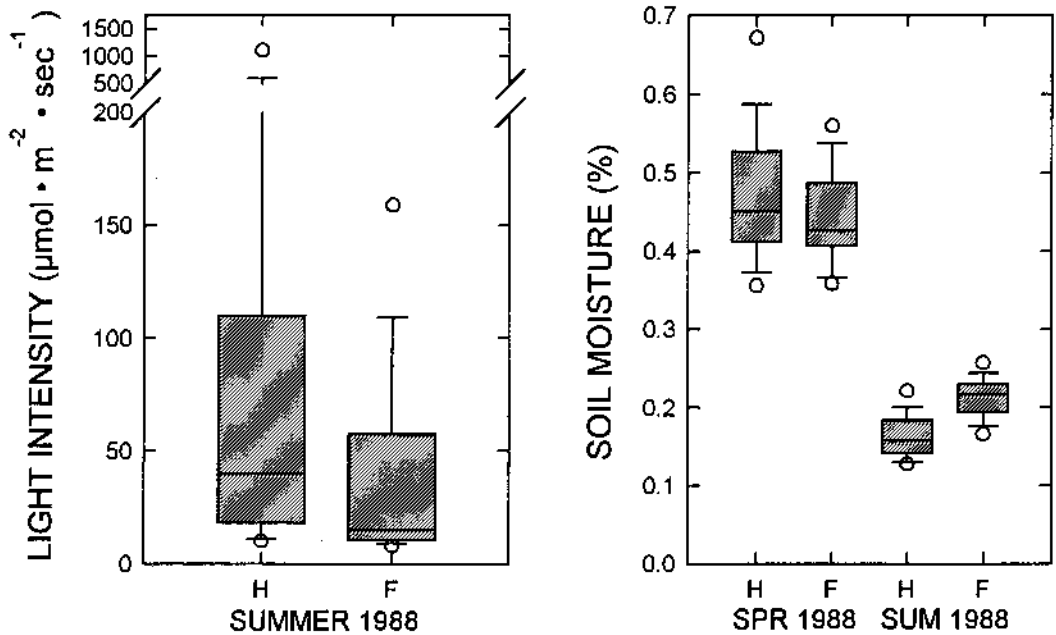
Fig. 2. Box plot summaries of microenvironmental characterization of hedgerow (H) and forest (F). Shaded box represents interquartile range (middle 50% of data), horizontal line is the median, vertical lines represent 95% CI, lower and upper circles, represent minimum and maximum values, respectively. Light intensity was measured at midday on a clear day (see text).

foragers do not rely on the aromatic husk as a scent cue. There was no relationship between diaspore condition and landscape position with regards to the proportion of nuts discovered ($G = 0.04$, df = 1, $P > 0.50$).

SEEDLING EXPERIMENTS. Log-linear analysis indicated that a model containing three factors was necessary to adequately describe seedling

Fig. 3. Summary of three years of live-trapping data for gray squirrels. Sub-adults have been compressed into juvenile category due to very small sample sizes. There is no significant relationship between age and location (G-test, $P > 0.10$). There is a significant ($P < 0.05$) sex bias towards male dominance in the forest.

survival patterns. Subsequent chi-square term analyses indicate that date, location, and exclosure are the most important elements in the model (Table 1). Shade may have been a contributing factor, but single order and higher models containing this term were generally not significant.

A detailed analysis of survival frequencies (Fig. 4) suggested that seedlings not protected from herbivores have the lowest probability of survival. Uncaged seedlings in the forest suffered disproportionately high mortality compared to those in the hedgerow (Table 1; Fig. 4). Seedling survival after 3 yr was quite low (4 to 20%). Survival in the hedgerow was almost 5 times greater than that of the forest after three years (Fig. 4).

While five modes of mortality were observed, only four (rooting, browsing, drought, and pulling) contributed 5% or more to overall mortality patterns. Unlike survival patterns, log-linear analysis suggests that first order models are generally adequate to describe mortality patterns, with the possible exception of drought death. Again, date, location, and exclosure were the most important terms (Table 2). Shading did not decrease mortality associated with drought in either location.
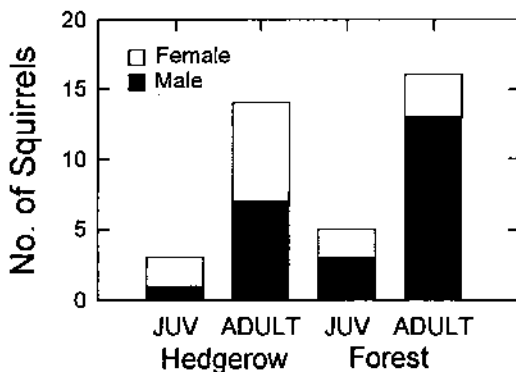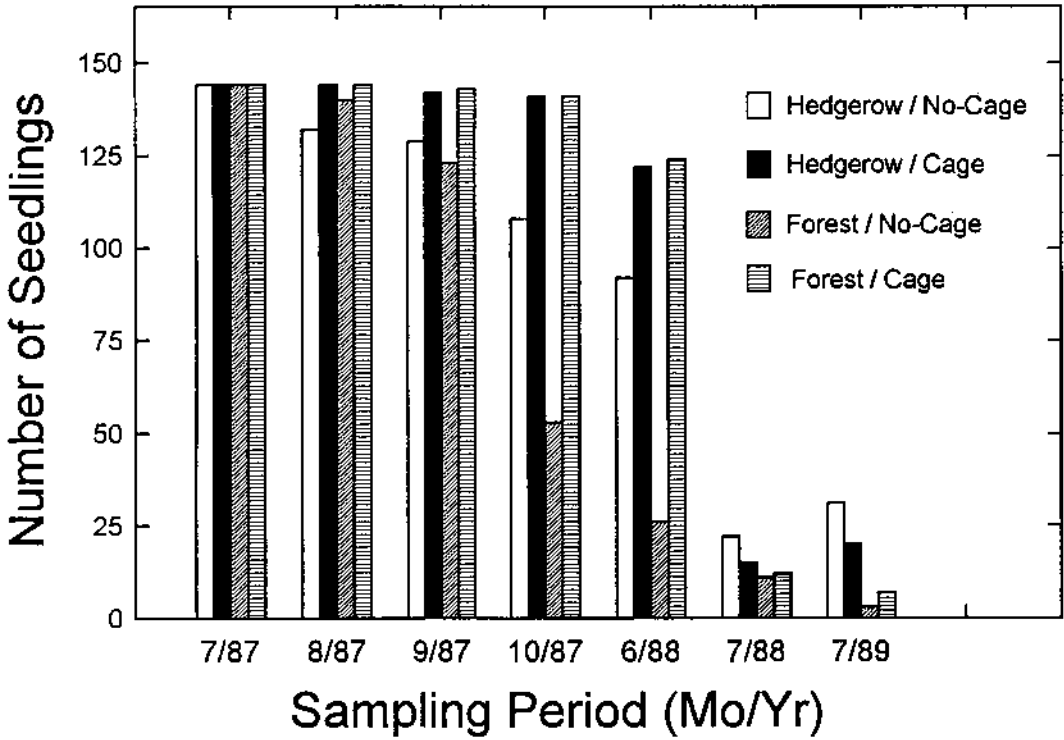
Fig. 4. Number of seedlings surviving for three years. There were 144 seedlings in each combination of location and exclosure treatment at the start of the experiment (576 total). Survival was measured by stem presence. Some treatments may have experienced an increase in later sample periods due to resprouting.

Seedling mortality patterns for the four modes of mortality indicate that root digging and plant pulling were an order of magnitude less important than browsing and drought stress (Fig. 5). Root grubbing only occurred during the first year and was more prevalent in the forest than the hedgerow (Table 2; Fig. 5). Root grubbing is most likely the result of squirrels attempting to acquire the seed while it is still in organic attachment to the young seedling. Whole plant removal by pull-

Table 1. Detailed chi-square term analysis and partial associations for best 3-way log-linear model describing hickory seedling survival. Levels of main effects are described in text.

| | | Partial association | |
| | | Chi- | |
Effect	df	square	P
Date	6	1057.88	0.0001
Location	1	11.23	0.0008
Shade	1	1.08	0.2993
Exclosure	1	31.22	0.0001
Date × Location	6	41.72	0.0001
Date × Shade	6	15.22	0.0186
Date × Exclosure	6	54.17	0.0001
Location × Shade	1	0.07	0.7861
Location × Exclosure	1	12.58	0.0004
Shade × Exclosure	1	0.24	0.6274
Date × Location × Shade	6	6.24	0.3973
Date × Shade × Excl	6	32.5	0.0001
Location × Shade × Excl	1	0.06	0.8009

Table 2. Detailed chi-square term analysis and partial associations for best 2-way log-linear model describing hickory mortality patterns. Levels of main effects are described in text.

| | Likelihood ratio probabilities† | | | |
K-terms	Rooting	Brows-ing	Drought	Pulling
Date	****	****	****	****
Location	****	****	****	****
Shade	*	**	ns	*
Exclosure	****	****	****	****
Date × Location	ns	ns	ns	ns
Date × Shade	ns	ns	ns	ns
Date × Excl	ns	ns	ns	ns
Loc × Shade	ns	ns	ns	ns
Location × Excl	ns	ns	****	ns
Shade × Excl	ns	ns	**	ns

† Probabilities: * = 0.05, ** = 0.01, **** = 0.0001, ns = not significant (P > 0.05).

Roots Dug Up

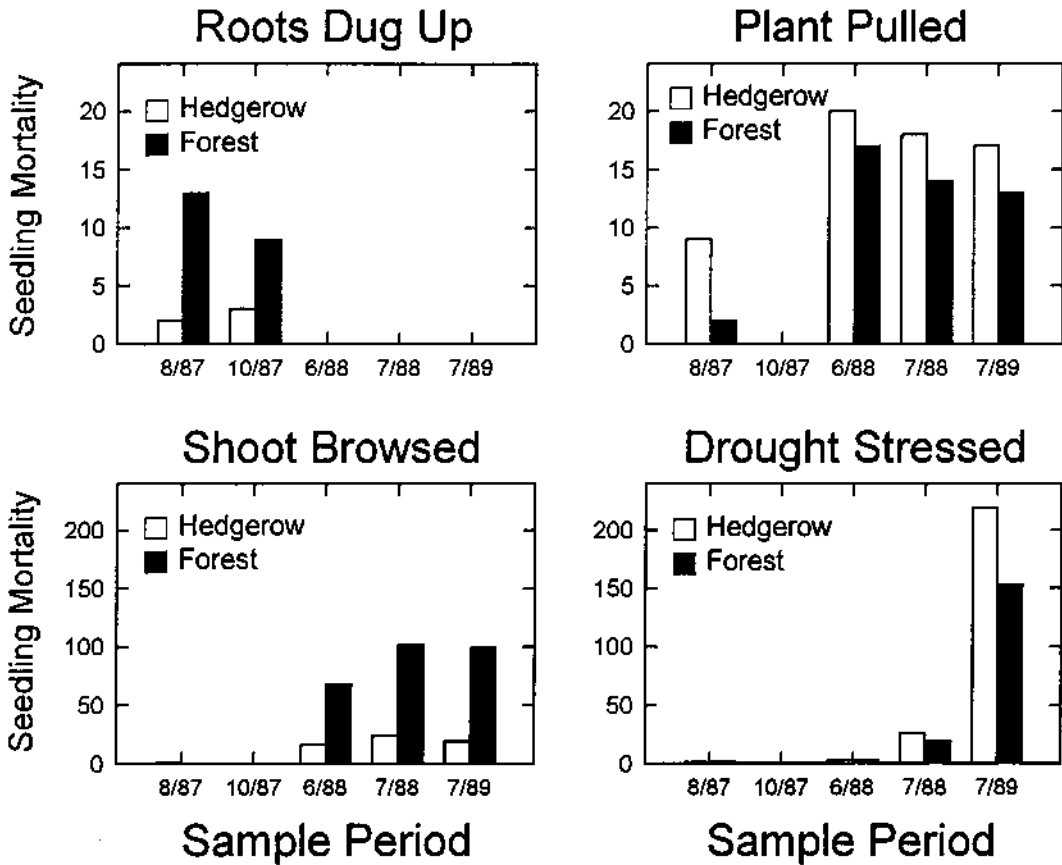## Plant Pulled

Shoot Browsed

Drought Stressed

Fig. 5. Number of seedlings dying as a function of rooting, pulling, browsing, and drought. Two seedlings died due to unknown causes and are not recorded here. Mortality frequency was recorded at five sample periods (month/year).

ing was more prevalent in the hedgerow. The vast majority of plants were lost due to browsing and drought, but mortality patterns differed by location. Mortality due to browsing was more common in the forest, while mortality due to drought was more common in the hedgerow (Table 2; Fig. 5).

Phytophagous insects did not result in the direct death of any seedling during the three years of this study. However, virtually every seedling (574 of 576) had some leaf area removed (LAR) at some time. Approximately 86% of all seedlings suffered <10% LAR, 9% suffered 10–50% LAR, and 5% had >50% LAR. No significant ($P >$ 0.05, G-tests) patterns associated with year, location, exclosure, or shading were observed.

Discussion. Previous studies of *Carya* at the same study site have demonstrated that 40–60% of potential seeds (pistillate flowers) are lost prior to fruit set (McCarthy and Quinn 1989, 1990);

an additional 50–80% of set fruits never reach full maturity (McCarthy and Quinn 1992), resulting in only 10–20% of potential seeds able to serve as new recruits prior to abscission from the tree. Results from this study indicate that probably less than 10% of seeds arriving at the ground are able to escape detection by seed predator-dispersers (what proportion is consumed and what proportion is dispersed and not recovered is unknown) and only 10% of those escaping predation remain as recruits three years after establishment. Thus, 99.9+% of all possible recruits appear to be lost during the first three years. The extent to which this pattern holds for other eastern hardwoods is unknown because considerably less demographic data are available for woody plants relative to herbaceous plants (Harper 1977; Fenner 1985).

SEED PREDATION. Post-dispersal seed predation appears to be a major factor limiting seed-

lings recruitment. Hickory nuts are large and extremely nutritious relative to the propagules of most other eastern hardwood tree species (Waino and Forbes 1941; Smith and Follmer 1972; Havera and Smith 1979; Abrahamson and Abrahamson 1989) and the fact that hickory nuts are a highly preferred food item for small mammals has been well documented (Martin et al. 1951; Nixon et al. 1968; Smith and Follmer 1972; Barnett 1977; Sork 1983b). Barnett (1977) reported that 90% of all hickory nuts are removed from the ground by squirrels. Sork (1983b) discovered that 7–29% of all nuts were removed by the end of the first wk; after 12 wk <40% of seeds remained, none of which were viable. I observed ca. 90% removal during the first 5 days and virtually complete removal after 2 wk using only viable seeds (pre-experiment float test). This suggests that viable nuts are discovered and removed almost immediately after abscission from the tree.

Barnett (1977) and Sork (1983a) concluded that artificial burial did not necessarily increase survival. Squirrels were equally likely to discover a nut whether they buried it or not. Squirrels apparently use scent cues to discover the location of nuts (Calhane 1942) so a large proportion of nuts will always be discovered even by naive animals. The scent cue is apparently not associated with the aromatic husks because nuts planted with and without husks experienced similar discovery rates. Evidently, any nut arriving on the ground or buried has a very low probability of escaping detection.

Previous studies by Lewis (1982) and Stapanian and Smith (1978, 1984) have demonstrated that nut survival decreases with an increase in nut density. This observation suggests that squirrels are able to recognize differences in nut densities and devote correspondingly more time to foraging in areas with high densities. Stapanian and Smith (1984) noted that foraging decisions could be as sensitive as one nut per 25–100 m^2 (i.e., 5–10 m internut planting distance). One might argue that my 1 m internut planting density biased the experiment towards complete removal. However, this ignores the density of the natural seed rain around mature hickory trees which is much greater than my planting density (pers. obs.). Thus, my density is much less than ambient and probably is a good reflection of the ability of squirrels to find nuts which have been abscised from a mature canopy tree. Further, squirrels rarely venture from the hedgerow to adjacent old-fields due to increased predation risk

(Newman and Caraco 1987) or from the hedgerow to the forest (no squirrels caught in this study migrated between the two patches) suggesting that most nuts dehisced from trees in the hedgerow are either consumed or dispersed in that hedgerow. Thus, nut densities are quite high on the hedgerow floor.

Clearly, seed dispersal and predation may vary in relation to habitat structure, squirrel foraging ability, and squirrel vulnerability to predation (Sork 1983b; Stapanian and Smith 1984). There appear to be distinct foraging constraints in gray squirrels relative to feeding behavior and patch-use patterns (Newman and Caraco 1987; Newman et al. 1988). In high risk patches (i.e., those with minimal cover), squirrels consumed seeds faster, handled seeds faster, and traveled faster among patches (Newman et al. 1988). One would therefore expect that seed discovery in hedgerows might be less because squirrels would spend less time foraging due to the increased exposure to predators. However, this was not observed in this study. I found that seeds were equally likely to be found in either the wooded hedgerow or forest. Structural and compositional characteristics of the hedgerow may be important in influencing squirrel feeding behavior. My study hedgerow was relatively wide (5–7 m), had a complex structure (3-storied), and had highly preferred food species. A narrower hedgerow with a more homogeneous structure and fewer preferred food species might experience quite different plant-animal interactions.

SEEDLING ESTABLISHMENT. There is a growing body of evidence which suggests that biotic and abiotic effects may have their greatest influence at the earliest stages of reproduction (Grubb 1977; Cook 1979). Assuming a seed can escape detection by a predator, or is not recovered by a caching disperser, there is still only a very small likelihood (<10%) that the seedling will be alive after 3 years. Large browsing vertebrates seem to exert a considerable influence on seedling survival and successional patterns (Crawley 1983). Over 50% of all seedling mortality in this study was attributable to vertebrate browsing. Likewise, Myster and McCarthy (1989) found that predation by browsers was the primary factor limiting establishment of *Carya* seedlings in old-fields.

The effects of shade on seedling survival in different habitats are unclear. I found virtually no effect of diffuse competition (simulated with 50% shade cloth) on seedling survival in either hedgerow or forest. Likewise, Myster and Mc-

Carthy (1989) found that shading by herbs did not significantly alter performance or survival of *Carya* seedlings in old-fields. While De Steven (1991a) and Gill and Marks (1991) found that herbs may actually facilitate woody seedling emergence and establishment by interfering with visually oriented foragers, both studies found that tall neighboring herbs did ultimately have a negative effect on survival and performance of certain tree species. *Carya* spp. are at the extreme end of the temperate seed size continuum and I suspect that the size of seed reserves is most important in determining early competitive ability (cf. De Steven 1991a, 1991b). Seedlings originating from large animal-dispersed seeds will perform better in the face of herbaceous competitors than will small wind-dispersed seeds.

To a certain extent, the effects of competition may be mitigated by microsite conditions. McCarthy and Facelli (1990) determined that there are certain "safe sites" (sensu Harper 1977) that will promote tree seedling survival. For example, seedling models placed under a thorny *Rosa multiflora* shrub had a much higher probability of survival than those in sparse to medium herb cover only. Thus, microhabitat plays an important role in establishment and survival.

In addition to direct biotic pressures, there are indirect biotic influences (e.g., trampling), abiotic stresses (drought, frost-heaving), and random mortality agents (falling macrolitter). Using seedling models, McCarthy and Facelli (1990) determined that these other agents can also contribute significantly to seedling mortality. Seedling damage or mortality due to falling litter was very low in this study (1 of 576 seedlings) presumably due to the presence of the experimental cages. Several cages had large branches (> 10 cm diam.) drop on them through the course of the study. These branches may have killed additional seedlings had they reached the ground.

While there are no detailed studies of the microenvironments of hedgerows (Forman and Baudry 1984), it is clear that these habitats experience considerably greater wind speeds, soil desiccation, solar radiation, and increased soil and air temperatures compared to a forest. Indeed, my measures of light and soil moisture demonstrated that hedgerows can receive significantly more light and have drier soils than in the forest interior. Many more seedlings suffered mortality in the hedgerow due to drought than in the forest; thus, survival data are consistent with microenvironmental regimes. An important point to note is the effects of multiple mechanisms. Physiological death in the hedgerow was only an important factor beginning in 1988 due to regional drought during various parts of the growing season. Under more normal rainfall conditions microhabitat differences may produce considerably different patterns. De Steven (1991a) found similar effects when examining dispersal times, emergence times, and moisture conditions for wind-dispersed tree species colonizing old-fields in North Carolina.

CONCLUSIONS. The primary goal of this study was to experimentally assess the influence of landscape element on the recruitment of hickory seedlings. General conclusions must be tempered by the limitations of the present study, i.e., landscape elements were not replicated. This caveat aside, I found that the major predator-disperser of hickory nuts, the gray squirrel, was equally abundant in both the hedgerow and the forest, and was equally likely to discover a nut in both areas. Seed discovery, presumably predation more so than dispersal, is uniformly high and apparently not influenced to any great extent by landscape element. On the other hand, the seedling establishment phase appears to be markedly influenced by the landscape or spatial context. Seedlings in hedgerows suffer greater physiological stress from drought compared to the forest. However, squirrels will disperse nuts into wooded hedgerows which are not subsequently subjected to the same browsing pressure by deer and rabbits at the seedling stage. Given the enormous browsing intensity found in the forest, a seedling has a 10-fold higher probability of establishment in a hedgerow if it can escape severe drought early in its life cycle. Presently, there are an inadequate number of experimental studies in different landscape elements to make strong generalizations; however, my data suggest that landscape configuration might have a significant effect on the regeneration ecology of hardwood trees. More studies taking a population-based approach to understanding landscape influences will help to clarify general patterns.

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