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GAP PARTITIONING AMONG MAPLES (*ACER*) IN CENTRAL NEW ENGLAND: SHOOT ARCHITECTURE AND PHOTOSYNTHESIS[1]

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Abstract. We measured shoot architecture and photosynthesis by three species of maple (*Acer pensylvanicum, A. rubrum, A. saccharum*) in response to understory and small canopy gaps in the mixed deciduous forests of central New England. Trees were felled to create six cleared gaps of two sizes (8 × 12 m, 75 m^2; 16 × 24 m, 300 m^2). 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 gaps and additional understory sites 1 yr before gap creation. Measurements of microclimates, architecture, photosynthetic performance, and seedling survival and growth were made over 1 yr before, and 2 yr following, gap release.

Architectural variation increased greatly over the 3-yr period. Striped maple (*A. pensylvanicum*) and red maple (*A. rubrum*) increased branch numbers, leaf numbers, and total leaf areas in gaps, especially large gaps, while sugar maple (*A. saccharum*) showed much smaller changes. Red maple tended to increase the number of leaves while leaf size decreased; striped maple increased leaf number but held leaf size constant.

Diurnal patterns of photosynthesis by these species differed within and between gap and understory sites. Red maple showed higher photosynthetic rates per unit leaf area than striped and sugar maple in all site/plot combinations except the large-gap south plots, where striped maple exceeded red maple. Estimated diurnal shoot-level assimilation differentiated species more than unit area assimilation rates and also altered the rank order of performance, with striped maple > red maple > sugar maple in all microsites except the large-gap north.

Population-level assimilation vs. irradiance response curves exhibited a similar pattern, with red maple dominating unit area rates in most plot microsites. In contrast, shoot assimilation curves showed striped maple > red maple > sugar maple in all microsites except the large-gap north, where red maple > striped maple.

Architectural variation among these species interacted with leaf-level assimilation rates to produce some differences among these species in shoot-level assimilation across the gap–understory microclimatic gradient. Since survival and growth patterns are usually correlated with differences in whole-plant carbon assimilation, our results suggest that there is some photosynthetic potential for gap partitioning among these three species of *Acer*.

Key words: Acer pensylvanicum; Acer rubrum; Acer saccharum; *forest canopy gaps; Harvard Forest; leaf photosynthesis; microenvironments; plant architecture; shoot photosynthesis.*

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 coexistence and community diversity are enhanced by disturbance-fostered niche specialization (Pickett 1983, Bazzaz 1984, 1987, Canham and Marks 1985, Denslow 1985, Petraitis et al. 1990). 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

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close to the ground, and (2) autecological traits of tree species, including seed size, dispersal ability, dormancy, germination behavior, and physiological responses such as photosynthesis, nutrient use, and overall shade tolerance. Both papers stressed the importance of seed and small seedling stages in discussing the 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 the original, narrower sense.

There are good reasons for expecting ecophysiological specialization by tree species on portions of the gap–understory gradient (Bazzaz and Sipe 1987). Studies of plant architecture, photosynthesis, water relations, and nutrient use have led to a general theory regarding the autecological traits that characterize early- vs. late-successional tree species (Bazzaz 1979) and large-gap vs. small-gap specialists (Bazzaz and Pickett 1980, Pickett 1983, Bazzaz 1984). The relationship between photosynthetic behavior and ecological performance has received the most attention. Four themes have dominated this work: (1) the degree to which apparent successional roles and/or gap size preferences of species correlate with the classic differences in sun vs. shade photosynthetic syndromes (Bazzaz 1979, Bjorkman 1981, Oberbauer and Strain 1984, Read and Hill 1985, Osmond and Chow 1988); (2) the degree to which physiological plasticity (different phenotypes when grown in unchanging different environments) and acclimation (ability to respond to changes in environment) differ among apparent generalists vs. large-gap or small-gap specialists (Bazzaz and Carlson 1982, Fetcher et al. 1983, Langenheim et al. 1984, Chazdon and Field 1987, Pearcy 1987, Walters and Field 1987, Field 1988, Thompson et al. 1988); (3) the importance of shoot-level and whole-plant measurements for understanding ecological performance (Mooney and Chiariello 1984, Küppers 1985, Field 1988, Givnish 1988), and (4) the degree to which carbon assimilation in fluctuating light environments differs from steady-state expectations, particularly in forest understories (Pearcy 1990 and references therein). The results from controlled environment experiments have demonstrated the potential for partitioning among species of contrasting autecology, but ecophysiological studies in the field have been less conclusive.

Our knowledge of forest microclimates, silvicultural regeneration, natural gap regeneration, tree ecophysiology, and tree growth is extensive, but it has not been possible to generalize on the degree to which gap partitioning actually occurs, particularly in the smaller gaps (<300 m^2) that dominate natural disturbance regimes in many temperate and tropical forests (Brokaw 1985, Runkle 1985). 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. 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.

The study presented here is an experimental test of the gap partitioning hypothesis for three species of maple (*Acer pensylvanicum, A. rubrum, A. saccharum*) in the mixed broad-leaved forests of central New England. We created elliptical canopy gaps of two sizes (8 × 12 m, 75 m^2; 16 × 24 m, 300 m^2) at the Harvard Forest in central Massachusetts and measured non-competitive architecture, photosynthesis, survival, and growth of 2160 transplanted seedlings in response to microclimatic patterns over a 3-yr period. Five questions were posed at the outset: (1) How do microclimates vary diurnally and seasonally across the understory and canopy gaps? (2) How do the maple species differ in shoot architectural and photosynthetic responses across the gap–understory microclimatological gradient? (3) Do the species exhibit differential survival and/or growth across the gradient? (4) What are the relationships among microclimate, photosynthetic performance, and survival/growth? (5) Is there specialization by the species along the gradient, i.e., does gap partitioning occur?

The results of this study are being reported in a series of papers. The first paper summarizes the gap–understory microclimatological gradient (T. W. Sipe and F. A. Bazzaz, *unpublished manuscript a*). This paper discusses shoot architectural dynamics and leaf-, shoot-, and population-level photosynthetic responses by these maple species to the microclimatological gradient. The third paper (T. W. Sipe and F. A. Bazzaz, *unpublished manuscript b*) discusses survival and growth and concludes with a study synthesis on the occurrence of gap partitioning in this 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* (striped maple, PEN), *A. rubrum* (red maple, RUB), and *A. saccharum* (sugar maple, SAC). A fourth shade-tolerant species, *A. spicatum* (mountain maple), can also be found with these three, but it is rare in the Harvard

Forest. The distributions of the three study species overlap across a substantial range in the eastern U.S., including New England, the Great Lakes Region, and the Appalachians (Burns and Honkala 1990). They cooccur in greatest abundance in moist forests where small gaps dominate the disturbance regime. These species play prominent roles in New England, including the Transition Hardwoods region where the Harvard Forest research station and our study site are located (Sipe 1990).

While they are all classified as tolerant or very tolerant of shade (Baker 1949), there are physiological, morphological, and life historical differences that suggest potential specialization in understory and small gap microenvironments. Sugar maple has been regarded as one of the most shade tolerant of the North American broad-leaved species (Burns and Honkala 1990). It is the largest and longest lived of our three study species. Sugar maple saplings can survive extended understory suppression and still respond to small canopy gap release (Barden 1983, Canham 1985), but may not respond as well in larger silvicultural gaps (Tubbs 1977). Of the three species, sugar maple appears to have the greatest water and nutrient requirements (Leak 1975).

Red maple's range and local physiographic distribution are greater than for sugar or striped maple. It is intermediate in longevity and maximum size, and it is widely thought to be less shade tolerant than sugar maple. Wallace and Dunn (1980) found that red maple responded quite well to gap conditions, and the general experience of foresters and ecologists is that red maple can grow rapidly in larger canopy openings.

Striped maple is primarily a subcanopy tree that is capable of reproductive output in the understory. Its longevity and maximum size are well below that of the other two species. Opinions differ on striped maple's shade tolerance, ranging from very tolerant (Hibbs 1979) to intermediate (Bormann and Likens 1979). Wilson and Fischer (1977) suggest that striped maple is able to respond well to small canopy gaps.

Germination and establishment in all of these species may occur after disturbance, especially by red maple, but advance regeneration (germination in the understory followed by release when a canopy gap forms overhead) is considered to be more important for canopy participation and/or reproductive maturity in all three species (Marquis 1982, Barden 1983, Canham 1985, White 1991).

In summary, the three maple species are all shade tolerant and typically employ advance regeneration, but they appear to respond differentially to canopy gaps of varying size, and thus represent a useful system for testing the gap partitioning hypothesis. We hypothesized that, if the microenvironmental gradient across the understory, single-tree (75 m^2) and small multiple-tree gaps (300 m^2) is sufficiently broad to be partitioned among these species, then 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. The species should also perform differentially across plot positions within the large and small gaps in response to within-gap microenvironmental patterns.

Site preparation and experimental plantings

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). Our experiment was done in 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, Prunus serotina, Fraxinus americana, Pinus strobus,* and *Tsuga canadensis.*

Six understory sites and six future gap sites were laid out in fall 1986 across three blocks in the experimental area. Three future gaps were small (8 × 12 m, 75 m^2) and three were large (16 × 24 m, 300 m^2). The rationale for these sizes and further information on experimental design are discussed in T. W. Sipe and F. A. Bazzaz (*unpublished manuscript b*). All gaps were designed to be elliptical with the long axis oriented east-west. Five transplant seedling plots were placed in each gap, at the center and near what would become the gap edge along all four subcardinal directions (northwest, northeast, southwest, and southeast). The edge plots were equidistant from the center plot. The "large understory" and "small understory" sites also had five seedling plots arranged like those in the corresponding gap size. All seedling plots were treated by removing all roots >0.5 cm in diameter and all rocks >2.5 cm in size. Care was taken to minimize inversion of the soil profile.

A total of 2160 naturally established seedlings (720 per species, 15–30 cm tall, 4–20 yr old) were lifted from the understory in several other areas of the Harvard Forest and transplanted into the 60 plots. All seedlings were unbranched and undamaged with an intact terminal meristem (leader). The seedlings were dug in October 1986 after leaf senescence and planted with bare roots into the 60 prepared plots over a 2-wk period a full year before gap creation. Each seedling plot contained 12 seedlings per species (36 total), randomized by position in four rows of nine seedlings each. Seedlings were separated by 25 cm in all directions to minimize competition. Edge seedlings also had 25 cm of growing space on the plot margins. Seedlings from the various source locations in the forest were nonsystematically randomized across the 12 sites and 60 plots.

Trees were felled to make the gaps in October 1987. All logs and branches were removed, all woody stems >50 cm tall were cut basally, and regrowth was cut back each year. This was done in order to study the primary effect of gap geometry on microclimatic patterns and species responses in the absence of the extremely variable structural heterogeneity of the downed and recovering gap community. Leaf and fine woody litter were left in place where they naturally fell except for lifting larger branches off seedlings to prevent damage. The plot margins were respaded in the late spring of each year, and the plots were weeded by hand regularly within each growing season.

Shoot architecture

Shoot architectural variables were measured in early fall of both 1987 (1 yr after transplanting, just before gap creation) and 1989 (two growing seasons after gap creation) on all surviving seedlings. The 1987 pregap data included shoot height, number of leaf pairs, number of leaves, and leader status (intact vs. dead or damaged). In 1989, the following architectural variables were added: (1) number of living primary and secondary branches; (2) the positions of branch origins on the stem, divided into upper, middle, and lower thirds; and (3) mean leaf (laminar) length.

Total leaf areas per shoot were estimated through species-specific regressions of leaf area on laminar length. Leaves were collected in midsummer from naturally established young seedlings of all three species. Their laminar lengths were measured to the nearest 1.0 mm, and their areas were determined individually to the nearest 0.01 cm^2 with a LI-COR 3100 leaf area meter. Quadratic curves were then fitted to data points for each of the first three leaf pairs within each species to check for divergent allometry across pairs. The coefficients did not differ greatly across pairs within species, so the leaf pairs were pooled and curves were fitted to the pooled data.

The means for the architectural data were compared across 1987 and 1989. In addition, a split-split-plot analysis of variance model (plots split within sites, species split within plots; T. W. Sipe and F. A. Bazzaz, *unpublished manuscript b*) was applied to 1989 stem height, mean leaf length, mean leaf area, and total leaf area. Tukey HSD tests (Day and Quinn 1989) were used for post hoc multiple comparisons among treatment groups.

Photosynthesis

Our objectives required photosynthetic data that could be related to cumulative survival and growth at the population level across the entire gap–understory gradient, involving several scaling problems. We sacrificed intensive study of photosynthetic mechanisms in order to achieve simultaneous broad comparisons of carbon assimilation by these species at both leaf and shoot levels.

All gas-exchange measurements were done in block 1 of the experimental area, which contained a large gap, small gap, large understory, and small understory site. We sampled diurnal patterns of assimilation at six site/plot positions, which spanned the gap–understory gradient: large gap north and south, small gap north and south, and large understory north and south. The large understory plots differed in mean irradiance levels (south > north), providing two points on the understory portion of the gradient.

All gas-exchange measurements were done with a LI-COR 6200 photosynthesis system, operating in absolute mode, on plants with intact leaders and normal architecture. The typical sampling scheme was to take three sequential 30-s measurements on one member of the oldest leaf pair for each seedling. These three measurements were averaged to provide mean net assimilation for that seedling at that time of day. Measurements were always replicated for species at the plot level (usually three seedlings per species, nine seedlings total). Measurements among plot positions were repeated to yield 3–5 points per species across the day.

We used the same set of seedlings on several days during 1988 to encompass seasonal variation in gas exchange. We sampled the northwest plots and the southeast plots on different days due to time limitations in the field. Two days were selected for presentation of diurnal patterns of net assimilation per unit leaf area across the six microsites, 25 June 1988 (northwest plots) and 8 August 1988 (southeast plots).

Estimates of total instantaneous shoot assimilation were calculated by multiplying the assimilation per unit area for a single leaf (measured in the field) by a shoot assimilation scaling factor (also per unit area) and then by total shoot leaf area. The shoot-level assimilation scaling factors were generated using data from four sample days in 1988 and 1989. Linear regressions were used to predict assimilation within and then across leaf pairs, based on a single gas-exchange measurement on one leaf of the oldest pair on the seedling. The within- and across-pair scaling factors were multiplied to yield a single combined shoot scaling factor for each species (Sipe 1990).

The 1987 and 1989 measurements of shoot architecture described above were unsuitable for photosynthetic scaling because (1) they encompassed all surviving seedlings, including many architecturally complex individuals with leader loss and variable regrowth, and (2) they represented only late-season architectural status. So shoot leaf areas for photosynthetic scaling were calculated from a separate set of architectural information, generated from phenological measurements on a subset of seedlings in all sites and plots taken every other week during 1988 and 1989. These 540 plants (three per species per plot × 60 plots) were selected before leafout in April 1988 as representative of mean age, height, and basal diameter for each species. Data for the 180 seedlings in block 1 of the experiment were used since the gas-exchange sampling was done in this block.

Mean laminar lengths for each leaf pair on each seedling were recorded at each sample (taken once every 2 wk), providing a seasonal course of leaf areas (through area : length regressions) for each leaf pair and for the entire shoot. The phenological samples closest to the dates of diurnal photosynthetic sampling were selected, so that scaled shoot photosynthesis estimates were as accurate as possible.

This shoot scaling technique yields maximum potential shoot assimilation since it does not take into account the effects of differential leaf orientation or self-shading by the species. For species of substantially different shoot architectures, this would be a problem. However, undamaged seedlings of the three maple species do not differ greatly in phyllotaxy. They are oppositely branched with consistent 90° angles between successive leaf pairs. They have relatively few nodes and leaves and tend to maintain their leaves horizontally except during periods of significant water stress. They are all relatively determinate in their leaf flushing within any given year, such that leaf ages do not vary widely on the shoot, especially in microsites with low irradiance.

In addition to diurnal assimilation comparisons, we explored how our species differed in photosynthetic responses to irradiance at the *population* level over *seasonal* time scales by generating leaf-level and shoot-level light response curves from data pooled across all diurnal sample days in 1988. This was possible because our diurnal sampling regime was always comparative among species, providing equivalent representation by the species in the pooled data. The measurements were partitioned into photosynthetic photon flux (PPF, in micromoles per square metre per second) intervals that provided the best breakdown of numbers of samples across the PPF continuum. Net assimilation (in micromoles of carbon per square metre per second) and PPF from the samples were averaged within each PPF interval and plotted for each species in each site/plot location. Curves were first generated for unit area assimilation rates. Then shoot scaling factors were applied in the same manner as for diurnal assimilation to yield estimated shoot-level assimilation vs. PPF response curves for 1989.

We did not attempt to fit hyperbolic curves to these data because they were more variable than data typically used for response curve analysis. The virtue of our approach is that it represents a powerful tool for direct comparison of population performance over seasonal time scales at various microsites in the field.

RESULTS

Shoot architecture

The species differed significantly but only slightly (<31 mm) in mean height at the end of the 1986–1987 pregap year in the understory, with SAC (sugar) > RUB (red) > PEN (striped). The species also differed in mean number of leaf pairs (RUB = 2.4, SAC = 1.8, and PEN = 1.1) and thus total number of leaves (RUB = 4.5, SAC = 3.4, and PEN = 2.1), representing species-specific tendencies under suppression by low irradiances in the understory environment.

Extensive architectural variation arose over the two seasons following gap creation (Fig. 1). By October 1989, only 723 of the surviving 1705 stems (42%) had intact leaders. The species differed greatly in maintaining their leaders, with PEN = 444, RUB = 76, and SAC = 203. Along with leader loss, there were some basal resprouts from dieback stems, secondary branching, and microsite-related branch initiation unrelated to shoot damage. The result of all these processes was more complicated shoots with larger numbers of active meristems, more leaf pairs, more leaves, and a greater diversity in leaf age and size on the same shoot as compared to pregap seedlings.

For all species together, seedlings were taller in both gap sizes than in the understory, and the best average height growth was achieved in the large gap centers. As compared to the 1987 pregap initial heights, only striped maple showed a positive increase, while red and sugar maple both declined, on average, due to dieback. This pattern held across the entire study as well as within each site.

The total of 1106 plants with branches in 1989 far exceeded the number of seedlings with branches in 1987. For all species combined, seedlings in both gap sizes exhibited more branching than in the understory, with the highest values in the large-gap north and center plots. This corresponded to the more frequent leader loss in these plots. Red maple had more branches on average than either striped or sugar maple across the study and within all sites (Fig. 1).

For the species combined, the three sites differed in total number of leaves, with the large-gap plants possessing 3 times as many leaves as the understory and 75% more leaves than the small gaps. The largest numbers of leaves occurred in the center, northwest, and northeast plots of large gaps. The species differed in total leaf number, with a RUB > PEN > SAC rank order that held across all sites (Fig. 1). Red maples in large gaps had over twice as many leaves (18.6) as the other species in any site, mostly due to the center plots.

The species differed greatly in mean laminar length, with striped maple leaves being over twice as long as either sugar or red maple in all sites (Fig. 1). Striped maple showed monotonically increasing laminar lengths from the large gaps to small gaps to understories, while red maple declined monotonically along this gradient. The results for mean leaf area paralleled those for mean leaf length across species and sites. But since leaf area is related to laminar length through quadratic allometry, the relative differences between striped maple and the other species were even greater than for laminar length (Fig. 1).

The species differed significantly in total shoot leaf area, with striped maple nearly twice that of red maple and over 5 times that of sugar maple overall (Fig. 1).

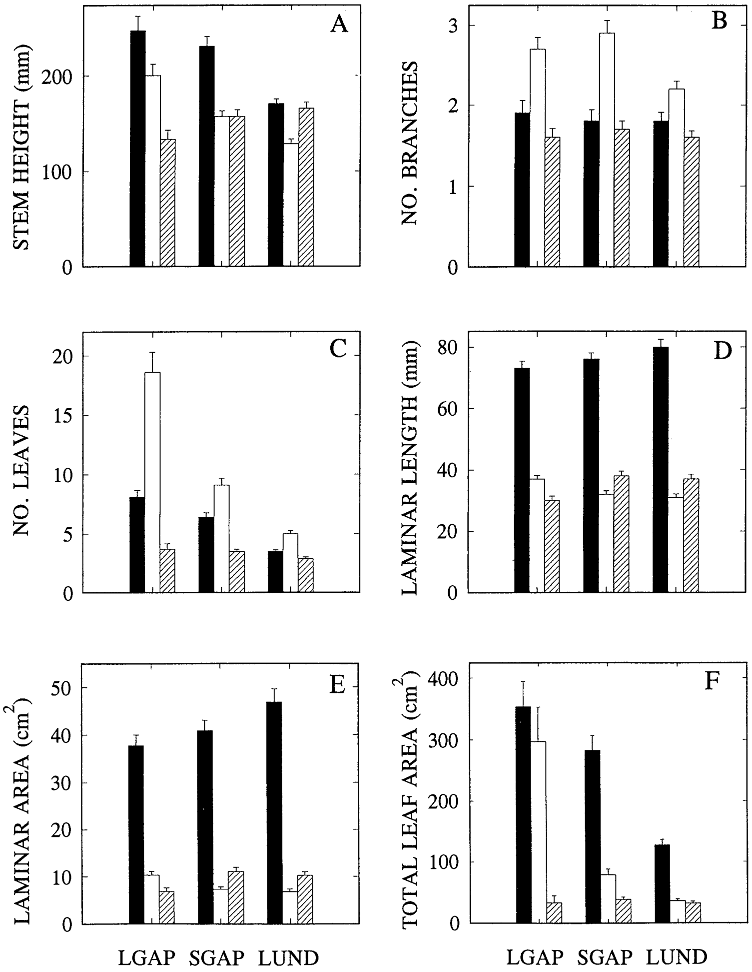

FIG. 1. Summary of shoot architecture for all surviving seedlings as of September 1989. (A) Stem height, (B) number of branches, (C) number of leaves, (D) leaf laminar length, (E) individual leaf area, (F) total shoot leaf area. LGAP = large gap, SGAP = small gap, LUND = large understory. *Acer pensylvanicum* = ■, *A. rubrum* = □, *A. saccharum* = ▨. Sample sizes range from 96 to 167. Data are means ± 1 SE.

This rank order held across all sites, but was most noticeable in the small gap. In contrast to mean leaf length and area, both striped and red maple showed monotonic declines in total leaf area from large gaps to small gaps to understory. Sugar maple showed almost no response to the gradient.

In summary, the three species differed significantly in mean stem height (PEN > RUB > SAC), mean leaf length (PEN > SAC > RUB), mean leaf area (PEN > SAC > RUB), and total leaf area (PEN > RUB > SAC) at the end of two seasons of growth following gap creation. There were several monotonic patterns across the large gap/small gap/understory gradient for all species combined. The number of leaves and total leaf area declined, while mean leaf length and area increased. But none of these monotonic differences were statistically significant overall due to the differential patterns among the species. Striped and red maple were much more responsive architecturally than sugar maple, and the divergences among species were greater in the gaps (especially large gaps) than in the understory.

Photosynthesis

Architectural data used in scaling photosynthesis to the shoot level.—In 1988, PEN > RUB > SAC in total leaf area (Table 1). But by 1989, striped maple had gained significantly (+94%), red maple gained modestly (+34%), and sugar maple lost significantly (−48%) in total leaf area. Both red and sugar maple increased the mean number of leaves overall from 1988 to 1989, but mean leaf areas declined. In contrast, striped maple maintained its mean leaf area but more than doubled leaf number. The result is that striped maple had the greatest leaf area in five out of the six site/plot positions used in photosynthesis measurements, with red maple the greatest only in the large-gap north. Sugar maple was last in all but the large-understory north and small-gap south.

TABLE 1. Shoot architectural data for a subset of seedlings in the north and south plots of the Block 1 large-gap (LGAP), small-gap (SGAP), and large-understory (LUND) sites (N = north, S = south). Total leaf areas for 1988 and 1989 in this table were used to scale upward from assimilation per unit leaf area to estimated shoot assimilation. PEN = striped maple, RUB = red maple, SAC = sugar maple.

		1988						1989					
Species	Site/plot	*n*	No. leaf pairs	No. leaves	Mean leaf length (mm)	Mean leaf area (cm^2)	Total leaf area (cm^2)	*n*	No. leaf pairs	No. leaves	Mean leaf length (mm)	Mean leaf area (cm^2)	Total leaf area (cm^2)
PEN	Total	35	1.1	2.2	79.8	37.8	79.5	30	2.5	5.0	77.5	37.4	154.5
RUB	Total	35	2.1	4.2	43.4	12.0	49.7	34	5.8	10.9	29.2	5.8	66.8
SAC	Total	35	1.4	2.9	58.6	27.2	78.3	27	1.8	3.3	32.7	10.0	40.5
PEN	LGAP-N	5	1.0	2.0	61.0	21.7	43.4	1	6.0	11.0	15.0	1.3	14.0
	LGAP-S	6	1.0	2.0	73.3	31.5	63.1	6	3.5	7.0	62.5	23.3	154.7
	SGAP-N	6	1.5	3.0	76.5	33.8	90.4	5	2.8	5.4	76.1	33.3	172.5
	SGAP-S	6	1.0	2.0	88.0	45.2	90.4	6	3.7	7.3	87.1	47.2	297.4
	LUND-N	6	1.0	2.0	90.2	47.4	94.7	6	1.0	1.8	86.8	45.4	77.3
	LUND-S	6	1.0	2.0	86.5	44.4	88.7	6	1.2	2.3	85.3	43.0	97.3
RUB	LGAP-N	6	2.5	5.0	41.8	10.5	52.6	6	8.5	15.7	31.8	6.2	109.2
	LGAP-S	6	2.2	4.3	42.1	11.3	46.3	6	9.7	18.5	27.4	4.7	72.5
	SGAP-N	6	2.0	4.0	52.6	17.4	72.6	4	6.5	11.8	30.5	6.6	73.5
	SGAP-S	5	2.2	4.4	38.0	9.5	42.0	6	5.3	10.0	34.8	8.2	92.8
	LUND-N	6	1.7	3.3	47.7	14.2	46.3	6	2.5	4.7	22.5	3.3	16.9
	LUND-S	6	2.0	4.0	37.0	8.7	36.9	6	2.7	4.8	28.7	6.2	38.3
SAC	LGAP-N	6	1.3	2.7	55.4	23.4	63.1	1	2.0	4.0	12.0	1.1	4.4
	LGAP-S	6	1.3	2.7	57.6	26.8	74.3	6	1.5	2.8	26.3	6.4	17.7
	SGAP-N	5	1.4	2.8	55.1	24.5	67.5	2	1.0	2.0	24.5	4.5	9.1
	SGAP-S	6	1.8	3.7	67.8	35.1	123.2	6	2.7	5.3	47.2	19.0	106.9
	LUND-N	6	1.3	2.7	65.0	33.4	81.8	6	1.8	3.3	40.8	13.1	38.7
	LUND-S	6	1.3	2.7	50.3	19.6	58.1	6	1.3	2.2	22.7	5.0	15.0

Microclimatological patterns across the gap–understory gradient.—A distinct irradiance gradient exists from the north sides of large gaps to the most shaded portions of the understory, especially on clear days (Table 2). The clear-day values are important for interpreting photosynthetic responses because the gas-exchange measurements were all made under clear to hazy sky conditions. However, leaf performance at any point in the season is conditioned by the cumulative effect of all preceding weather conditions. So the combined-day (clear plus overcast) PPF values are also relevant, especially for the population light response curves, which are based on gas-exchange data from across the season. Mean air temperature and the duration of air temperature >25°C on clear days also show a clear gradient due to the great differences in direct beam exposure. Mean PPF and mean air temperature showed a particularly strong correlation across these six microsites ($R^2 = 0.993$). These patterns are described more completely in T. W. Sipe and F. A. Bazzaz (*unpublished manuscript a*).

Diurnal leaf and shoot assimilation.—The species showed parallel diurnal patterns of leaf assimilation except in the most exposed (large-gap north) and darkest (large-understory north) sites (Fig. 2). Red maple had the highest rates in all microsites except the large-gap

TABLE 2. Microclimatological conditions across the six gas-exchange plot positions that span the gap–understory gradient. Data are means for 5 clear, 5 overcast, or 10 combined clear and overcast 12-h sample days spread across the growing season (T. W. Sipe and F. A. Bazzaz, *unpublished manuscript a*). Measurements made at northwest and northeast plots were averaged to provide "north" values. Data from southeast and southwest were averaged to provide "south" values. Direct beam durations refer to how long direct beam arcs shone on each plot position across the growing season (seasonal duration) or on clear days near summer solstice (diurnal duration). PPF = photosynthetic photon flux.

Site/plot*	Seasonal duration direct beam (wk)	Diurnal duration direct beam (h)	Mean PPF clear days	Mean PPF overcast days	Mean PPF combined days	Mean air temp. clear days	Mean air temp. overcast days	Duration clear day air temp. >25°C (min)
LGAP-N	29.0	5.75	611	139	375	24.7	20.5	341
LGAP-S	0	0	190	117	154	22.1	20.6	219
SGAP-N	7.5	2.25	280	48	164	22.9	20.0	172
SGAP-S	0	0	74	54	64	21.5	19.7	138
LUND-N	0	0	22	9	16	21.0	19.7	136
LUND-S	0	0	72	23	48	21.4	19.7	114

* LGAP = large gap, SGAP = small gap, LUND = large understory, N = north, S = south.

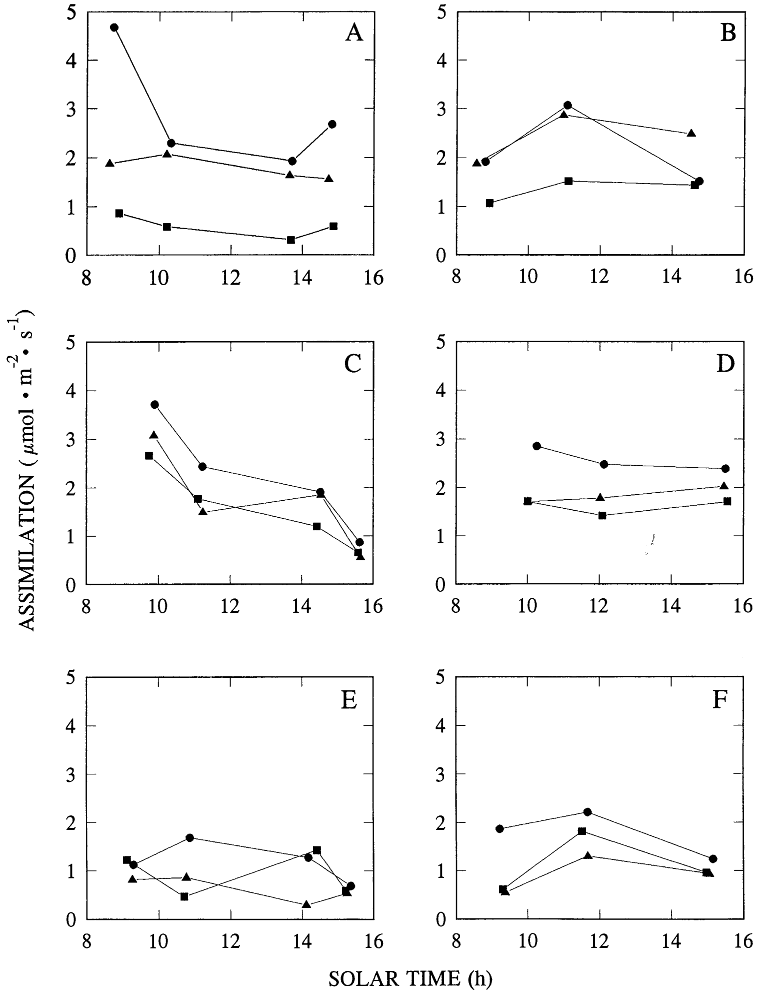

FIG. 2. Diurnal patterns of leaf assimilation on 28 June 1988 (northwest plots) and 8 August 1988 (southeast plots). (A) Large-gap northwest, (B) large-gap southeast, (C) small-gap northwest, (D) small-gap southeast, (E) large-understory northwest, (F) large-understory southeast. *Acer pensylvanicum* = ▲, *A. rubrum* = ●, *A. saccharum* = ■. For all plots, $n = 3$ seedlings and 3–9 assimilation measurements per data point.

south, where PEN > RUB. The clearest differences were in the large gap, where red maple possessed its greatest advantage in the early morning and late afternoon, with an apparent midday depression. Sugar maple exhibited the lowest rates in all gap sites and was second to red maple in the understory.

Estimated shoot assimilation in 1989 showed greater differences overall, and significant changes in relative performance among the species, as compared to unit area rates (Fig. 3). Red maple was still superior in the large-gap north plots, but striped maple outperformed the other species in all other microsites except the darkest understory (north), where the three species were indistinguishable.

The leaf-level data did not distinguish the species as well as shoot-level rates in the second season after gap release. Furthermore, the differences in shoot assimilation among species increased over the two sample years (data not shown for 1988). Scaling to the shoot level not only clarified species relationships, but altered species rank orders. This was most often true because red maple had higher unit area rates but smaller shoot leaf areas than the other species.

Population light response curves at leaf and shoot levels.—As a combined group, the three species exhibited a clear preference for plot microsites with intermediate levels of irradiance (Fig. 4). They generally performed best, in terms of overall light response curves, in the small-gap north and large-gap south plots. The three species were suppressed in the understory, especially in the deeply shaded north plot, and they were inhibited in the north plots of large gaps. The large-gap south plots were more favorable than the small-gap south plots due to the generally higher diffuse irradiances and greater frequency of direct beam in the former. The small-gap south plots do receive slightly higher diffuse irradiances than the understory due to the canopy opening (T. W. Sipe and F. A. Bazzaz,

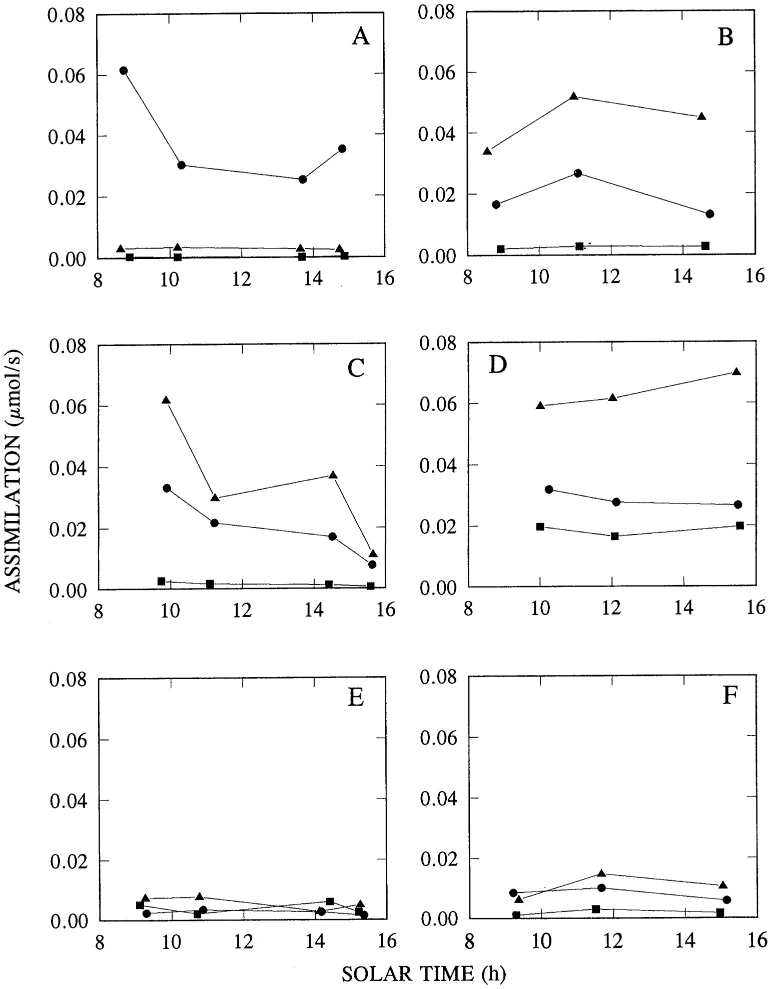

FIG. 3. Diurnal patterns of estimated shoot assimilation in 1989. (A) Large-gap northwest, (B) large-gap southeast, (C) small-gap northwest, (D) small-gap southeast, (E) large-understory northwest, (F) large-understory southeast. Symbols defined in Fig. 2. For all plots, $n = 3$ seedlings and 3–9 assimilation measurements per data point.

unpublished manuscript a), and this may have accounted for their rank above the understory plots in leaf assimilation.

With the exception of the understory north (species indistinguishable) and the large-gap south, where PEN > RUB > SAC, red maple exceeded striped and sugar maple in leaf assimilation for all microsites. Peak assimilation and apparent saturation irradiance were highest for all species at the four microsites intermediate in mean daily PPF. But the species did not show parallel patterns, implying microsite-specific differences in adjustment of photosynthetic capacity. Across all microsites, red and striped maple reached comparable peak carbon assimilation (4.5 $\mu mol \cdot m^{-2} \cdot s^{-1}$), while sugar maple never exceeded 3.25 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Saturation irradiances were mostly <500 $\mu mol \cdot m^{-2} \cdot s^{-1}$, even for the large-gap north plots. Apparent compensation points, visually estimated from scatterplots of all data points used in this analysis (data not shown), generally declined across the microsite–irradiance gradient, from 25–50 $\mu mol \cdot m^{-2} \cdot s^{-1}$ in the large-gap north plots to <10 $\mu mol \cdot m^{-2} \cdot s^{-1}$ in the understory north, with no clear differences among species.

Scaling the population light curves to the shoot level for 1989 clearly separated the species and showed that striped maple dominates red and sugar maple in five of the microsites (Fig. 5). Red maple was superior only in the large-gap north, and sugar maple showed very little response to the gradient. The species were least distinguishable in the darkest understory.

The population light response curves support the interpretations from the diurnal sampling. In both cases shoot assimilation estimates distinguished species more clearly than leaf assimilation and produced different rank orders of superiority, especially in the second season following gap release. Red maple usually possessed higher leaf-level assimilation, but striped maple's greater total leaf area gave it the advantage in shoot assimilation in all microsites except the large-gap north. Sugar maple was competitive only in the most shaded un-

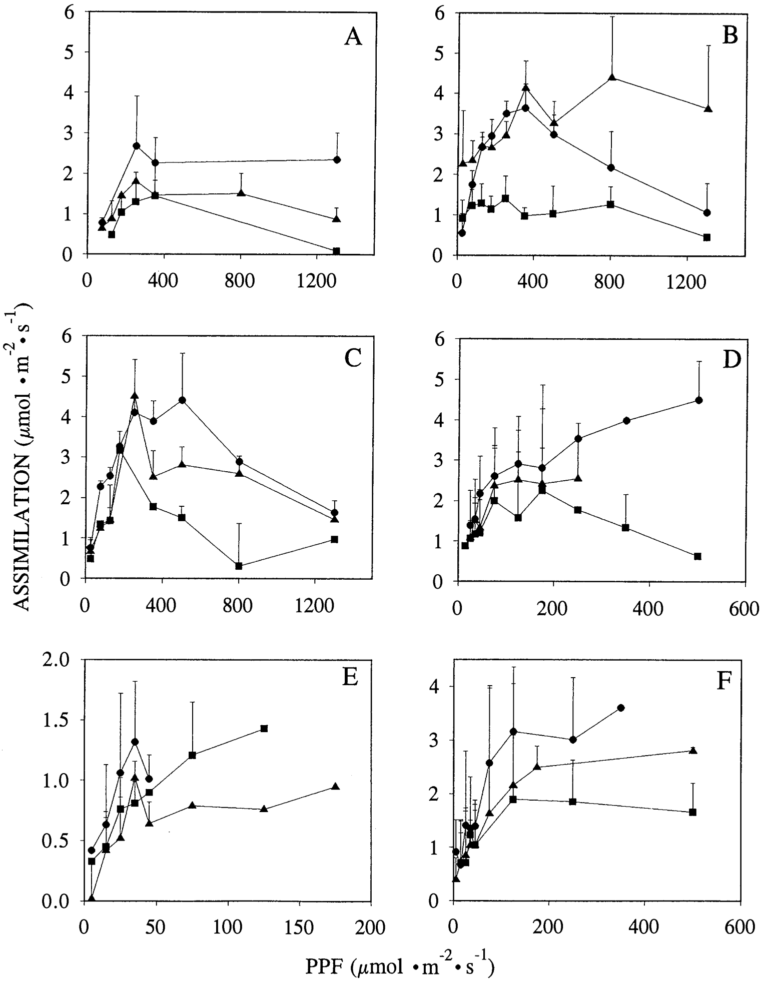

FIG. 4. Population light response curves for leaf assimilation. (A) Large-gap northwest, (B) large-gap southeast, (C) small-gap northwest, (D) small-gap southeast, (E) large-understory northwest, (F) large-understory southeast. Sample size ranges from 1 to 53 for individual data points. Symbols defined in Fig. 2. Data are means ± 1 SE. Note differences in scale on both the x and y axes.

derstory environment, where all species were suppressed considerably.

DISCUSSION

Shoot architecture results from the interaction between genotypically regulated ontogeny and environmental conditions. Architectural variation may be significant even within closely related congeners and may affect understory vs. gap responses (e.g., Sakai 1987). While species tend to exhibit distinctive architectures when undamaged, they also differ in architectural plasticity (different phenotypes when grown in different, unchanging environments) and acclimation ability (phenotypic alteration caused by exposure to changing environmental conditions). Presumably, species capable of architectural plasticity and/or acclimation should possess an advantage over less flexible species, and should thus be more successful across different microsites and/or under changing environmental conditions.

We observed marked differences in architectural responses to the gap–understory gradient among our three species. Striped maple exhibited the most distinct architectural adjustment, especially in small gaps and on the south sides of large-gaps. Our field observations indicate that suppressed seedlings up to 20+ yr old in the understory usually possess no branches and only one pair of relatively large leaves. But when released in our gaps, striped maple switched to much faster shoot elongation and also began to develop short shoots (Wilson and Fischer 1977). Both striped and sugar maple appeared to maintain coordinated control over lateral meristems, even after the death of terminal leaders, such that shoot architectures were not complex. In contrast, red maple often exhibited extensive lateral bud release and the development of large numbers of leaves, especially in large-gaps and particularly when leaders

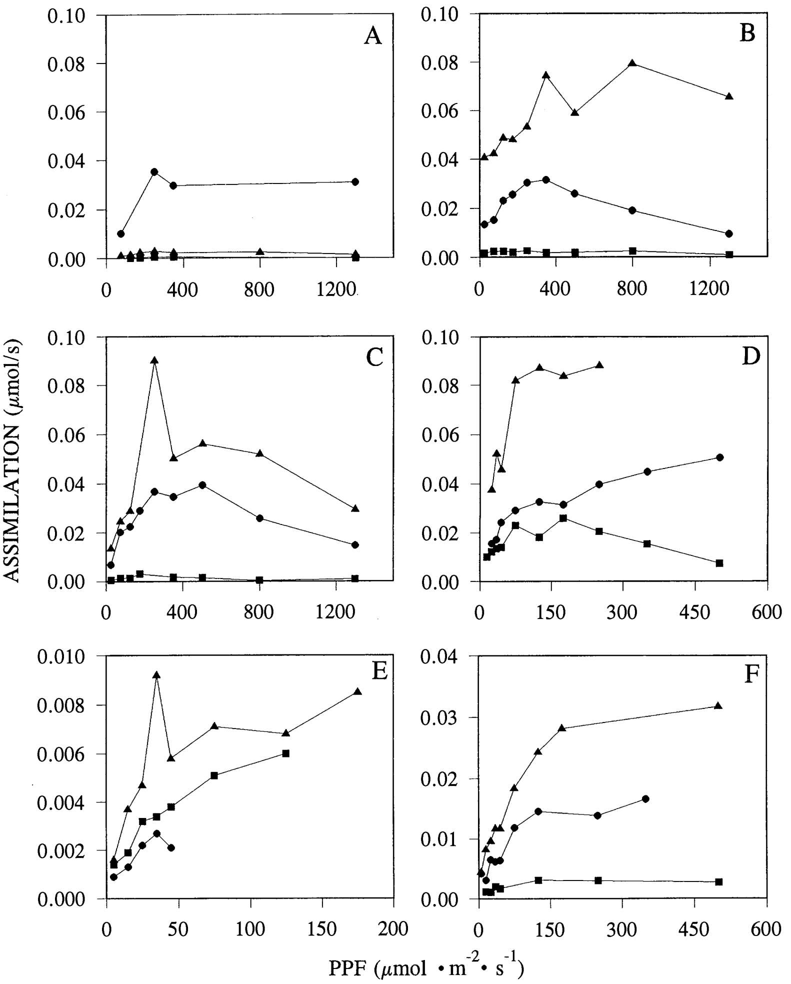

FIG. 5. Population light response curves for estimated shoot assimilation in 1989. (A) Large-gap northwest, (B) large-gap southeast, (C) small-gap northwest, (D) small-gap southeast, (E) large-understory northwest, (F) large-understory southeast. Symbols defined in Fig. 2. Sample size ranges from 1 to 39 for individual data points. Note differences in scale on both the x and y axes.

were lost. Because of the temporally asynchronous initiation of new leaf pairs on released lateral branches, leaf age and size varied widely across red maple shoots. The visual impression was that red maples were "out of control" architecturally. In spite of this, red maple appeared to recover best in terms of shoot growth from leader loss or full dieback (T. W. Sipe and F. A. Bazzaz, *unpublished manuscript b*). Our results for red maple are supported by Wallace and Dunn (1980), who concluded that red maple was well suited to growth in either understory or gap environments because of architectural (and some physiological) plasticity. In contrast, we did not observe the morphological adjustment and efficiency of sugar maple architecture in small gaps suggested by Steingraeber (1982) and reported by Canham (1988). This may be due to the relatively small size of our seedlings as compared to the larger saplings studied by these authors.

The general belief regarding shade tolerance among these species has been that red maple is the least tolerant and sugar maple the most tolerant. Concurrent with this is the long-standing principle that "shade-adapted" species should exhibit higher net assimilation at low PPF than "sun-adapted" species, largely due to differences in dark respiration rates (Boardman 1977, Bazzaz 1979). A substantial body of data has supported the idea that sugar maple is highly tolerant of the understory (e.g., Weber et al. 1985), but is less likely to perform as well photosynthetically at higher irradiances compared to other co-occurring tree species (e.g., Logan and Krotkov 1968). The conclusion from numerous field and glasshouse studies is that sugar maple is sensitive to tissue water loss, closing stomates quickly beyond relatively narrow ranges of optimal irradiance, temperature, vapor pressure, and possibly relative humidity. The negative impact of stomatal closure by sugar maple in environments such as forest gaps is lower assimilation and water use efficiency in comparison to competing species (Geis et al. 1971, Wuenscher and Kozlowski 1971, Davies and Kozlowski 1974, 1977, Kozlowski et al. 1974, Pereira and Kozlowski 1977, Hinckley et al. 1978, Ellsworth and Reich 1992).

Our results for sugar maple are consistent with these studies in that sugar maple showed a clear preference for the less exposed microsites across the gap–understory gradient. In both large- and small-gap north plots, it typically closed stomates sooner than the other species after direct beam irradiance began to strike plots in the morning and maintained the lowest conductances of the three species throughout clear days. It showed its highest peak assimilation rates in the understory and south sides of small gaps.

However, we also found that both striped and red maple exceeded sugar maple in leaf assimilation across much of the gap–understory gradient, including the understory microsites. Furthermore, red maple had consistently higher leaf assimilation rates than either of the other species, even in the understory. These results would not have been predicted based on shade tolerance designations and the classic sun–shade photosynthetic syndromes. Our results agree with Jurik et al. (1985), who found the same rank order (RUB > PEN > SAC) of unit area assimilation rates for saplings in the understory of northern Michigan hardwood forests. Therefore, sugar maple does not seem to be better suited photosynthetically than the other two species to understory irradiances, at least in terms of unit area assimilation rates.

Our data are relevant to Lei and Lechowicz's (1990) conclusion that sugar maple is not as well adapted to mesic understory conditions as either striped or mountain maple (*Acer spicatum,* understory tree). These authors argue that overstory and understory tree species face different degrees of evolutionary constraint related to specialization on vertical irradiance environments. Their interpretation is that sugar maples, as long-lived overstory dominants, must be capable of adjustment to the higher irradiances and temperatures of exposed crown conditions as mature adults and therefore retain several sun-adapted traits even as understory juveniles. In contrast, the understory maples (striped and mountain) can complete their life histories in the shade and should be less constrained in their ability to specialize on understory environments. While this may help explain sugar maple's low photosynthetic performance in the shade, our data suggest three problems with this interpretation for the other species. First, it implies that striped maple should exhibit a narrower physiological niche than sugar maple. We would not expect striped maple to be capable of rapid growth in intermediate-to-large canopy openings if it has specialized on the understory. But our work and other studies (e.g., Bicknell 1982) suggest that striped maple is very plastic across the understory–large gap gradient, apparently experiencing little loss in competitiveness in exposed sites. Red maple performed better than striped maple in our large-gap north plots in terms of leaf assimilation, shoot assimilation, and survival, but striped maple sustained better height growth even in this most exposed microsite (T. W. Sipe and F. A. Bazzaz, *unpublished manuscript b*). Second, striped maple was superior to sugar maple for both assimilation and growth in all but the darkest understory microsite, which runs counter to the interpretation by Lei and Lechowicz (1990). Finally, silvicultural and ecological experience (Burns and Honkala 1990) suggests that red maple, another overstory species, requires even more light for life history completion than any of the other three maple species encompassed by Lei and Lechowicz (1990) and our study, and thus should exhibit even less tolerance for understory conditions than sugar maple. However, we found that red maple also had higher leaf assimilation (as well as shoot assimilation in all but the most shaded microsite) and survived and grew better than sugar maple in the understory. It is clear that our knowledge of the physiological reasons for differential survival and growth is still incomplete for these species.

We have discussed in another paper the possibility that nutrients may be limiting sugar maple more than the other two maple species in our system (T. W. Sipe and F. A. Bazzaz, *unpublished manuscript b*), especially in small gaps where published literature suggests that it should be more competitive in terms of photosynthesis, architectural acclimation, and growth. Carbon assimilation is strongly affected by nutrient availability, particularly nitrogen, and species differ greatly in the degree to which nutrient limitations lower carbon assimilation (Field and Mooney 1986). However, sugar maple leaf assimilation rates in our study are comparable to values reported for both understory and small-canopy gap environments (Lei and Lechowicz 1990, Ellsworth and Reich 1992), and we found similar patterns of survival and growth by the three maples in a natural gap experiment on a more fertile soil series (T. W. Sipe and F. A. Bazzaz, *unpublished data*). So it does not appear that nutrients are a major limitation for sugar maple in our study.

The soils in both our experimental and natural gap study sites are well-drained sandy loams, and thus sugar maple's documented sensitivity to tissue water deficits also may have contributed to its poor performance as compared to red and striped maple. The roots of our experimental seedlings were generally located within the upper 20 cm of the soil at the time of transplanting. Soil water deficits could have been influential in the upper horizons, particularly under the more exposed conditions of our cleared gaps. Experiments involving interactions among irradiance, water, and nutrient gradients in the field are needed to clarify the degree to which soil resources alter assimilation patterns and ultimately growth differences among these species.

It is evident that ecological behaviors such as shade tolerance and response to canopy gaps cannot be predicted accurately on the basis of leaf-level assimilation since whole-shoot carbon balance depends on leaf numbers, ages, sizes, orientations, and water and nutrient status (Mooney and Chiariello 1984, Küppers 1985, Chazdon and Field 1987, Field 1988, Givnish 1988, Walters et al. 1993). The microenvironmental fluxes typical of a given microsite set the conditions for ecophysiological strategies that would maximize shoot assimilation. Because growth is usually more strongly correlated with total shoot assimilation than with unit area rates (e.g., Logan and Krotkov 1968 for sugar maple) and because growth generally enhances plant success, especially in competitive situations, architectural effects on shoot assimilation may play key roles in trade-offs among tree species across gap–understory gradients. Since the development of architecture occurs across the longer time scales of days to months and because current season growth is partly determined by primordial development patterns in the previous year for determinate and partially indeterminate woody species in temperate zones, differences in seasonal courses of microenvironmental conditions across the gap–understory gradient may significantly influence architectural responses (T. W. Sipe and F. A. Bazzaz, *unpublished manuscript a*).

The relative impact of differences in photosynthetic performance on survival and growth patterns is not easily determined, given the many other physiological processes and biotic interactions that influence the fates of juvenile trees (Field 1988, Ramos and Grace 1990). However, our population-level light response curves reinforced conclusions from diurnal sampling and captured species photosynthetic comparisons at biological levels (i.e., population) and temporal scales (across entire seasons) relevant to survival and growth. The differences in shoot assimilation suggest at least some photosynthetic partitioning of the gap–understory gradient by these species, with red maple superior in the most exposed microsite (large-gap north), no species dominant in the most shaded understory, and striped maple superior in all other microsites. The degree to which survival and growth paralleled photosynthetic differences is discussed in the final paper of this series (T. W. Sipe and F. A. Bazzaz, *unpublished manuscript b*).

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