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GAP PARTITIONING AMONG MAPLES (*ACER*) IN CENTRAL NEW ENGLAND: SURVIVAL AND GROWTH¹

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Abstract. We measured survival and growth of three shade-tolerant species of maple (*Acer pensylvanicum*, *A. rubrum*, and *A. saccharum*) in response to understory and experimentally created small canopy gaps of two sizes (8 × 12 m, 75 m²; 16 × 24 m, 300 m²) in central New England. Seedlings of the three species (2160 total, 720 per species) were transplanted into five plot locations (center plus northwest, northeast, southwest, and southeast gap edges) within all gap and understory sites. Measurements of microclimates, architecture, photosynthetic performance, survival, and growth were made over 1 yr before, and 2 yr following, gap release.

Red maple (*A. rubrum*) survived better overall across the study due to greater persistence in the north and center plots of large gaps. The small gaps and understories showed no differences among the species. Survival rates exceeded 80% in most sites and plots, with low values (30–65%) only in the exposed plots of large gaps. There were no relationships between post-gap survival and previous age, height, or basal diameter.

By the end of 2 yr of gap release, both gap sizes induced greater distinctions among the species in all growth variables than the understory. Striped maple (*A. pensylvanicum*) exhibited greater leader extension, absolute stem height, net height change, absolute basal diameter, and net basal diameter change than red maple and sugar maple (in that order) in nearly all sites and plots. The exception was large-gap center and north plots, where red maple equalled or exceeded striped maple in net basal diameter change, but not net height increase. Sugar maple (*A. saccharum*) was the least responsive of the species to the gap–understory gradient. As with survival, there were no predictable relationships between pre-gap age or size and post-gap growth.

Photosynthetic performance paralleled growth by these species across the gradient, particularly for shoot assimilation. When growth variables were plotted against irradiance and temperature measured at seedling plot positions, there were consistent and clear distinctions among species across the gap–understory gradient, providing limited evidence for gap partitioning in our system. Striped maple appears to be a superior generalist, red maple is a weaker generalist, and sugar maple shows the poorest performance in a manner that is nearly insensitive to the gap–understory gradient in our experimental system.

Key words: *Acer rubrum*; *Acer saccharum*; *Acer pensylvanicum*; forest canopy gap; gap partitioning; growth; species diversity; survival.

INTRODUCTION

The gap partitioning hypothesis was proposed in 1977 as a mechanism for enhancing tree species diversity in closed-canopy forests. The hypothesis suggests that species differ in their autecological responses along the gap–understory microenvironmental gradient generated by canopy disturbance. These autecological differences lead to trade-offs along the gradient, such that species will show distinct preferences for gaps of different size or positions within larger gaps (Ricklefs 1977, Bazzaz and Pickett 1980, Denslow 1980). The trade-offs imply shifting advantage among small-gap vs. large-gap specialists, such that tree species coex-

istence and community diversity are enhanced by disturbance-fostered niche specialization (Pickett 1983, Bazzaz 1984, Denslow 1985, Canham and Marks 1985, Bazzaz 1987, Petraitis et al. 1989). Underlying this hypothesis are the expectations that the gap–understory gradient is too broad for a single species to be competitively superior throughout, and that some degree of niche specialization is more advantageous than being a generalist.

In the original versions of the gap partitioning hypothesis Ricklefs (1977) and Denslow (1980) emphasized (1) above- and belowground microenvironmental heterogeneity, with a particular focus on conditions close to the ground, and (2) autecological traits of tree species, including seed size, dispersal mechanisms, dormancy, germination behavior, and physiological responses such as photosynthesis, nutrition, and overall shade tolerance. Both papers stressed the importance of seed and small seedling stages in discussing the

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potential for niche specialization and thus gap partitioning.

During the last 15 yr, the concept of gap partitioning has informally expanded to include any kind and source of differential performance by species within and across gaps of different size. While it is true that the full spectrum of abiotic and biotic factors affects tree seedling success in interactive, complex ways, this expansion of scope has obscured the focus that the gap partitioning hypothesis originally had on microenvironments and ecophysiology. Throughout this paper, we refer to the "gap partitioning hypothesis" in this narrower sense. Our questions and our highly controlled field experiment are a test of this narrower version of the hypothesis, involving a restricted number of environmental variables and physiological responses. There are limitations on extrapolating our results to gap partitioning under natural gap regeneration, which we discuss at the end of this paper.

There are good reasons for expecting ecophysiological specialization by tree species on portions of the gap-understory gradient (Bazzaz and Sipe 1987). But even though our knowledge of forest microclimates, silvicultural regeneration, natural gap regeneration, and tree ecophysiology is extensive, it has not been possible to generalize on the degree to which gap partitioning actually occurs, particularly in the smaller gaps (<300 m²) that dominate natural disturbance regimes in many temperate and tropical forests (Brokaw 1985b, Runkle 1985). There are several reasons for this (Sipe 1990), but the central problem is that a complete test of the gap partitioning hypothesis requires simultaneous measurements of (1) spatial-temporal microenvironmental variation, (2) physiological and morphological responses, and (3) survival and growth in the field.

Published studies on natural gap partitioning (Barton 1984, Brandani et al. 1988, Núñez-Farfán and Dirzo 1988, Denslow et al. 1990, Brown and Whitmore 1992) differ greatly in purpose, methodology, and scope and thus no clear picture of the overall significance of partitioning has emerged. Most of these studies have made use of naturally established juvenile trees, involving limited control over experimental plant locations and densities. With the exception of Denslow et al. (1990), the studies represent a search for differential patterns of species distribution according to the broader interpretation of gap partitioning discussed above. There has been no comprehensive test of gap partitioning for tree species that involves simultaneous measurements of microenvironments, ecophysiology, and growth responses in a fully controlled field experiment.

The study presented here is an experimental test of the gap partitioning hypothesis for three species of maple (*Acer pensylvanicum*, *A. rubrum*, and *A. saccharum*) in the mixed deciduous forests of central New England. Five questions were posed at the outset: (1) How do microclimates vary diurnally and seasonally across the understory and small canopy gaps? (2) How

do the maple species differ in shoot architecture and photosynthetic performance across the gap-understory microclimatic gradient? (3) Do the species exhibit differential survival and/or growth across the gradient? (4) What are the relationships between microclimates, photosynthetic performance, and survival/growth? (5) Is there specialization by the species along the gradient, i.e., does gap partitioning occur?

This paper discusses noncompetitive survival and growth of 2160 transplanted maple seedlings in gaps and understory for 1 yr before (1987) and 2 yr after (1988–1989) gap creation. We conclude with a project synthesis, where connections are made among the microclimatic patterns (T. W. Sipe and F. A. Bazzaz, *unpublished manuscript*), photosynthetic behavior (Sipe and Bazzaz 1994), and survival and growth, in order to interpret the occurrence of gap partitioning in our system.

METHODS

Study species

Acer is the only North American tree genus that has at least three co-occurring species rated as tolerant to very tolerant of shade: *A. pensylvanicum* L. (striped maple), *A. rubrum* L. (red maple), and *A. saccharum* Marsh. (sugar maple). The distributions of the three study species overlap across a substantial range in the eastern U.S., including central New England, and they play important roles in our study system. They co-occur in greatest abundance in moist forests where small gaps dominate the disturbance regime.

The three maple species tend to behave similarly in autecological terms in comparison to common co-occurring tree genera. But while they are all classified as tolerant or very tolerant of shade, there are physiological, morphological, and life historical differences that suggest potential specialization across the understory and canopy gaps (Sipe and Bazzaz 1994). Based on published information, we predicted that sugar maple would outperform the others in the understory, striped maple would dominate in the small gaps, and red maple would be superior in the larger gaps. We also predicted that the species would perform differentially across plot positions within the large and small gaps, and possibly in the understory, in response to spatial variation in microenvironments.

Study site

We conducted our study at the Harvard Forest in central Massachusetts (42°30' N, 72°15' W), located in the Transition Hardwoods-White Pine-Hemlock forest type zone (Spurr 1956, Westveld et al. 1956). The forest in our study area is a relatively mature stand that originated after clear-cutting in 1890. The stand is currently dominated by *Quercus rubra*, *Acer rubrum*, *Fagus grandifolia*, *Betula allegheniensis*, and *Betula papyrifera*, with scattered individuals of *Betula lenta*,

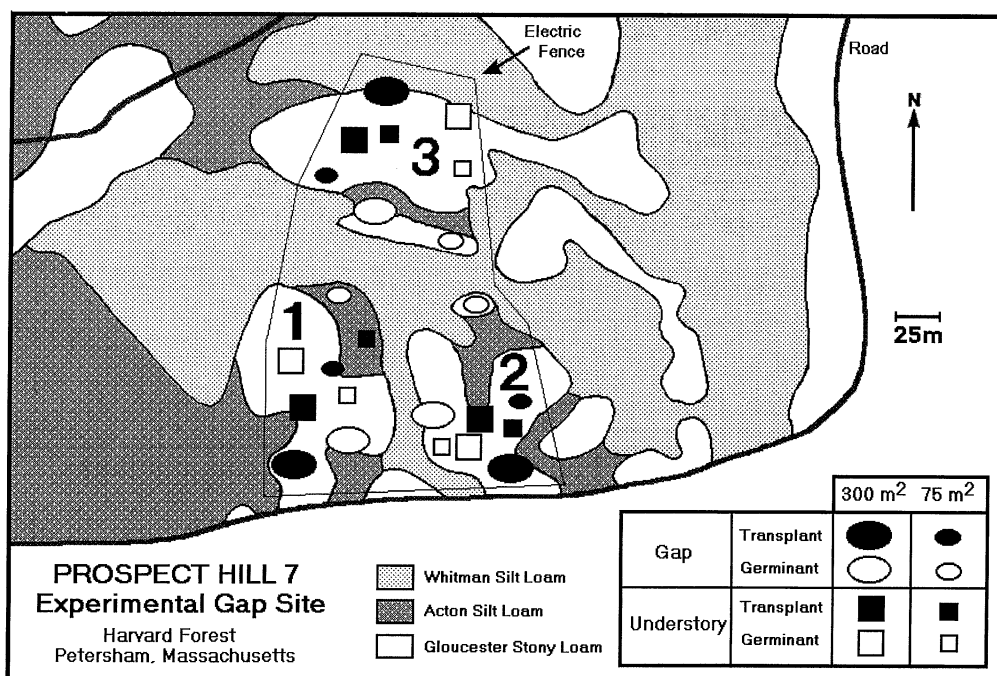


FIG. 1. Study site layout in the Prospect Hill 7 compartment of the Harvard Forest. Twelve gaps (6 large, 6 small) and 12 understory sites (6 large, 6 small, with plot positions matching that of corresponding gap sizes) are intermingled throughout the study area across three blocks of higher ground. Older seedlings of our three *Acer* study species were transplanted into half of the 24 sites ("transplant" sites), while seeds were planted in the other half ("germinant" sites).

Prunus serotina, *Fraxinus americana*, *Pinus strobus*, and *Tsuga canadensis*. Three main portions of slightly higher ground are separated by shallow ravines with small intermittent streams in the study area (Fig. 1). Our experimental gap and understory sites are located on the higher portions of the study area with minimal to no slope. The soil catena is derived primarily from granitic glacial till. Gloucester stony loams, which dominate the higher ground, are coarse, well drained, shallow, prone to drought, and relatively infertile.

A total of 24 gap and understory sites were positioned within the study area a year before gap creation (Fig. 1). Shade-tolerant tree species can exhibit both pre-gap establishment (advance regeneration) or post-gap establishment, and the relative performance among species in gaps may differ for these two regeneration modes. Half of the 24 sites received transplanted older seedlings before gap formation to study the response of advance-regenerated individuals to gap release. The transplant half of the experiment is the subject of this paper. Seeds from our three *Acer* species were planted in the remaining half of the experiment after gap creation. The results for germinants are described in a separate paper (T. W. Sipe and F. A. Bazzaz, unpublished data). The two halves of the experiment (transplant, germinant) were spatially intermixed across the three blocks of higher ground in the study area. Each block contained a full complement of four transplant and four germinant sites.

The 12 transplant sites included six gaps (three small, three large) and six understory sites (three small, three large). We chose two gap sizes, 75 m² (8 × 12 m) and 300 m² (16 × 24 m), based on published studies of natural gap regimes in temperate forests. Gaps ranging up to 300 m² in area typically represent 80–90% of all gaps encountered randomly during surveys in old-growth forests in the eastern U.S. (Barden 1983, Runkle 1985). The median area of single-tree gaps in these studies ranges from 75 m² to 130 m², while median multiple-tree gap areas are ≈240–290 m². Our two experimental sizes therefore encompass the most commonly encountered single-tree and multiple-tree gap sizes in eastern forests.

The experimental gaps are elliptical since natural gaps tend to be elongated and elliptical functions have been widely used to estimate gap area (e.g., Barden 1979, Runkle 1982, Brokaw 1985a). The gap areas differ by a factor of four and their elliptical dimensions by a factor of two, with a length:width ratio that is the same for both gap sizes (1.5). All gaps were oriented uniformly, with long axes east-west. The locations, sizes, shapes, and orientations of these 12 gaps were controlled through meticulous selection of overstory trees to be felled.

Five 1 × 2 m seedling plots were positioned in all understory and gap sites a year before gap creation. The plots included a center (C) position plus one plot equidistant from the center in all subcardinal directions

(northwest [NW], northeast [NE], southwest [SW], southeast [SE]). The gap plots were placed where the subcardinal axes would intersect the expected elliptical margin for each gap size. Even though plots were positioned in the field prior to gap formation, careful selection of gapmaker trees resulted in all marginal plots being on or very close to the gap canopy edge after tree felling.

The large and small understory sites differed only in distances among seedling plots, which corresponded to the same distances in large and small gaps. We used two sizes of understory sites to simplify analysis of variance and to provide two different scales for judging spatial variability in the understory. Gap and understory sites of the same size were treated independently (i.e., not paired).

All seedling plots were treated to remove root competition and rocks. The plot margins were sliced vertically to a depth of 25 cm with flat spades, and the soil profile was then chopped to the same depth with mattocks. Care was taken to minimize inversion of the soil profile. Small and large woody roots, herbaceous and shrubby perennials, and any rock fragments >2.5 cm in diameter were removed. The surface layer (\approx 5 cm deep) was mixed and smoothed across the plots.

Then 2160 naturally established seedlings (720 per species, 15–30 cm tall, 4–20 yr old) were lifted from various understory locations in the Harvard Forest and transplanted into the seedling plots. All seedlings were unbranched and undamaged with an intact terminal meristem (leader). The seedlings were dug with a small soil ball after leaf senescence and transplanted with bare roots into the 60 prepared plots over a 2-wk period in October 1986, a full year before gap creation. This provided 18 mo for adjustment to transplant shock before exposure to high irradiances in gaps in summer 1988. Seedlings from the various source locations in the forest were nonsystematically randomized across the 60 plots.

We created all 12 gaps during 25 September through 2 November 1987. Understory saplings and shrubs >0.5 m tall were cut basally prior to felling the overstory trees. Transplanted seedlings were protected from falling trees by surrounding the plot margins with cordwood. No seedlings were damaged during tree felling. Sawlogs and cordwood were removed carefully from the gaps with very little soil disruption. Remaining brush was spread in the understory 5–10 m beyond the gap margins, well away from seedling plot positions. All regrowth was cut back regularly. The entire study area was protected from herbivory by white-tailed deer (*Odocoileus virginianus*) by installing a five-stranded electric fence (Fig. 1.).

Survival and growth of the transplanted seedlings were measured through complete surveys at the end of each growing season from 1987 through 1989. Since all hierarchical levels in the design contained the same initial number of seedlings, survival analyses were

TABLE 1. Split-split-plot ANOVA model used for all growth and architectural variables. See Fig. 1 for study site design. A total of 2160 transplanted seedlings were used.

Level	Source of variation	df
Main	Block (1, 2, 3)	2
	Site (LG, SG, LU, SU)*	3
	Error(1) = Block \times Site	6
Split	Plot (NW, NE, C, SW, SE)†	4
	Site \times Plot	12
	Error(2) = (Block \times Plot) + (Block \times Site \times Plot)	32
Split-split	Species (PEN, RUB, SAC)‡	2
	Plot \times Species	8
	Site \times Species	6
	Site \times Plot \times Species	24
	Error(3) = Residual	2060
Total		2159

* LG = large gap; SG = small gap; LU = large understory; SU = small understory.

† NW = northwest; NE = northeast; C = center; SW = southwest; SE = southeast.

‡ PEN = *Acer pensylvanicum*; RUB = *Acer rubrum*; SAC = *Acer saccharum*.

based on raw numbers and not percentages. The survival data were analyzed for the effects of treatments across time using one-way and two-way contingency analysis (chi-square and *G* statistics). The same methods were used to test whether or not survival varied with initial seedling age, height, or basal diameter. Seedlings were partitioned into 10 classes within each variable: (1) 2–20 yr for age, in 2-yr intervals, (2) 4–40 cm for height, in 4-cm intervals, and (3) 1.40–5.00 mm for basal diameter, in 0.40-mm intervals.

The pre-gap age, height, and basal diameter (1 cm above root collar) of all surviving seedlings were recorded in September 1987 just before gap creation. Leader extension and basal diameter were measured again in early October 1988. These and several additional variables were measured for the final time in October 1989, including: (1) branch extension in 1989; (2) total living branch extension since October 1986; (3) total living shoot extension since October 1986 (leader plus branches); and (4) stem height (highest living meristem, regardless of leader or branch origin). Yearly increments in height and basal diameter were calculated from these data.

Post-gap growth was plotted against pre-gap seedling size and age to determine the relationships between prior growth history and gap response. The growth data were also analyzed for treatment effects using a split-split-plot analysis of variance (ANOVA) with selected interactions (Table 1). Growth was analyzed for four time periods: 1987 pre-gap status, 1988 season alone, 1989 season alone, and cumulative 1987–1989 change. The three species differed statistically in pre-gap age, height, height growth rate, basal diameter, and basal diameter growth rate. But the absolute differences were not large and the species did not show the same rank order across these variables, suggesting there was no

initial advantage that would bias relative performance among species during the experiment.

Annual growth in 1988 and 1989 is discussed in Sipe (1990) and only the cumulative performance over 1987–1989 is reported here. The analysis of cumulative growth included all survivors as of October 1989 ($n = 1705$). Results are presented for leader extension, branch extension, total shoot extension (leader plus branch), net height change, and net basal diameter change over the 3-yr period. Negative values are possible for both net stem height change and net basal diameter change because only live stems were measured, and a stem with dieback followed by regrowth could have a smaller new stem than the dead precursor.

Each growth variable was checked for normality and outliers by (1) plotting raw data histograms, (2) calculating skewness and kurtosis, (3) fitting the ANOVA model, and (4) inspecting both normal probability plots of the residuals and plots of residuals against predicted scores. All growth variables were \ln transformed to achieve normality. Homoscedasticity was confirmed by applying the F_{\max} (Sokal and Rohlf 1981) to residuals following model fitting. The explanatory power of the model was determined by calculating the squared correlation coefficient (R^2) for the scatterplot of residuals vs. normalized scores.

Post-hoc multiple comparisons of groups within treatments were done using Tukey box plots (Sokal and Rohlf 1981) and pairwise Tukey hsd tests. The hsd tests preserve experiment-wise error rate, they are robust enough to handle unequal cell sizes (with the Tukey-Kramer adjustment), and individual Tukey hsd tests are valid even if the overall F test is not significant (Wilkinson 1986, Day and Quinn 1989).

Large understory and small understory results were nearly identical across all analyses. Although some tables and figures contain data for both understory site sizes, the discussion is streamlined by contrasting the three main types of conditions: large gap (LG), small gap (SG), and understory (U). These three sites encompass 15 plot positions, considered here as microsites along the gap-understory gradient. Throughout the remainder of the paper, species abbreviations are PEN for *A. pensylvanicum*, RUB for *A. rubrum*, and SAC for *A. saccharum*. "Site" effects will refer to the response of all species combined to the three main site types (large gap, small gap, understory). "Plot" effects will refer to the response of all species combined to the 15 individual plot positions (microsites) spread across the large gap, small gap, and understory.

RESULTS

Survival

There were no significant differences in survival across initial age, height, or basal diameter classes for all hierarchical breakdowns of sites, species, and species within sites. The 57 probability values (19 tests

per initial status variable \times 3 variables) ranged from $P = 0.90$ to $P = 0.99$, demonstrating a complete lack of any effect of previous age or size on post-gap survival.

Total survival during the year following transplanting was 95%, with no notable differences among species or sites, while the overall survival rate after 35 months was 79%. Mortality rates increased from 5% in 1986–1987 to 7% in 1987–1988 and 9% in 1988–1989.

Survival differed among site types (Fig. 2, Table 2). The large gaps diverged noticeably from the other sites following gap creation. As a consequence of the 20% greater losses in large gaps and slightly higher survival in the understory than small gaps, survival differed significantly across sites by the end of 1989, with $U > SG > LG$.

Plot positions within sites yielded some significant differences for all species combined (Fig. 2, Table 2), but only in the large gaps, where $SE = SW > C > NE > NW$ as of 1989. The maximum difference between plots was 60% in large gaps, but only 9–14% in the small gaps and understory. All plots in the understory and small gap sites showed $>75\%$ survival through 1989, and the south plots of the large gap showed $>90\%$ survival. But the large-gap C, NE, and NW plots showed only 30–56% survival. There was a clear north-south gradient of survival in the large gaps, but no such pattern occurred in the small gaps.

The three species showed divergent survival patterns over the 3 yr (Fig. 3, Table 2). Mortality rates did not change markedly for any of the three species during the first growing season following gap creation, but the species differed significantly by the end of the second season, with $RUB > PEN > SAC$ overall. Although sugar maple declined noticeably during 1988–1989 in the small gap and understory, the species differed significantly only in the large gaps ($RUB > SAC = PEN$). The pattern of $PEN \Rightarrow RUB > SAC$ was consistent, though nonsignificant, in the small gaps and understory. Species differed in survival among plots only in the large gaps, where $RUB > PEN = SAC$ in the NW, NE, and C plots.

Growth

Growth vs. previous age and size.—We found no predictive relationships among any of the five 1987–1989 net growth variables vs. pre-gap age, stem height, or basal diameter, which parallels the results for survival. The only recognizable pattern was that the extremes (very young or old, very small or large) were somewhat less likely to show large post-gap growth rates or net change in height or basal diameter (Sipe 1990).

Site and plot differences for all species combined.—Leader extension did not differ significantly across sites overall, but Tukey hsd tests showed $LG = SG > U$ (Table 3, Fig. 4). Plots did not differ in the understory

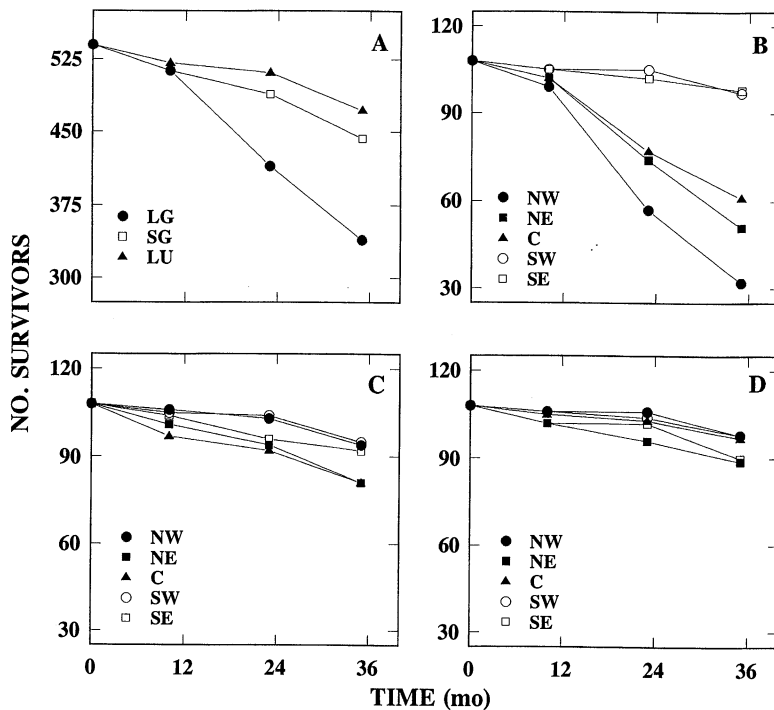


FIG. 2. Survival of all species combined by site types (A) and by plots within large gaps (B), small gaps (C), and large understories (D). The points represent full censuses taken in the fall (late September or early October) of each of the years 1986–1989.

or small gap, but the center plot diverged from all other plots in large gaps ($C > SE = NE = SW = NW$).

Branch extension also did not differ overall across sites, but Tukey tests showed $LG > SG > U$ (Table 3, Fig. 5). Plot positions were significantly different only in the large gap, where $C > NW = NE > SE = SW$. Seedlings in the large-gap centers showed unusually

high cumulative branch growth, with a combined species total that was 2.5 times that of any other site/plot. The significant difference between large and small gaps was largely due to this one plot position.

In contrast to leader and branch extension, the sites differed significantly in total shoot extension, with $LG > SG > U$ (data not shown). There were no noticeable

TABLE 2. Chi-square and G test results for differential survival across the 3 yr by groups in various breakdowns. NSD = no significant difference at $P = 0.05$.

Comparison	Site*	Chi-square or G	P	Rank order
Sites		24.85	<0.001	LU > SU > SG > LG*
Plots within sites	LG	49.77	<0.005	SE = SW > C > NE > NW†
	SG	2.22	>0.500	NSD
	LU	0.87	>0.900	NSD
	SU	1.90	>0.100	NSD
Species		8.98	<0.025	RUB > PEN > SAC‡
Species within sites	LG	12.79	<0.005	RUB > SAC = PEN
	SG	5.80	>0.100	NSD
	LU	1.81	>0.100	NSD
	SU	1.79	>0.100	NSD
Species within plots within sites	LG	15.36	=0.052	RUB > PEN = SAC in NW, NE, C
	SG	0.33	>0.990	NSD
	LU	0.78	>0.990	NSD
	SU	1.26	>0.990	NSD

* LU = large understory; SU = small understory; SG = small gap; LG = large gap.

† SE = southeast; SW = southwest; C = center; NE = northeast; NW = northwest.

‡ RUB = *Acer rubrum*; PEN = *Acer pensylvanicum*; SAC = *Acer saccharum*.

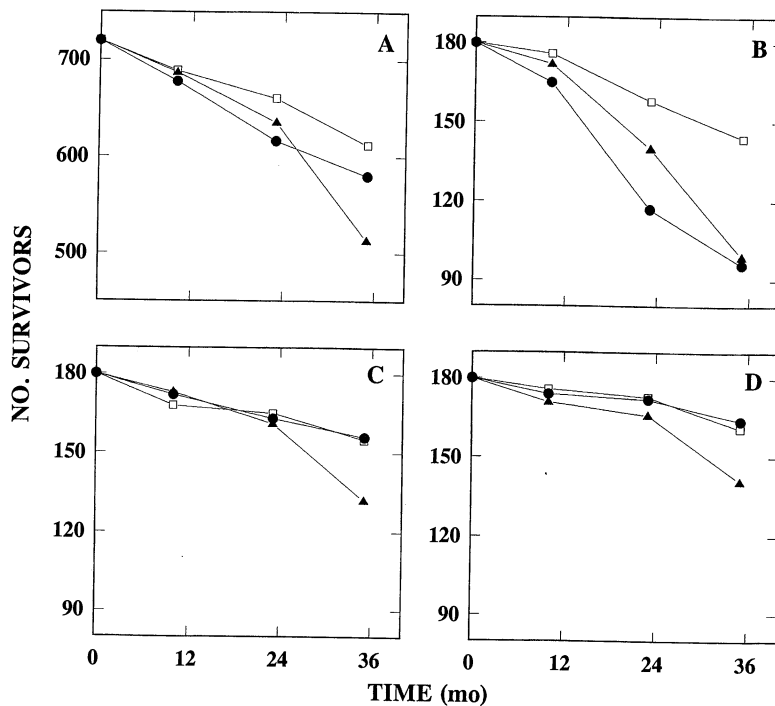


FIG. 3. Survival by individual species over the entire study area (A) and within large gaps (B), small gaps (C), and large understory (D). ● = *Acer pensylvanicum*, □ = *A. rubrum*, ▲ = *A. saccharum*. The points represent full censuses taken in the fall (late September or early October) of each of the years 1986–1989.

plot differences in the understory or small gaps, but the marked response in large-gap centers produced a significant site \times plot interaction. The contributions of leader and branch growth to total shoot extension differed among the species and sites. In large gaps, branch growth was a greater contributor to total growth for striped maple and red maple in all plots, while sugar maple exhibited nearly equal leader and branch contributions. In small gaps, striped maple showed much greater leader growth, red maple had greater branch growth, and again sugar maple had equal components.

All species showed consistently greater (but very small) branch growth than leader growth in the understory plots.

The rank orders for species in any of the three extension variables (leader, branch, and total shoot) require careful interpretation, since they may not reflect absolute gains in height. Branch extension for many individual seedlings represented recovery from leader loss and substantial dieback. Since total shoot extension includes this recovering branch growth, seedlings with the greatest dieback in stem height sometimes

TABLE 3. ANOVA results for 1987–1989 cumulative growth variables. For df, “res” refers to residual df, which varied with total df among variables.

Source	df	Leader extension	Branch extension	Total extension	Net height change	Net basal diam. change
Block	2, 6	0.97	0.26	0.33	0.93	0.04
Site	3, 6	3.18	2.45	6.54*	0.67	5.61*
Plot	4, 32	1.77	2.11	2.25	1.24	0.67
Species	2, res	114.09***	219.40***	343.70***	130.09***	119.47***
Site \times Plot	12, 32	2.56**	3.46**	2.94**	1.03	0.61
Site \times Species	6, res	10.35***	9.92***	20.90***	8.45***	12.91***
Plot \times Species	8, res	3.12**	2.36*	3.23**	3.16**	7.12***
Site \times Plot \times Species	24, res	0.98	1.89**	1.24	1.43	4.80***
Total df		1696	242	1698	1703	1689
Variance (%) accounted for by the model		98.7	99.5	9.0	91.0	91.8

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$.

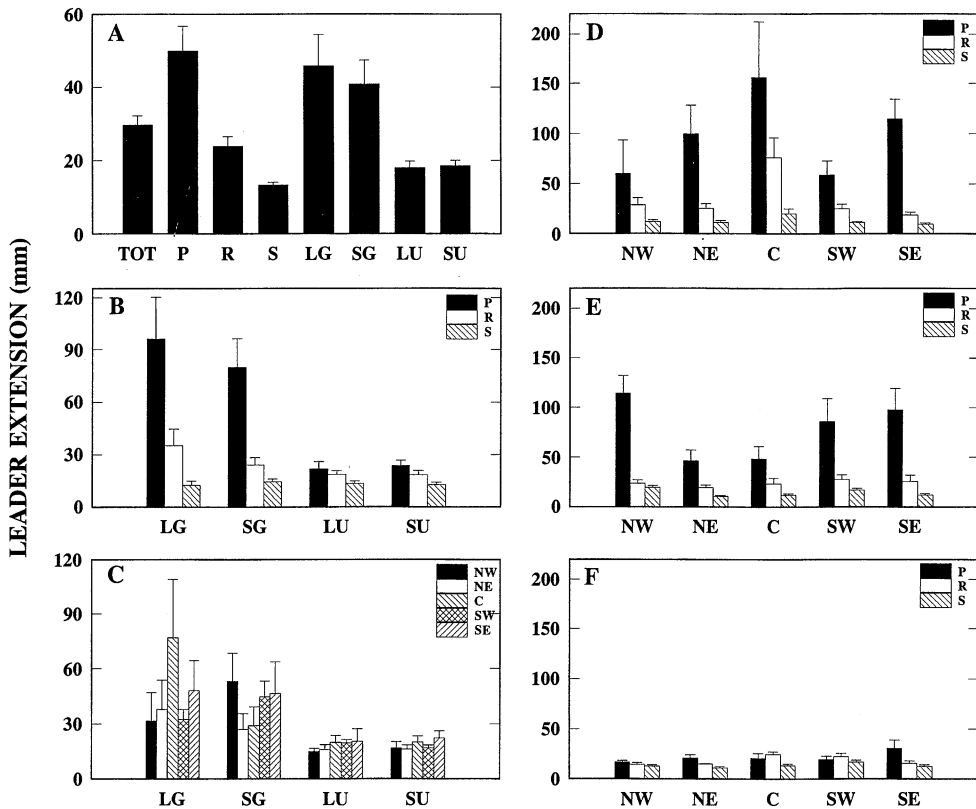


FIG. 4. Total leader extension (mean ± 1 SE) by seedlings surviving with intact leader to October 1989. (A) By species and site type totals, (B) by species within site types, (C) by plots within site types, (D-F) by species and plot positions in large gaps, small gaps, and large understories, respectively. Abbreviations: TOT = entire study area, P = *Acer pensylvanicum*, R = *A. rubrum*, S = *A. saccharum*, LG = large gap, SG = small gap, LU = large understory, SU = small understory, NW = northwest (plot positions), NE = northeast, C = center, SW = southwest, SE = southeast.

showed the largest total shoot extension, even though they actually lost net stem height over the 1987–1989 period.

There was a nonsignificant difference overall among sites in net height change by seedlings, but the two gap sizes produced net height gains and differed significantly from the understory, which yielded net height losses (Table 3, Fig. 6). Net height change was significantly different for plots within sites only in large gaps, where $C > NE = SE = NW = SW$. The maximum mean height change in any site was only ≈ 9 cm, in any plot only ≈ 12 cm, and by any species in any plot only ≈ 19 cm. Overall, the entire community of surviving seedlings showed a net height gain over 2 yr of < 0.5 cm.

Seedlings differed significantly in net basal diameter change among sites, with $LG = SG > U$ (Table 3, Fig. 7). No significant plot differences occurred in the small gaps or understories, but seedlings in the center plots of large gaps showed higher basal diameter growth than in all other plots ($C > NE = SE = NW = SW$).

Species differences.—The three species differed significantly in leader extension when compared across the entire study area, with $PEN > RUB > SAC$ (Table

3, Fig. 4). The same pattern occurred at the site level in large gaps and small gaps, but species did not differ in the understory. All large gap plots showed $PEN > RUB > SAC$, while all small-gap plots showed $PEN > RUB = SAC$. Striped maple leader extension was most responsive to site differences ($LG > SG > U$), while red maple diverged primarily in large gaps ($LG > SG = U$), and sugar maple showed no preference.

The species showed significant differences in branch extension overall, with $RUB > PEN > SAC$ (Table 3, Fig. 5). This same rank order occurred in both gap sizes, but the species did not differ in the understory. The order $RUB = PEN = SAC$ applied in all sites and plots except for the large-gap NW, where $PEN > RUB > SAC$.

Total shoot extension paralleled branch extension (data not shown). There were significant differences among species, with $RUB > PEN > SAC$. The species showed the same pattern in both gap sizes ($RUB > PEN > SAC$) but slightly different relationships in the understory ($RUB > PEN = SAC$). Red and striped maple showed the same site preferences overall for total shoot extension ($LG > SG > U$), while sugar maple did not differ among sites.

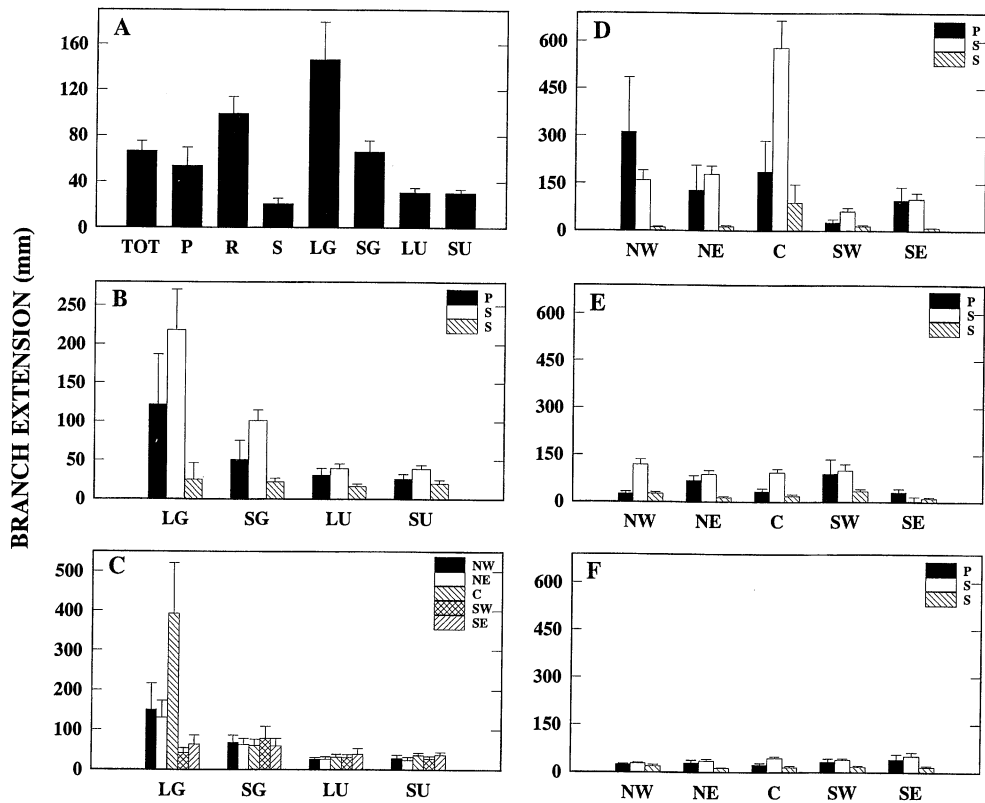


FIG. 5. Total branch extension (mean \pm 1 SE) by seedlings surviving to October 1989. (A) By species and site type totals, (B) by species within site types, (C) by plots within site types, (D-F) by species and plot positions in large gaps, small gaps, and large understories, respectively. See Fig. 4 for abbreviations.

There were significant differences among species in 1987–1989 net height change, with PEN > RUB > SAC overall (Table 3, Fig. 6). Species rankings varied among sites, with PEN > RUB > SAC in large gaps, and PEN > RUB = SAC in all gaps and understory. An unexpected result is that only striped maple showed a net gain in height (46.2 mm), while both red maple (-8.8 mm) and sugar maple (-29.7 mm) actually declined in mean height for all surviving seedlings. Across the 15 plot positions in the large gap, small gap, and understory, striped maple always showed positive gains in height, sugar maple always showed losses, and red maple showed mostly losses (3 plots with gains, 12 plots with losses). The differences among species were the greatest in the large-gap plots, less in the small-gap plots, and dampened most in the understory plots.

There were significant differences among species in net basal diameter change, with PEN > RUB > SAC overall (Table 3, Fig. 7). Species differed significantly within sites: PEN = RUB > SAC in large gaps, PEN > RUB > SAC in small gaps, and PEN = RUB = SAC in the understory. At the plot level the pattern was PEN > RUB > SAC in nearly all site/plot combinations. The exceptions were RUB > PEN > SAC in large-gap centers, and occasionally RUB > SAC in

the understory. Unlike net height change, all species showed positive basal diameter change in all sites and plots. While the average gains by species did not exceed 1.00 mm, these values still represented 9–35% increases, which were greater than the proportional gains/losses in height.

In summary, both gap sizes induced greater distinctions among the species in all growth variables than the understory by the end of the second season of gap release. Striped maple exhibited greater leader extension, net stem height change, and net basal diameter change than red maple and sugar maple (in that order) in nearly all sites and plots. The exception was large-gap center and north plots, where red maple equalled or exceeded striped maple in basal diameter growth, but not in net height growth. In general, red maple exhibited more frequent dieback, which produced branch extension and total shoot extension values that exceed the other species in most of the 15 plot positions. However, even though it showed a better ability to respond to leader loss, red maple was not able to recover completely and show net increases in height and basal diameter as large as striped maple across the sites. Sugar maple was the least responsive of the species to the gap-understory gradient, and was usually last for all growth variables in all microsites.

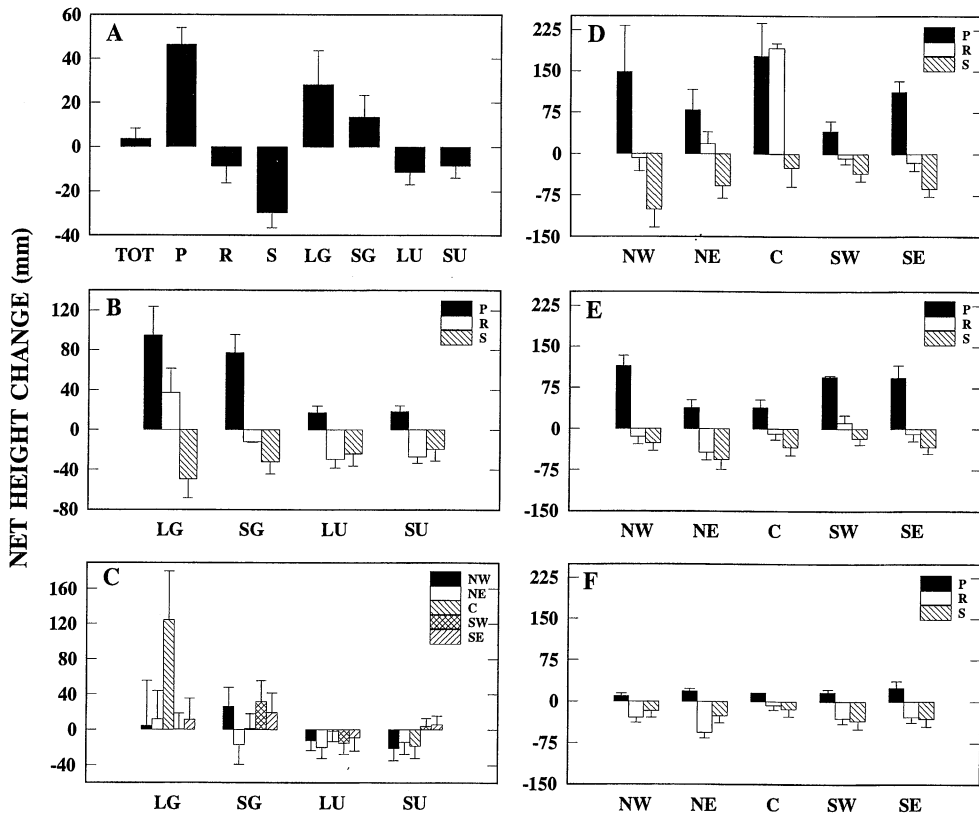


FIG. 6. Net height change (mean ± 1 SE) for seedlings surviving to October 1989. Data represent the difference between 1987 (pre-gap) and 1989 highest living meristem, measured perpendicular to the ground. (A) By species and site type totals, (B) by species within site types, (C) by plots within site types, (D-F) by species and plot positions in large gaps, small gaps, and large understories, respectively. See Fig. 4 for abbreviations.

DISCUSSION

Our results suggest that pre-gap status is a poor indicator of post-gap growth for these species. This contrasts with Marquis (1982), who found positive correlations between initial size, age, and growth rates vs. subsequent survival and growth for red and sugar maple seedlings when released in large silvicultural gaps in north-central Pennsylvania. The potted seedlings Marquis used were mostly smaller (6–21 cm tall, 0.50–2.54 mm basal diameter) than the transplants we studied, but his results suggest that survival in even the center and north plots of our large gaps at the Harvard Forest should have been higher for both these species. The ground-level conditions of the clear-cut area were not described by Marquis, and it is possible that debris and regrowth in the silvicultural cut ameliorated the conditions at the small seedling level somewhat as compared to our completely cleared experimental gaps.

With few exceptions, the large-gap centers were the most favorable environment for most growth variables for all three species in our study. The north plots of large gaps are exposed to direct beam irradiance the entire growing season (T. W. Sipe and F. A. Bazzaz, unpublished data), with irradiance and temperature levels (Table 4) that were clearly inhibitive for the seed-

lings in our size classes. Survival in the large-gap center was not as high as in the south, but growth by survivors was much greater in the center. The center plots receive the highest diffuse light levels on both clear and overcast days, and it is likely that seasonal and diurnal periods of direct beam are not as inhibitive as in the north. Direct beam radiation reaches the centers before leafout in early May, so the seedlings there have no advantage in terms of gradual acclimation to full irradiances. But it is possible that the cessation of direct beam in the centers (generally the 3rd wk of August; T. W. Sipe and F. A. Bazzaz, unpublished data) reduces late-season radiation stress more than in the north plots, where direct beam continues through September.

Our hypothesis that striped maple would perform better than the other species in small gaps was supported, but it is also clear that striped maple surpassed the other species in net size increase across nearly all of the gap-understory gradient. This result is supported by published data that shows that striped maple is capable of both prolonged understory survival (Hibbs 1979) and moderate to rapid growth in gap sizes ranging from <100 m² (Wilson and Fischer 1977, Hibbs et al. 1980) to larger patch cuts (Marquis 1964) and even

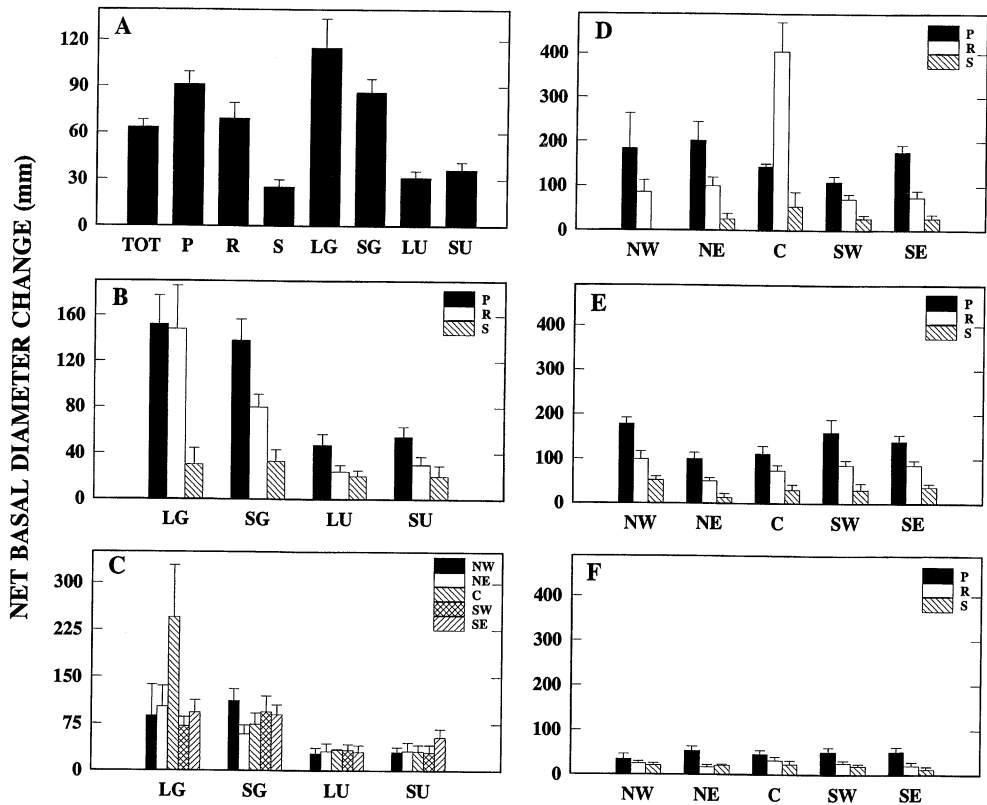


FIG. 7. Net basal diameter change (mean \pm 1 SE) for seedlings surviving to October 1989. Data represent the difference between 1987 (pre-gap) and 1989 stem diameters measured 1 cm above the ground surface. Differences of 0.1 mm or less are within the experimental error in resampling unmarked points. (A) By species and site type totals, (B) by species within site types, (C) by plots within site types, (D-F) by species and plot positions in large gaps, small gaps, and large understories, respectively. See Fig. 4 for abbreviations.

full watershed clear-cuts (Bicknell 1982). Red maple is known to be capable of colonization and rapid growth in both overstory thinning and large patch cut situations (e.g., Leak and Solomon 1975), and its survival and persistence following dieback were predictable (Burns and Honkala 1990).

Sugar maple's general lack of differential response to the two gap sizes concurs with the literature (e.g., Logan 1965, Canham 1985), but its net losses in height do not mirror the more marked responses to small gaps noted by Canham (1988, 1989). Sugar maple's poor ranking in understory growth compared to red and striped maple is one of the most unexpected results of this study, because the long-standing belief has been that sugar maple is the most shade tolerant of these three species. Our results support the more recent interpretation by Lei and Lechowicz (1990) that sugar maple is not as well adapted to mesic understory conditions as are both striped maple and mountain maple (*Acer spicatum*), which are understory trees. They suggest that this is due to the different degrees of evolutionary constraint for overstory vs. understory species. As a long-lived overstory dominant, sugar maple must be able to perform well with crowns in high-irradiance

environments, and Lei and Lechowicz's argument is that this constrains the ability of sugar maple juveniles to adapt to understory conditions as compared to understory species such as striped maple.

However, according to this view striped maple should not be as capable of rapid growth in large canopy openings if it is regarded as an understory specialist. Our work and other studies (e.g., Bicknell 1982) suggest that striped maple is very plastic across the understory-large gap gradient, apparently experiencing no significant loss in competitiveness in exposed sites. Furthermore, red maple also survived and grew better than sugar maple in the understory. Red maple, another overstory species, is thought to require even more light for life history completion than sugar, striped, or mountain maple, and thus should exhibit less tolerance for understory conditions than sugar maple. Our conclusion that red maple is flexible enough physiologically and architecturally to perform well across a wide range of environments is supported for larger saplings by Wallace and Dunn (1980).

One reason for sugar maple's poor performance in our study site could be that the soils are not favorable enough to permit sugar maple to express its growth

TABLE 4. Mean daily photosynthetic photon flux (PPF), air temperature, surface soil temperature (1 cm), and deep soil temperature (15 cm) for combined clear and overcast days throughout the 1989 season.

Site*	Plot†	PPF ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	Air temp. ($^{\circ}\text{C}$)	Surface soil temp. ($^{\circ}\text{C}$)	Deep soil temp. ($^{\circ}\text{C}$)
Total		144	21.2	19.1	17.2
LG		285	22.2	22.3	18.8
SG		113	21.0	18.1	16.5
U		33	20.4	17.0	16.2
LG	NW	407	22.7	22.7	18.9
	NE	343	22.6	21.8	18.1
	C	365	23.0	22.8	20.4
	SW	182	21.3	22.2	19.5
	SE	126	21.4	21.1	17.2
SG	NW	173	21.6	18.8	16.8
	NE	156	21.3	19.1	17.0
	C	106	21.1	18.8	16.5
	SW	69	20.7	17.4	16.2
	SE	60	20.6	15.9	15.9
U	NW	16	20.4	15.5	15.5
	NE	15	20.4	17.3	15.9
	C	42	20.2	19.8	16.2
	SW	47	20.6	16.6	16.6
	SE	48	20.5	16.1	16.7

* LG = large gap; SG = small gap; U = understory.

† NW = northwest; NE = northeast; C = center; SW = southwest; SE = southeast.

potential in response to gap or even understory conditions. Mature sugar maples are more physiographically selective in central Massachusetts than either red or striped maple, occurring on moister, more fertile soil series and a narrower range of drainage conditions. This corresponds to the patterns studied extensively by Leak (1975) in New Hampshire. The well-drained sandy loam soils in our study area are somewhat prone to drought. Even though precipitation is fairly evenly distributed throughout the year in this region, it is conceivable that the seedling rooting zone (upper 20 cm for our plants) could show very low water potentials, particularly in large gaps on clear days. Soil moisture is often thought to be less limiting in the understory than in open sites, but interception by the overstory and root competition among all strata of plants may reduce understory soil moisture to levels that could inhibit seedlings of species sensitive to tissue water stress, such as sugar maple (Ellsworth and Reich 1992).

It is evident that our understanding of both the patterns and processes of differential performance by tree species across the gap-understory gradient is still incomplete, even among superficially similar congeners. Contrasting results among studies may be in part due to the differences in size of the experimental plants. Studies by Canham (1988, 1989), Wallace and Dunn (1980), Steingraeber (1982), and Lei and Lechowicz (1990) have involved saplings older and larger than the seedlings we used. Of the three species, sugar maple may be the most shade tolerant in the early juvenile

phases although it is least likely to exhibit flexible responses to the gap-understory gradient in terms of height growth and architectural plasticity. Both of these characteristics could be related to its tendency to allocate considerable resources to root growth (Burns and Honkala 1990).

STUDY SYNTHESIS: GAP PARTITIONING IN ACER

The gap partitioning hypothesis requires clear relationships among microenvironmental patterns, eco-physiological responses, and survival/growth if we are to conclude that partitioning is occurring. Photosynthetic performance in response to the microenvironmental gradient has already been discussed in Sipe and Bazzaz (1994). The remaining connections between microclimates, photosynthesis, and survival and growth are discussed here, with a conclusion on the occurrence of gap partitioning under the conditions of our study.

Survival and growth vs. photosynthesis

We quantified photosynthetic performance at three scales: leaf, shoot, and population (Sipe and Bazzaz 1994). We measured assimilation per unit leaf area on undamaged seedlings of all species on the north and south sides of the large-gap, small-gap, and large-understory transplant sites in Block 1 of the experiment (six positions total). We also scaled leaf area rates to estimated shoot assimilation rates using seedling architectural data. The rank order for leaf assimilation was RUB > PEN > SAC in all six microsites, but the order for shoot assimilation was PEN > RUB > SAC in all but the large-gap north, where RUB > PEN > SAC. The species differed more in shoot assimilation than in rates per unit leaf area, and the shoot assimilation differences increased from 1988 to 1989. Because shoot assimilation is a better measure of whole-plant performance than leaf area rates, survival and growth are compared to shoot assimilation in the remainder of this section.

Survival patterns did not parallel shoot assimilation well. They agreed only in the large-gap north, where RUB > PEN > SAC for both variables. There were no significant differences in species survival in the small gap and understory, even though there were marked differences in assimilation.

The interpretation for photosynthesis vs. growth is more difficult due to our gas-exchange sampling regime and to the prevalence of dieback, branching, and resprouting. As emphasized in a previous paper (Sipe and Bazzaz 1994), our gas-exchange measurements and shoot assimilation calculations apply directly only to undamaged seedlings with intact leaders and relatively simple shoot architecture. Furthermore, we did not measure photosynthesis in large-gap centers where all species eventually exhibited relatively good growth and red maple in particular dominated over striped and

sugar maple. So the connection between assimilation and growth is not definitive until we have better data on gas exchange by more complicated shoots at more points along the gradient.

With this caution in mind, we observed that shoot assimilation differences among species paralleled the 1987–1989 growth variables, with the same rank order of $PEN > RUB > SAC$ in nearly all sites and plots. Red maple had higher shoot assimilation and greater net basal diameter change than striped maple in large-gap north plots. However, striped maple showed greater total leader extension, final stem height, and final basal diameter than red maple in these plots as well.

*Survival and growth vs.
microclimatological gradients*

Seasonal means of photosynthetic photon flux (PPF), air temperature at 25 cm, surface soil temperature (1 cm) and deep soil temperature (15 cm, seedling rooting zone) across the gap–understory gradient are summarized in Table 4 for combined clear and overcast days. These data were measured simultaneously in the large-gap, small-gap, and large-understory transplant sites in Block 1 of the study area. There is a clear gradient in mean daily PPF, which is paralleled to varying degrees by mean daily air and soil temperatures. The differences among gap plots were due to the interaction among plot position, gap geometry, and solar movement, while differences among the understory plots were due to spatial heterogeneity in overstory and soil composition (T. W. Sipe and F. A. Bazzaz, *unpublished data*).

We plotted survival and growth variables against these microclimatic data for all 15 site/plot positions, treating the study area as a continuous gradient rather than as categorical treatments for chi-square analysis or ANOVA. We used eight microclimatological variables, including those shown in Table 4 plus four additional variables: mean daily duration of PPF in the compensation, optimal, and superoptimal ranges for photosynthesis by our study species, and mean daily duration of air temperature above 25°C, an approximate temperature optimum for photosynthesis by our species (T. W. Sipe and F. A. Bazzaz, *unpublished data*). The survival and growth patterns were consistent for all eight microclimatological factors. We illustrate this result by plotting survival, leader extension, branch extension, total extension, net height change, and net basal diameter change against mean daily PPF (Fig. 8).

Survival is reduced substantially only at the extreme exposure end of the gradient (large-gap NW, NE, and C). The species show nearly parallel responses and the same rank order ($RUB \Rightarrow PEN \Rightarrow SAC$) in all site/plot positions.

The three species are distinctly separated across the gradient, with few crossovers, for all five growth variables. The rank order among species is consistently $PEN > RUB > SAC$ for leader extension and net height

change. The order applies for net basal diameter change as well, except for large-gap centers. Since total shoot extension was highly correlated with branch growth due to dieback, and since red maple exhibited the greatest ability to recover from leader loss, the graphs for branch and total shoot extension show $RUB \Rightarrow PEN > SAC$ across most of the PPF gradient.

Conclusions on gap partitioning

Our study provides little evidence for gap partitioning by small, advance-regenerated seedlings of striped, red, and sugar maple across the microenvironmental gradient resulting from the experimental creation of small- (75 m²) and medium-sized (300 m²) canopy gaps in the mixed deciduous forests of central Massachusetts. The rank order across most of the gradient was $PEN > RUB > SAC$ in shoot assimilation and net increase in both height and basal diameter. There were some weak trade-offs in species performance in the north and center plots of the large gaps, where red maple had higher survival, estimated shoot photosynthesis (north plots only), and/or total extension growth (center plot only). However, because of the more extensive dieback by red maple, striped maple surpassed red maple in net height increase in all plots, and exceeded red maple in net basal diameter increase in all plots but large-gap center. A separate analysis of growth by seedlings without dieback showed an even clearer $PEN > RUB > SAC$ performance ranking across the entire microenvironmental gradient (Sipe 1990). We conclude that striped maple is a superior generalist, red maple is a weaker generalist, and sugar maple shows the poorest performance in a manner that is relatively insensitive to the gap–understory gradient. The nearly complete absence of significant site \times plot \times species interaction terms in the ANOVA results for 1988, 1989, and cumulative 1987–1989 growth data supports this result. Field observations in 1994 confirm that this pattern of species responses has continued through 6 yr of gap release.

Extrapolating our results to natural gaps raises several questions due to the clearing of the experimental gaps and seedling management. We removed all felled biomass and periodically cut back regrowth to clarify the impact of gap geometry on microclimatic patterns. This eliminated structural heterogeneity (dead, dying, and regrowing), created more exposed conditions at ground level, and suppressed competition between different size classes of advance regeneration and sprout regrowth. The seedling plot preparations minimized belowground competition and probably affected moisture and nutrient availability.

Under the expanded interpretation of gap partitioning discussed in the *Introduction*, these manipulations are problematic because they alter many factors and biotic interactions, such as competition, which influence species success in natural gaps. Our experiment would thus be viewed as a study of the ecophysiological

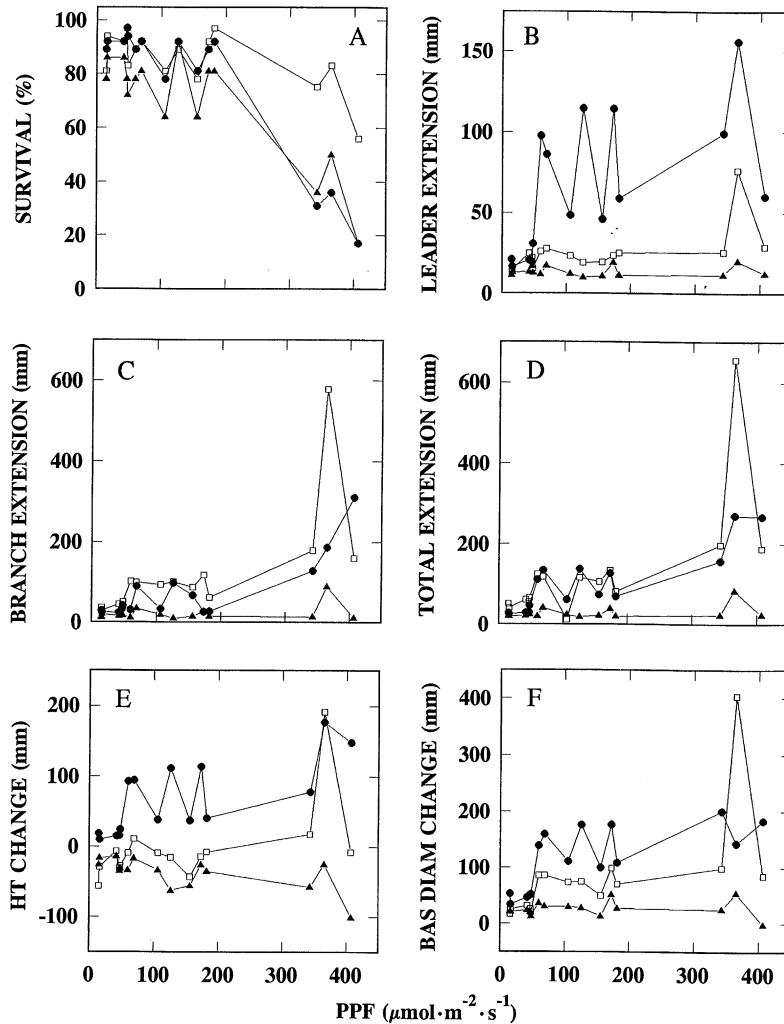


FIG. 8. Survival and growth vs. mean PPF across the gap-understory gradient: (A) survival, (B) total leader extension, (C) total branch extension, (D) total shoot extension, (E) net height change, (F) net basal diameter change. ● = *Acer pensylvanicum*, □ = *A. rubrum*, ▲ = *A. saccharum*.

potential for partitioning involving a small subset of all possible mechanisms for spatial differences in species performance. But the original gap partitioning hypothesis (narrow interpretation) is fully autecological, involving a sequence of connections between (1) predictable microenvironmental variation, (2) differential ecophysiological responses to this variation, and (3) spatial trade-offs among species in noncompetitive survival and/or growth that are clearly linked to differential ecophysiological performance. The generally unpredictable nature of structural heterogeneity and biotic interactions in natural gaps would make it difficult to quantify the effects of gap geometry on microenvironmental patterns and to detect any underlying trade-offs in ecophysiological responses to these patterns. The narrow version of the gap partitioning hypothesis requires the kind of controlled experimentation repre-

sented by our study, and our conclusions on gap partitioning are made with this in mind.

We do have empirical support for the results of this study from a companion experiment in three small (60–107 m²), uncleared natural gaps at the Harvard Forest (T. W. Sipe and F. A. Bazzaz, unpublished data). We simulated gap release by moving potted seedlings of all three maple species from understory to gap plot positions that were arranged in the same spatial pattern as in the experimentally created gaps. Striped maple again exceeded the other species in height and basal diameter growth across the entire understory-gap gradient. Sugar maple's response was comparable to red maple in gaps and exceeded red maple in the understory.

Our transplanted seedlings were of a limited age and size range compared to the breadth of advance re-

gerant status in uneven-aged forests. Longer term studies of gap processes, which include measurements of microenvironments and ecophysiology under both competitive and non-competitive conditions for juvenile trees of varying age/size, are needed. This would clarify the degree to which natural gap partitioning affects regeneration patterns and the maintenance of community tree species diversity in central New England.

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