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Gap Partitioning Among Maples (*Acer*) in the Forests
of Central New England

A thesis presented

by

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to

The Department of Organismic & Evolutionary Biology

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ABSTRACT

The gap partitioning hypothesis was proposed in 1977 as a mechanism for enhancing tree species diversity in closed-canopy forests through differential autecological responses by species to the heterogeneous microenvironments generated by canopy gap disturbance. Previous ecological, silvicultural, and physiological research suggested that partitioning may occur, but there have been no direct experimental tests of the hypothesis in the field.

The objective of this research was to test the gap partitioning hypothesis among three shade-tolerant species of maple (*Acer pensylvanicum*, *A. rubrum*, *A. saccharum*) in the mixed deciduous forests of central New England. Trees were felled to create six cleared, elliptical canopy gaps of two sizes ($75\text{m}^2 = 8 \times 12\text{m}$, $300\text{m}^2 = 16 \times 24\text{m}$) at the Harvard Forest in Petersham, Massachusetts. Naturally-established seedlings of the three study species (2160 total, 720 per species) were transplanted into five plot locations (center and NW, NE, SW and SE gap edges) within all six gaps and matching understory sites one year before gap creation. Measurements of microclimates (photosynthetic photon flux density, windspeed, vapor pressure, air and soil temperatures), photosynthetic performance, and non-competitive seedling survival, growth, and architecture were made over three growing seasons, including one season before (1987) and two seasons following (1988-89) gap creation.

Although the gap-understory microenvironmental gradient was complex and broad enough to elicit species differences, *Acer pensylvanicum*

consistently performed better than *Acer rubrum* and *Acer saccharum* (in that order) in nearly all sites and plot positions. Patterns of survival and growth were supported by shoot-level photosynthesis measurements. The results from the experimental gaps were supported by a companion experiment in unmanipulated natural gaps. Thus gap partitioning did not occur for these species in central Massachusetts. This result has several implications for predicting forest regeneration under natural or silvicultural disturbance regimes.

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CHAPTER 1

INTRODUCTION

1.1. COMMUNITY THEORY AND NICHE SPECIALIZATION

Ecologists have long sought to understand the forces that generate and maintain species diversity in natural ecosystems. Central in this search has been the concept of niche. Enormous empirical and theoretical efforts have been devoted to probing the ways in which community composition and structure are affected by species' niche differences. This is true in spite of the difficulty of defining 'niche' precisely and measuring it comprehensively (Hurlbert 1981). From the classic ideas of niche breadth, overlap, and competitive exclusion (Gause 1934) to trophic relationships (Paine 1966), evolutionary niche divergence and species packing (MacArthur and Levins 1967; Whittaker 1977), and multivariate analysis of n-dimensional hypervolumes (Hutchinson 1957; Dueser and Shugart 1979), niche relationships have dominated community ecology.

This emphasis has paralleled the pervasive view that positive and negative biotic interactions play a stronger role in regulating community structure than abiotic conditions. The earlier debate over the importance of environmental versus biotic regulation (Andrewartha and Birch 1954; Hairston et al. 1960) was played down during 1960-1975 as community theorists developed mathematical predictions about niche dimensions, competition and predation dynamics, and the assumed positive relationship between community diversity and stability. Much of this theory was developed by animal community ecologists, who did not agree with plant ecologists on the individualistic nature of species

distributions and abundances and the fortuitous nature of community composition on any given site (McIntosh 1985).

By the middle 1970's contradictory empirical evidence had accumulated for many of the major predictions of mathematical community ecology. Furthermore, theoretical analyses had revealed that the proposed relationship between diversity and stability was complex (May 1973), that models based on the equilibrium assumptions of Lotka-Volterra equations of population growth, predation, and competition were misleadingly simple, and that various forms of spatial and temporal heterogeneity as well as non-linear dynamics could induce unpredictable variations in population fluctuations and community structure (McIntosh 1985; Kareiva 1989).

Consequently the last decade has witnessed a serious reassessment of the degree to which community dynamics are biotically regulated in a consistently predictive manner. Several major edited volumes of papers by prominent ecologists have strongly emphasized that former ideas regarding biotic regulation are too narrow, and that the many forces that induce heterogeneity and spatial and temporal unpredictability are critical in most ecosystems (Saarinen 1980; Salt 1983; Strong et al. 1984; Diamond and Case 1986; Gee and Giller 1987; Roughgarden et al. 1989). Non-equilibrium dynamics are now considered to be more common than equilibrium dynamics (Connell 1979; Pickett 1980; Wiens 1984; Chesson and Case 1986).

The significance of this shift in perspective should not be underestimated. It represents the willingness to accept fundamental indeterminacy in community behavior and enforces the need to quantify not only the absolute role of any particular process, but the relative

roles among many interacting processes. The latter is, of course, much more difficult. These enlargements of theoretical scope and flexibility represent a necessary maturation of ecology as a discipline (Simberloff 1980).

Foremost in ecologists' thinking about these non-equilibrium forces has been the role of disturbance in causing localized mortality, spatially variable resource environments, and opportunities for colonization and growth to maturity (Whittaker and Levin 1977; Grime 1979; White 1979; Paine and Levin 1981; Sousa 1984; Pickett and White 1985). Terrestrial plant and marine intertidal ecologists have led the way in developing disturbance theory because of the importance of disturbance in communities dominated by sessile organisms. Stochastic disturbance events of varying frequency and magnitude disrupt species interactions and place a greater emphasis on dispersal, colonization, and the ability to adjust to environmental fluctuations. Since disturbance effects have come to be regarded as prominent at all scales in most ecosystems, the relationship between disturbance and community diversity has also been explored (Connell 1978; Fox 1979; Denslow 1980b; Hastings 1980; Abugov 1982; Miller 1982; Hubbell and Foster 1986; Petraitis et al. 1989).

1.2. DISTURBANCE AND PLANT SPECIES DIVERSITY IN CLOSED-CANOPY FORESTS

Ecologists' attempts to clarify the broad principles governing community diversity have been motivated in large part by the effort to understand why tropical rainforests are so diverse, or to be more precise, why rainforests are so much more diverse than all other ecosystems on earth. For most of this century, the belief was that

rainforests were the prime example of the positive feedback between stability and diversity. Lowland tropical climates were regarded as having been equable and stable on immense time scales (10^6 years), fostering evolutionary niche divergence and niche packing through both competitive and cooperative mechanisms (Ashton 1969; Richards 1969). Diversity, in turn, was thought to enhance stability even further. The occurrence and possible significance of natural disturbances were noted by several authors working in both tropical (Aubreville 1938; Richards 1964; Schulz 1960) and temperate (Jones 1945; Bray 1956; Loucks 1970) forests, but disturbance was clearly regarded as secondary to niche relationships in regulating community diversity and structure.

Then an opposing viewpoint arose in the late 1970's, along with the reassessment of biotic regulation discussed in Section 1.1. Many ecologists began to emphasize patterns of disturbance and functional responses of tree species as unifying links between the temperate and tropical broadleaved forests of the world, despite striking differences in climate, physiography, plant species diversity and floristic affiliations (Whitmore 1978, 1982; Brokaw 1985; Runkle 1985). This view paralleled the increasing emphasis on disturbance regimes in all communities (Levin and Paine 1974; Connell 1979; White 1979; Oliver 1980; Bazzaz 1983; Sousa 1984; Pickett and White 1985). Disturbance was seen to generate spatially and temporally unpredictable mortality and patchiness in communities in ways that could prevent competitive exclusion from occurring and thus reduce the pressure for niche divergence among plant species. This would allow coexistence in the absence of significant niche differences due to the chanciness of seed dispersal, establishment, and highly variable competitive neighborhoods.

The idea that intermediate disturbance regimes yield highest diversities (Connell 1979; Fox 1979) and that disturbance-mediated coexistence may be common (Denslow 1985; Petraitis et al. 1989) were supported by numerous conceptual and theoretical treatments of the effects of environmental grain and variability (MacArthur 1975; Levins 1979; Wiens 1976,1977), patch dynamics (Levin and Paine 1974; Schaffer and Leigh 1976; Caswell 1978; Pickett and Thompson 1978; Armstrong 1988), stochasticity (Chesson 1985), and the differential abilities of species to move among patches (Levin 1974,1976,1981). Many of these ideas were not new, but were assembled into a more persuasive argument for the role of natural disruptions and heterogeneity in structuring communities (Strong 1983; Diamond and Case 1986).

It became clear that Gaussian ideas of niche overlap, which had dominated ecological theory for so long, were far too constraining, at least for terrestrial plant communities. Plant ecologists reversed the classic question of how different species' niches had to be for indefinite coexistence and asked how similar species could be and still co-occur due to disturbance-generated heterogeneity in space and time (Shmida and Ellner 1984; Bazzaz 1987). Ecologists who had had deep reservations about explaining rainforest diversity on the basis of the "one species, one niche" axiom now saw a more reasonable, comprehensive mechanism for the maintenance of diversity in these systems. Rather than shoehorn each species into its own supposed niche, ecologists considered it likely that many species were autecologically very similar, and that competitive differences within such guilds were insignificant (Hubbell and Foster 1986).

Tilman (1982,1988) has presented the most detailed recent argument

for niche separation among plant species, based on fine differences in the requirements for different resources. His theoretical analysis and empirical tests are noteworthy, but they are based on several questionable underlying assumptions, among them (1) resource supplies do not fluctuate, (2) resources are perfectly substitutable for each other, and (3) plants make complete use of all resources available. Furthermore, the models are designed for herbaceous annuals and perennials, and the degree to which large woody perennials would follow the predictions, given the substantial differences in structure and function between trees and herbs (Schulze 1982,1983), is unknown.

Ashton (1969,1988) has argued that tree species' niches are narrow and distinguishable in the aseasonal dipterocarp rainforests of Malaysia and that edaphic factors play a significant role. Ashton (1988) cited Tilman's (1982) theory as potential support for observed correlations between community diversity and soil nutrient levels and, in many cases, the restricted physiographic distributions of dipterocarp species. However, his conception of regeneration dynamics allows for the existence of autecologically very similar species whose success in gap-phase regeneration is determined partially by chance. Furthermore, he has suggested that there has been an overemphasis on the species level in the search for niche specificity in rainforests, that competitive selection acts at taxonomic levels other than species, and in particular that competition occurs at the family level in Malaysian rainforests (Ashton 1988).

The question of how diversity is generated, as opposed to maintained, was not resolved by the new emphasis on disturbance. But whatever the mechanisms of speciation, it seemed clear that disturbance,

along with the equable tropical climate, could significantly reduce the effectiveness of competitive exclusion and allow the accumulation of plant taxa in increasingly diverse systems (Hubbell 1979).

1.3. THE GAP PARTITIONING HYPOTHESIS

The intense interest in species niche differences versus disturbance led to a clearer consideration of forest disturbance regimes and how plant species respond in disturbed and recovering environments (e.g., Bazzaz 1984b). In effect, the debate sharpened the focus on niche relationships and the conditions under which distinct niche differences could contribute to community diversity.

Physiological specialization by seedlings along the complex microenvironmental gradient from the understory to the centers of large gaps offers one possible means of differentiation. Ricklefs (1977) hypothesized that this gradient was especially broad in tropical rainforests and that the existence of specialization could result in tradeoffs of dominance among such specialists across gap sizes or positions within large gaps, thereby maintaining a greater community diversity. Bazzaz and Pickett (1980) discussed the physiological ecology of tropical forest dynamics and focused on the important differences among large-gap and small-gap specialists. Denslow (1980a) enlarged on this theme in a taxonomic survey of apparent gap size preferences for tree species in rainforests around the world. Since her 1980 paper, this idea has become widely known as the gap partitioning hypothesis.

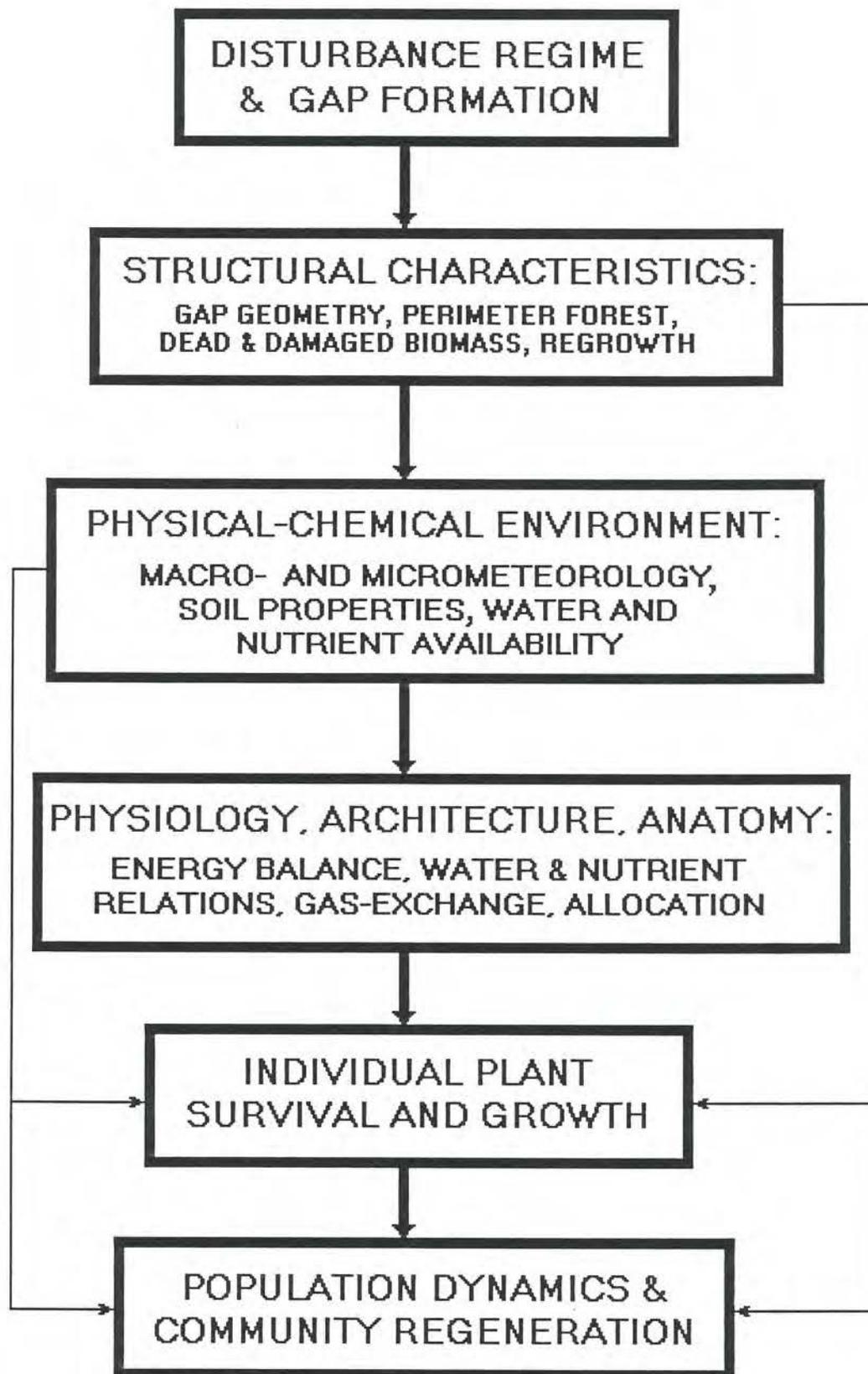
Gap partitioning is truly a hybrid hypothesis, combining elements of both the niche difference and disturbance viewpoints. The hypothesis acknowledges the importance of disturbance-generated uncertainty in

colonization opportunities, resource availability, and competitive neighborhoods, but clearly posits that species' niches differ autecologically in ways that produce shifting advantages along the gap-understory microenvironmental gradient, advantages that, on average, regularly override the stochasticity to yield predictable patterns of species success. The focus is on the performance of younger, smaller individuals during the recovery phase, and thus on regeneration niches (Grubb 1977).

The gap partitioning hypothesis also links state and process approaches to forest disturbance and response (Figure 1-1). The vast majority of existing research on forest gap dynamics has focused on structural variables of the disturbance regime, and on species and community correlative responses to variables such as gap size (Brokaw 1985b; Runkle 1985). This is represented by the smaller arrows on the right side of Figure 1-1 (also discussed in Section 1.4.). However, plants do not respond directly to structural variables, but to the physical and chemical flux mosaic generated by structural variation. Thus it is necessary to quantify how patterns of resources and physical modifiers of resource availability differ from the understory to gaps of different size and positions within gaps. Then ecophysiological processes can be connected to both the resource environment and subsequent survival and growth by individual plants. If enough data are available on the age/size structures of populations, spatial distributions, and population variability in autecological behavior, then individual behavior can be scaled to population and community patterns.

While several ecologists have noted the need to quantify

Figure 1-1. Conceptual linkages for understanding plant species responses to forest gap disturbance.



microenvironments in forest gap research (e.g., Denslow 1980a; Pickett 1983), the general importance of this linkage between state and process has been emphasized by only a few (Vitousek and White 1981; Bazzaz 1984b; Johnson 1985; O'Neill et al. 1986; Bazzaz and Sipe 1987). As suggested above, the gap partitioning hypothesis is one of the few concepts in plant community ecology that requires this linkage so explicitly.

There are good reasons for expecting specialization and adaptive tradeoffs in moist forests, in spite of the spatial-temporal unpredictability in resource environments generated by disturbance. First, the effects of closed canopies on the complex microenvironmental gradient from the disturbed areas of large natural gaps to the intact forest understory are pervasive. A multi-layered canopy structure alters the ranges and spatial-temporal patterns in air and soil temperatures; windspeed; ambient [CO₂]; irradiance; spectral distribution; soil moisture; nutrients; and relative humidity. Canopy gap disturbances disrupt this regulation and create complex three-dimensional patterns of microclimates and resource availability (Figure 1-1).

The breadth and steepness of gap-understory microenvironmental gradients are functions of disturbance frequency, size, and magnitude. Gap size, shape, orientation, and the remnant community interact to produce enormous heterogeneity in patterns of physical and chemical fluxes (Bazzaz and Pickett 1980; Denslow 1980a; Bazzaz 1983, 1984b; Pickett 1983; Brokaw 1985b; Bazzaz and Sipe 1987). Disturbance frequency affects the gradient breadth since the pre-gap community structure forms one end of the gradient and the development of the community from gap to building and mature phases is a function of the amount of time since the

last disturbance (Whitmore 1978,1982). Disturbance size (areal extent) is crucial since the gradient broadens as gap size increases (Jackson 1959; Minckler and Woerheide 1965; Tryon and Trimble 1969; Ricklefs 1977; Bormann and Likens 1979; White 1979; Bazzaz and Pickett 1980; Oliver 1980; Smith 1981; Bazzaz 1983,1984; Runkle 1985). However, the relative strength of the disturbance agent (intensity) and the extent to which the multi-layered pre-gap community is destroyed (severity), including the seed bank, must also be considered because of their effects on the nature of the remnant community and initial microenvironmental patterns.

Gap and understory environments pose problems of resource acquisition and use by plants for which different combinations of physiological, morphological, and architectural traits are required as solutions (Figure 1-1). Physiologists have demonstrated the distinction at the leaf level between an emphasis on light-harvesting and reduced enzymatic systems in the shade versus electron transport and carbon reduction capability in the sun (Boardman 1977; Bjorkman 1981). Ecologists have expanded this generalization to include all resources and plant responses, using terms such as "exploitive versus conservative" (Bormann and Likens 1979), "opportunist versus equilibrist" (Colinvaux 1973), and "small-gap versus large-gap specialist" (Bazzaz and Pickett 1980; Denslow 1980a) species. These tendencies are often presented as a clear dichotomy, but it is more realistic to regard species as overlapping broadly along a complex continuum (Loach 1967; Canham and Marks 1985).

No temperate tree species has the ability to grow steadily in dense shade (1-5% of full sun in moist forests) and force its way into the

overstory (Runkle 1985). The carbon balance is not favorable; water and nutrients may also be limiting. Thus all overstory species require a canopy opening to attain reproductive maturity, regardless of any preferences along the gap-understory gradient. Species very tolerant of shade, such as sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and eastern hemlock (*Tsuga canadensis*) may need two or more gaps to reach the overstory (Spurr and Barnes 1973; Canham and Marks 1985; Canham 1988b). Conversely, though gaps provide more light, water, and nutrients for growth, the potential for shoot thermal and water stresses is much greater, due to increased irradiance.

Most tree species can survive across the majority of this gradient, if growing alone. But the gradient is apparently too broad for species to grow rapidly under all conditions (Canham and Marks 1985). This may be largely due to the extensive differences in photosynthetic behavior that are required for survival and growth at the gradient extremes (Bjorkman 1981, Field 1988). Thus there are apparently no generalist tree species in temperate and tropical forests that can outcompete all potential specialists at their preferred locations along the understory-gap gradient. In the absence of such superior generalists, specialists and weaker generalists can both succeed. But since significant competition occurs in moist forests, a distinct advantage should result for any species with traits that allow it to establish sooner and/or grow faster than competitors under at least some of the microenvironments produced by the current forest structure and disturbance regime. Given enough time and a non-catastrophic disturbance regime over a large region, we might expect specialization to be favored over generalization, at least toward the distinction of several

physiological guilds (sensu Hubbell and Foster 1986).

The present co-occurrence of specialists (or specialist guilds) may be brought about by this scenario of coevolved niche divergence (Ashton 1969). An alternative is that co-occurrence may reflect the current juxtaposition of taxa with largely independent evolutionary and migrational histories, particularly in glaciated temperate and boreal regions (Davis 1986; Foster et al. 1990). In either case, to the extent that tree species respond differently to portions of the understory-gap gradient for establishment and early growth, the disturbance regime regulates opportunities for regeneration to maturity (Whitmore 1982). A more precise knowledge of the patterns and mechanisms of species responses would yield more accurate predictions of forest composition and structure under different disturbance regimes, and provide a direct test of the gap partitioning hypothesis. This requires the quantification of all the main connections in Figure 1-1.

1.4. PREVIOUS RESEARCH

We can now consider whether or not existing data are adequate for testing the gap partitioning hypothesis. Table 1-1 lists the major sources of information. There are many excellent studies that fulfill one or more of these criteria, and much circumstantial evidence that gap partitioning occurs. However, there is no published experimental test of the gap partitioning hypothesis for tree species.

Thompson et al. (1988) planted seeds of four tree species of varying shade tolerance in three gap sizes produced by selective logging in North Queensland, Australia. The rainforest in this region is remarkable in the dominance by shade-tolerant advance-regenerating

Table 1-1. Sources of existing data relevant to the gap partitioning hypothesis, with the most important limitations.

CONTROLLED ENVIRONMENT PHYSIOLOGY & GROWTH (Garden, Glasshouse, Chamber)

1. Continuous full sun and partial shade light treatments, without diurnal shifts in diffuse and direct beam radiation typical of forest gaps
2. Mostly single-factor gradients with few states (2-4)
3. Physiological and architectural traits not connected to growth and survival
4. Often have not used co-occurring species
5. Few long-term environmental switches from understory to gap conditions (simulating release) or vice versa (simulating gap closure and competition)

FIELD PHYSIOLOGY & GROWTH

1. Naturally-established plants, with little control over location or growth history
2. Very low numbers of individuals, too small for concurrent growth and demography
3. Not related to adequate spatial and temporal microenvironmental sampling
4. Limited range of forest environments, especially as related to disturbance

MICROENVIRONMENTAL SAMPLING STUDIES

1. Often restricted to one factor (usually light or moisture)
2. Few measurements over site replicates
3. Too few sensors to capture spatial and temporal heterogeneity simultaneously
4. Detailed measurements often not repeated across seasons
5. Not connected to growth and physiology simultaneously
6. Gap microenvironments usually measured in larger silvicultural openings

ECOLOGICAL SURVEYS OF COMMUNITY RESPONSE TO GAP DISTURBANCE

1. Not controlled for seed input or advance-regenerant community
2. End-state measurements (density, height, etc.) without mechanistic understanding
3. Microenvironmental data lacking
4. Focus usually on larger seedlings ($\geq 1\text{m}$ tall) or saplings

FORESTRY EXPERIMENTS (Particularly Harvest & Regeneration)

1. Not controlled for seed input or remnant vegetation (esp. stump sprouts) in gaps
 2. End-state measurements (Density, height, etc.) without mechanistic understanding
 3. Microenvironmental data lacking
 4. Focus usually on larger seedlings ($\geq 1\text{m}$ tall) or saplings
 5. Canopy openings usually larger than about 90% of natural gaps
-

species, in that only 20 of 700 total species colonize and grow rapidly in large openings. In fact, the primary goals of the study were to determine (1) the degree to which the intolerant species required "wide gaps" (~40% full sun on an annual basis) for colonization, and (2) the abilities of the tolerant species to acclimate to "wide gap" environments. Since the study was begun in 1979, it was not designed as an explicit test of the gap partitioning hypothesis. The results did show clear minimum gap size requirements among the species.

The large number of silvicultural studies that have focused on the effects of the size and shape of harvest cuts on regeneration have not involved experimental planting of tree seedlings (and thus the control of seedling size, age, location, and abundance), and have not included comprehensive sampling of understory and gap microenvironments. Furthermore, harvest cuts typically exceed the sizes of the majority of natural gaps (i.e. $>300\text{m}^2$), produce variable structural heterogeneity in the downed biomass that is left in place, and usually do not control for the rapid resprouting of cut stems. These points apply to the gap study published recently by Phillips and Shure (1990), in which four gap sizes (160, 800, 4000, and 20000m^2) were created by felling overstory trees and cutting all stems $\Rightarrow 5\text{cm}$ in diameter at breast height. The large boles were removed, but all remaining slash was left behind, such that microenvironments at the seedling level do not reflect opening size alone.

The only study designed to test the hypothesis explicitly was done with understory shrubs in Costa Rica (Denslow et al. 1990). Seven species of *Miconia* and *Piper* that included both shade-tolerant and intolerant representatives were planted as rooted cuttings at three

different plot locations (gap center, gap edge, understory) in and around four natural gaps (275-335m²). Measurements of PPFD and nutrients showed significant differences in light availability but not nutrients among plot locations. The shade tolerance classes within each genus did not exhibit predicted responses to irradiance levels, and differences in photosynthetic capacity (measured in the field) were not correlated with growth rates. The authors concluded that these shrub species did not cleanly partition the understory and gaps, possibly due to the shortened breadth of the light gradient.

It is evident from the forestry and ecology literatures that no experimental study has been done in which (1) the size, shape, and orientation of canopy gaps were controlled within size ranges applicable to most natural gaps, and (2) the downed biomass and regrowing community were eliminated, such that the primary effect of gap size on microenvironments and species responses could be determined. The removal of the remnant and regenerating community is not mimicked by natural disturbance agents in temperate broadleaved forests, with the exception of fire. To do so experimentally is thus to distance the results in part from natural gap processes. However, such a controlled experiment would yield clear information on the potential for gap partitioning in response to gap size and positions within gaps. Given the practical difficulties of replication in large-scale experimental gap creation, plus the tremendous seedling-scale heterogeneity induced by allowing the remnant biomass and regrowing community to interfere with microenvironments and target species responses, the tradeoff in information gained versus the semi-artificial nature of the experimental gaps is justified. This is particularly important for the attempt to

connect microenvironments to ecophysiology and growth.

Tree physiology and silvicultural experiments have demonstrated that co-occurring tree species do differ in physiological and demographical responses to the extreme conditions of deep shade or full sun. However, previous data are not adequate in several ways for determining the occurrence and significance of physiological specialization by trees in response to the full range of disturbed and undisturbed forest microenvironments (Table 1-1). First, most work has emphasized the gradient extremes (e.g., constant high or low light), which do not occur often under natural disturbance regimes. Second, most of the available physiological data are based on constant growth environments and steady-state measurements, since fluctuating environments and plant responses are more difficult to simulate or quantify (Pearcy 1988). Third, the vast majority of tree growth and demographical data in gaps in both temperate and tropical regions comes from silvicultural or agricultural gap formation, where (as mentioned above) gap geometry, elimination of remnant vegetation, and substrate disruption are markedly different from natural gap processes. Fourth, there is a major lack of data on the species-specific relationships between leaf-level and whole-plant physiological performance (Field 1988; Givnish 1988; Osmond and Chow 1988). Fifth, there are essentially no data on architectural variation within natural seedling populations or differential seedling leaf demography and shoot phenology between species. Finally, field measurements of physiological performance have not been simultaneously coupled to growth and demographic responses (Bazzaz 1984a).

We cannot determine the degree or significance of physiological

specialization and accurately predict forest response to disturbance until several of the inadequacies in Table 1-1 are addressed. This is especially important for canopy gaps smaller than 300m^2 in area, which can represent 80-90% of all gaps in both temperate (Barden 1979, 1980, 1981, 1983; Runkle 1981, 1982, 1984, 1985) and tropical (Hartshorn 1978; Brokaw 1985b; Brokaw 1987; Hubbell and Foster 1986; Sanford et al. 1986; Uhl et al. 1988) mature broadleaved forests. Clearly no single study can meet all these criteria, but the research presented below fulfills several important requirements.

While there is now little doubt about the existence of physiological specialization by species on the extremes of forest environments, much less is known about specialization within species groups that characterize the extremes. In moist forests with disturbance regimes dominated by small gaps, only the infrequent larger gaps ($>500\text{m}^2$) provide enough photosynthetically active radiation for large-gap specialists ("pioneers") (Bormann and Likens 1979; Whitmore 1983; Runkle 1985; Canham and Marks 1985). Thus understory (shade) tolerance is an important physiological strategy that seems to involve conservative resource use while seedlings are suppressed and the competitive advantage of advance establishment when seedlings are released in gaps. The disadvantages are a slower maximum growth rate (relative to pioneers) and the problem of adjusting to gap environments when released. The importance of advance regeneration has been known to silviculturists for most of this century, and ecologists have recently begun to emphasize the role that all pre-gap sub-canopy processes play in gap dynamics (Thompson et al. 1988; Uhl et al. 1988; Brokaw and Scheiner 1989; Canham 1989; Connell 1989)

Although the mechanisms of shade tolerance are partially understood, especially the anatomy and steady-state photosynthetic performance of leaves, much less is known about (1) responses to spatially and temporally variable field environments, and (2) physiological and architectural responses to gap release (Canham 1989; Poulson and Platt 1989). How different are species classified as shade-tolerant? Do the differences support the hypothesis that physiological specialization within a group of superficially similar species can contribute to species coexistence and higher community diversity? These questions, and thus the gap partitioning hypothesis, are best addressed by studying closely related co-occurring species which represent variations on the shade-tolerant theme.

1.5. OBJECTIVES

The objective of this research was to test the gap partitioning hypothesis among three shade-tolerant species of maple (*Acer*) in the mixed broadleaved forests of central New England. The following questions were posed:

- (1) How do microclimates vary diurnally and seasonally within and between the understory and small canopy gaps of two sizes (75m^2 and 300m^2) in mature broadleaved forests?
- (2) Do the species exhibit differential survival, growth and/or architecture within and between the understory and small gaps?
- (3) How do the species differ in diurnal gas-exchange and leaf- and shoot-level net photosynthesis within and between the understory and small gaps?
- (4) What are the relationships among (1) microclimates, (2) survival,

growth, and architecture, and (3) photosynthesis?

- (5) Is there specialization across the understory-gap microenvironmental gradient - i.e., does gap partitioning occur?
- (6) What are the implications of the presence or absence of specialization, for (a) community diversity and (b) the prediction of forest composition, in temperate forests with disturbance regimes dominated by small canopy gaps?

These questions were addressed by felling trees to create controlled canopy gaps of two sizes (75m^2 , 300m^2) at the Harvard Forest in central Massachusetts. Naturally-established seedlings of the three maple species were transplanted into five plot locations within all gap and matching understory sites one year before gap creation. Measurements of microclimates, photosynthetic performance, and seedling survival, growth and architecture were made over three growing seasons, including one season before (1987) and two seasons following (1988-89) gap creation. The key features of this experiment are listed in Table 1-2. Sections 2.4 through 2.6 discuss these features and provide more detail on the methods employed.

Rejecting the null hypothesis that gap partitioning does not occur ideally involves more than just demonstrating differential survival and growth among gap sizes and positions within gaps. The hypothesis requires that the differences in growth be clearly correlated with predictable patterns in the gap-understory microenvironmental gradient. Such a gradient will be a complex interaction between above- and belowground physical and chemical fluxes, including consumable resources and physical modifiers of resource availability (Bazzaz and Sipe 1987). Consequently a full description of the gradient is very difficult.

Table 1-2. Key features of the experimental gap research at the Harvard Forest.

-
1. Control of Gap Geometry (Size, Shape, Orientation) and Timing
 2. Replication (n=3) of All Gap and Understory Sites
 3. Within-Site Spatial Resolution - 5 Plot Positions Each
 4. Multiple Temporal Scales (Diurnal, Seasonal, Annual) for Comparisons of Microclimates and Species Responses
 5. Simultaneous High-Resolution Sampling of Microclimates Within and Between Understory and Gaps of Different Size
 6. Comparative Species Performance Throughout the Study (2160 Transplants, 720 per Species, 3 Species)
 7. Allowance for Transplant Acclimation: One Year Before Gap Creation, 1.5 Years Before Gap Exposure
 8. Non-Competitive Performance in Response to Gap Geometry and Within-Site Position: Gap Regrowth Suppressed and Seedling Plots Isolated From External Root Competition
 9. Multiple Measurements on the Same Study Plots & Plants: Microclimates, Gas-Exchange, Architecture, Growth, Survival, Phenology, Leaf Herbivore/Pathogen Damage
-

This project focused on the physical microclimate (photosynthetically active radiation, air and soil temperature, vapor pressure, windspeed) rather than soil resources (water, nutrients) for two reasons: (1) physical variables are more easily measured with the accuracy and spatial/temporal resolution and comprehensiveness required for describing the gradient; and (2) microclimatic variation is expected to be more responsible for differences in photosynthetic performance (discussed below) than soil resource variation over the controlled physiographic site positions in the study area. This is particularly true because of the cleared gaps and homogenized non-competitive plot conditions utilized in this project (Sections 2.5. and 2.6.). Variations in nutrient availability caused by the crown, bole, and tip-up treefall zones (Bazzaz 1983; Vitousek and Denslow 1986) were eliminated by cutting the trees at the base and removing the downed trees completely. This treatment does limit the extrapolation to natural treefall gaps, however.

The gap partitioning hypothesis also proposes that ecophysiological differences among species are responsible for different survival and growth along the gap-understory gradient. While biotic interactions (dispersal, herbivory, pathogens, mycorrhizae) probably vary as well along the gradient and are no doubt involved in most patterns of survival and growth, the hypothesis focuses on autecological responses to the gradient. Thus a successful test of the hypothesis requires that at least some ecophysiological behaviors be directly correlated with survival and growth.

Of the processes involved in whole-plant response to microenvironmental variation, photosynthetic carbon acquisition and

allocation are paramount, since they are necessary for all other activities (Mooney 1972; Schulze et al. 1983). Water and nutrient economies are intimately related to photosynthesis, and should be included in the ideal comprehensive study. But such comprehensiveness is difficult to achieve in an experiment as complex and physically large as the one described here. Therefore, the research focused on the sampling of leaf-level photosynthesis in the field and the manner in which architectural differences among species affected estimated shoot photosynthesis.

Carbon acquisition and allocation are clearly linked through feedbacks. Acquisition occurs at both leaf and shoot levels. Differences in species' architectures may lead to quite different shoot-level carbon assimilation as compared to unit leaf area rates (e.g. Logan and Krotkov 1968). Even if species exhibit comparable total shoot carbon gain, they may differ in allocation in ecologically significant ways. The differences among species cannot be understood by studying leaf acquisition, shoot acquisition, or whole-plant allocation in isolation (Schulze et al. 1982; Mooney and Chiariello 1984; Küppers 1985; Givnish 1988).

Leaf carbon acquisition varies with the ability to absorb photosynthetically active radiation, reduce CO_2 , and regulate water and thermal balance. Shoot acquisition results from two integrated kinds of allocation: (1) component allocation, the amount of biomass (and the resources necessary to produce that biomass) to alternative organs and their functions; and (2) architectural allocation, the arrangement of component mass in space. Diurnal variation in total plant carbon assimilation is a function of leaf behavior, since, with the exception

of leaf orientation due to turgor loss, pulvinal hinging, and/or sun tracking, shoot architecture does not change substantially over one day. However, seasonal variation in shoot assimilation does depend on the timing of allocation to plant components, and the interactions between architecture and microenvironment.

Species differ greatly in the developmental regulation of component and architectural allocation, particularly across different environments. The three study species used here are generally determinate in leaf primordial development and seasonal phenology, but there are indications in the literature that they may differ in architectural response to gap release (Wilson and Fischer 1977; Wallace and Dunn 1980; Canham 1988b).

In summary, this research tests the gap partitioning hypothesis by creating experimental gaps of controlled size, shape, and orientation in which the three-way interactions among physical microclimates, photosynthetic behavior, and survival and growth of transplanted seedlings are quantified within and between the understory and gaps of two sizes. The null hypothesis of no gap partitioning will be rejected if differences in species survival or growth are correlated with microclimatic patterns, and especially if photosynthetic variation in response to the microclimates supports the survival and growth results.

Although it is unlikely, it is possible that differential survival and growth will be detected in patterns that suggest species tradeoffs, but without any clear relationship to the measured microclimatic variables or photosynthetic patterns. In this case, the null hypothesis will still be rejected, and it will be concluded that gap partitioning occurs, but that other microenvironmental variables, ecophysiological

processes, and possibly other biotic interactions are responsible. Conversely, microclimates may vary consistently, and species may differ clearly in photosynthetic behavior, but no tradeoff in survival or growth emerges. Then the null hypothesis will be accepted and the discussion will focus on why species do not partition the gap-understory gradient.

CHAPTER 2

STUDY SYSTEM AND METHODS

2.1. FOREST COMMUNITIES AND DISTURBANCE IN NEW ENGLAND

Continental, regional and local variables generate a complex pattern of potential forest communities in New England. These variables include: (1) a temperate to boreal latitudinal range; (2) a SE to NW oceanic-continental gradient in regional weather patterns; (3) N-S trending mountain ranges and thus elevational gradients; (4) a glacial history that left heterogenous substrates and was followed by differential northward species migration; and (5) a natural disturbance regime that includes hurricanes, other windstorms and icestorms, fire, and insect and pathogen epidemics. The presettlement forests were diverse in composition and structure. Human disturbance has altered the landscape and left very few old growth forest remnants that could be used as standards to decipher the controls on community organization (Bromley 1935; Raup and Carlson 1941; Cline and Spurr 1942; Raup 1966).

Nonetheless it is useful to recognize species dominance of current community types (Figure 2-1). The three maple species used in this study play significant roles in three of the six forest types shown in Figure 2-1. These roles are summarized in Table 2-1.

Disturbance in New England forests has received significant study since about 1910. The best results have been obtained by intensive reconstruction on sites where forest histories are known (e.g., the Harvard Forest) and/or extensive experimentation where forest disturbance and development are controlled (e.g., Hubbard Brook, Bormann and Likens 1979). Specific points that have direct bearing on the

Figure 2-1. The forest types of New England, with the location of the Harvard Forest (modified from Smith 1979, based on Westveld 1957).

-  Spruce-Fir-Northern Hardwoods (#1 a,1b)
-  Northern Hardwoods-Hemlock-White Pine (#2)
-  Transition Hardwoods-White Pine-Hemlock (#3)
-  Central Hardwoods-Hemlock-White Pine (#4)
-  Central Hardwoods-Hemlock (#5)
-  Pitch Pine-Oak (#6)

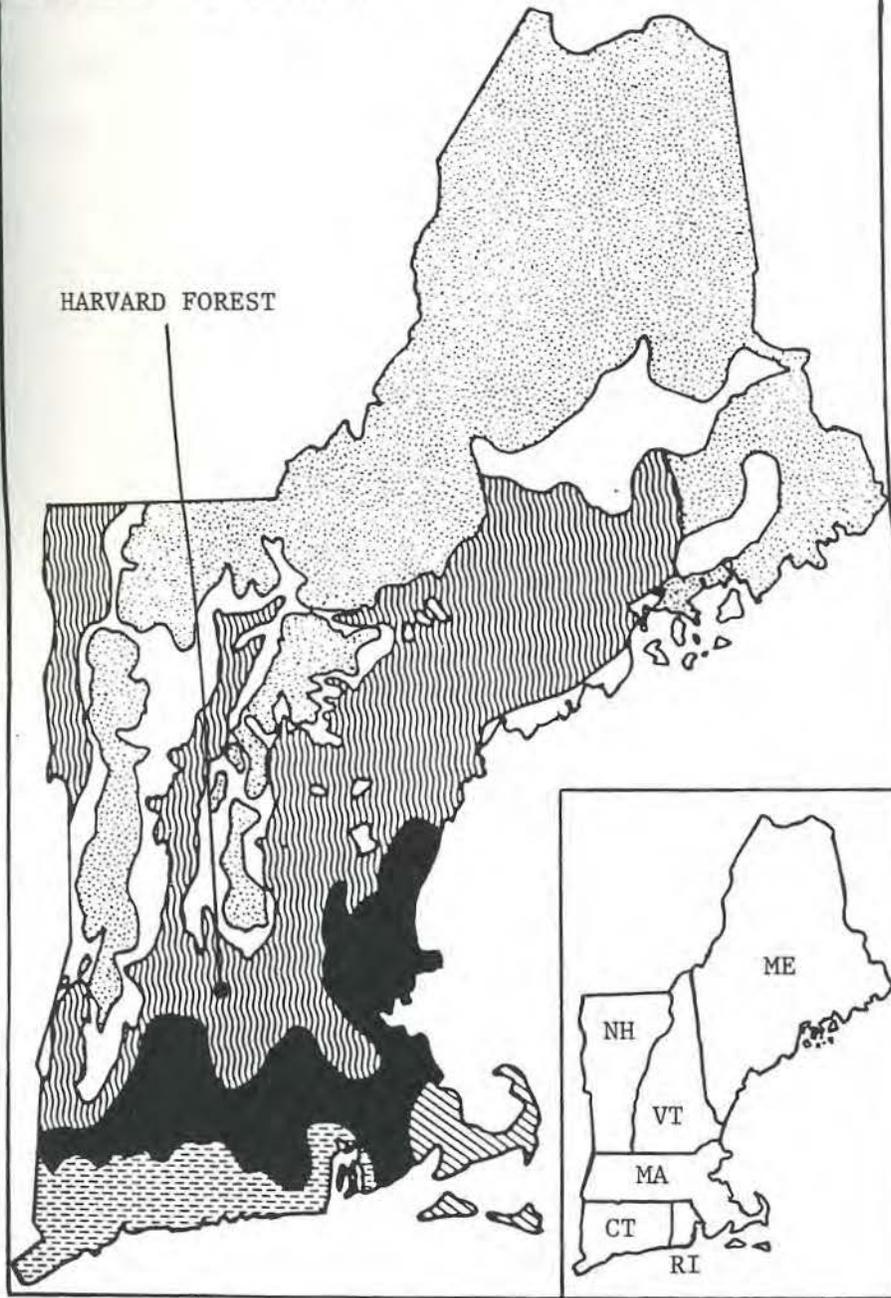


Table 2-1. Community roles of the three study species in the three forest types of New England in which the species are relatively abundant. These roles are based on the ecological and forestry literatures, as well as personal experience.

WESTVELD et.al. (1957) FOREST TYPE	MAJOR ROLE *	MINOR ROLE
Spruce-Fir-Northern Hardwoods, Tolerant Subdivision	A. saccharum (C) A. pensylvanicum (U,S)	A. rubrum (C)
Northern Hardwoods- Hemlock-White Pine	A. saccharum (C) A. rubrum (C) A. pensylvanicum (U,S)	
Transition Hardwoods- White Pine-Hemlock	A. rubrum (C,S)	A. saccharum (C) A. pensylvanicum (U,S)

* Abbreviations: C = Significant mostly as a canopy dominant,
especially in older forests
U = Significant mostly as an understory dominant, reaching
canopy co-dominance only rarely
S = Significant mostly as a successional dominant

research are summarized here.

The relative roles played by disturbance agents varies in a complex way throughout New England. Hurricanes are significant forces in southern New England, and decline in frequency and severity with increasing latitude. Tornadic windstorms, convective thunderstorms, and icestorms occur throughout, with few generalizable patterns. Insect and pathogen epidemics occur in all types, though the frequency, size and magnitude of these disturbances may be greater in the northern conifer-dominated forests (Baldwin et al. 1952). The exception to this is the exotic gypsy moth (*Porthetria dispar*), which has decimated oak-dominated forests in central and southern New England on an irregular basis at least once each decade since its introduction in 1869. The convergence of variables that predispose a forest to significant fire is not common in New England. This is largely due to the even temporal distribution of precipitation and compositional dominance by faster-decaying hardwoods, especially in the three forest zones relative to the study species (#1b,#2,#3). Fire is more significant in the zones not addressed by this research (#1a, #4,#5,#6) (Bormann and Likens 1979).

The return interval for major disturbance varies widely in New England. The northern portions of the intolerant subdivision of the Spruce-Fir-Northern Hardwoods (#1a) may experience severe fires at intervals of roughly 100-150 years (Heinselman 1981). The tolerant subdivision of this type (#1b) and the Northern Hardwoods-Hemlock-White Pine type (#2) have similar disturbance patterns and are argued to be among the few forest communities in the eastern U.S. where a steady-state mosaic could have been in place in presettlement times, with return intervals of several hundred years or more (Lorimer 1977; Bormann

and Likens 1979). Bormann and Likens (1979) define steady-state in terms of relatively constant ecosystem biomass. Their model of a mature forest, where "endogenous disturbance" produces mostly smaller gaps that are recaptured by shade-tolerant species such as sugar maple (*Acer saccharum*) or beech (*Fagus grandifolia*), allows for the indefinite persistence of early successional species (such as yellow birch, *Betula allegheniensis*) due to infrequent larger ("exogenous") gap formation (Forcier 1975). The scale of their shifting mosaic steady-state designation is thus larger than individual stands, and their model represents one of the best-studied examples of potential landscape equilibrium.

The Transition Hardwoods-White Pine-Hemlock forest (#3), in which this study took place, exhibits a shorter return interval of about 100 years or so, with hurricanes as the major disturbance (Foster 1988a,b). The same return interval probably characterizes the two Central Hardwoods zones (#4, #5), where fire may once again be a more significant factor along with wind. Finally, the Pitch Pine-Oak community (#6) may have the highest disturbance frequency at roughly 25 years due to hurricanes and fire (Westveld et al. 1956).

Forest development in the smaller gaps that are typical of zones #1 and #2 and that occur locally throughout New England shows either (1) maintenance of the dominant shade-tolerant canopy, most often by upgrowth of advance regeneration, or (2) transfer of dominance from less to more tolerant species, but not the recruitment of intolerant species. Development after larger blowdowns, fire, or clearcutting allows large-gap opportunists to dominate initial phases of recovery. Shifting canopy dominance then occurs through differential growth rates and longevities

as species more tolerant of shade eventually overtop and claim the stand (Henry and Swan 1974; Forcier 1975; Oliver and Stephens 1977; Bormann and Likens 1979; Oliver 1980; Bicknell 1982; Hibbs 1983; Foster 1988a).

The reason for this discussion of disturbance regimes is to establish that small- to medium-sized canopy gaps caused by windstorms, icestorms, or defoliation are typical of the three forest types relevant to this study. Even hurricanes, which produce the largest canopy openings in the Transition Hardwoods region, generate a heterogeneous pattern of damage that includes significant representation by small- and medium-sized gaps (Foster 1988b).

Some tree species in New England show a strong ability to endure prolonged overstory suppression and still grow quickly after canopy opening (*Abies balsamea*, *Acer pensylvanicum*, *Acer saccharum*, *Fagus grandifolia*, *Picea rubens*, and *Tsuga canadensis*). Several species of varying shade tolerance can show rapid seedling or stump sprouting following disturbance (*Acer rubrum*, *Acer spicatum*, *Castanea dentata*, *Quercus alba*, *Quercus rubra*, *Quercus velutina*, and *Tilia americana*). A few species can establish in the understory and are moderately tolerant of shade as young seedlings, but must be released within 3-6 years (*Fraxinus americana*, *Prunus serotina*, and *Ulmus* spp.). Finally, other species generally must establish and attain competitive canopy height during the same disturbance event (*Betula allegheniensis*, *Betula papyrifera*, *Betula populifolia*, *Pinus strobus*, *Populus grandidentata*, *Populus tremuloides*, and *Prunus pennsylvanica*). But few species use a single mode; most employ two or more regeneration tactics (Bormann and Likens 1979), thereby blurring their autecological niche relationships.

2.2. THE HARVARD FOREST

The 1200-hectare Harvard forest in north-central Massachusetts has been operated as a silvicultural and ecological research facility by Harvard University since 1907. The Forest lies in the New England Upland physiographic region, with moderate local relief ranging from 120m to 410m above sea level. A bedrock dominated by granite, gneiss, and schist is generally overlain by sandy loam glacial till, producing soils that are moderate to well drained, acidic, and average three meters in thickness. Variations in parent materials, textures, alluvial and colluvial deposits, and slope produce poorly drained and excessively drained sites as well. The regional climate is cool temperate (summer mean 20°C, winter -4°C) and humid, with precipitation (annual mean 110cm) distributed fairly evenly throughout the year (Rasche 1958; Sipe, unpublished data).

The forest is situated in the Transition Hardwoods-White Pine-Hemlock zone (#3, Figure 2-1), where floristic elements from both north and south intermingle to yield diverse communities. The compositions and successional relationships of forest types in the Harvard Forest have been summarized by Spurr (1956a). Table 2-2 gives the dominant tree species on upland sites in the Forest. Since 1907, research at the Forest has included studies of land use history; compositional and structural variation in relation to site; detailed soil structure, soil moisture, and root behavior; micrometeorological patterns; forest response to diverse types of silvicultural management; functional wood anatomy and branching patterns of trees; and community response to natural disturbances such as pathogen epidemics, insect damage, icestorms, and tornadoes, and hurricanes. Thus there is a substantial

Table 2-2. Primary tree species roles across the Harvard Forest in central Massachusetts, based on Spurr (1956), Harvard Forest records, and personal experience.

MATURE OVERSTORY DOMINANTS WIDESPREAD ABUNDANT	LOCALLY ABUNDANT	EARLY SUCCESSIONAL DOMINANTS	UNDERSTORY DOMINANTS (SMALL TREES)
Acer rubrum Betula lenta Fraxinus americana Quercus rubra Tsuga canadensis	Acer saccharum Betula allegheniensis Betula papyrifera Carya glabra Carya ovata Fagus grandifolia Pinus strobus Prunus serotina Quercus alba Quercus velutina	Betula papyrifera Betula populifolia Populus tremuloides Populus grandidentata Prunus pennsylvanica	Acer pensylvanicum Castanea dentata Cornus spp. Hamamelis virginiana Ostrya virginiana

background of information for interpreting the results of the experimental gap research.

The major strength of the Forest for current ecological research lies in the diversity of community compositions and structures and the records that summarize stand histories for the period 1907 to present. These records are unparalleled in comprehensiveness and detail, as all forest operations, plantings, experiments, and significant natural disturbances have been mapped and described for each year in all of the 28 Forest compartments. These descriptions have been supplemented by periodic complete forest inventories; 275 maps of site variables, forest composition and structure, and land use history; extensive archived photographs; and over 475 unpublished studies. This data base was used to interpret community variation throughout the Forest and select the study species and field site for the gap research.

2.3. STUDY SPECIES

The genus *Acer* is the only North American tree genus that has at least three co-occurring shade-tolerant species: *A. pensylvanicum* (striped maple), *A. rubrum* (red maple), and *A. saccharum* (sugar maple). A fourth shade-tolerant species, *A. spicatum* (mountain maple), can also be found with these three, but its distribution and abundance in the Harvard Forest were not great enough to justify its inclusion in the research. 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 higher elevations of the Appalachians as far south as Georgia (Fowells 1965). They co-occur in greatest abundance in forests where small gaps dominate the disturbance regime. These species

play prominent roles in three of the forest types discussed in Section 2.1. (Table 2-1).

While they are all classified as tolerant or very tolerant of shade, there are physiological, morphological, and life historical differences that suggest potential specialization on understory and small gap microenvironments (Table 2-3). Sugar maple is regarded, along with American beech (*Fagus sylvatica*), as the most shade-tolerant of the North American broadleaved species. It is the largest and longest-lived of the three study species. Tubbs (1968), Forcier (1975), Barden (1983), Canham (1985), and Woods and Whittaker (1983) have all reported on the ability of sugar maple to survive extended understory suppression and still respond with rapid growth to small canopy gap release. However, sugar maple seedlings may not be able to cope well in larger silvicultural gaps (Godman and Tubbs 1973; Tubbs 1977). Of the three species, sugar maple appears to have the greatest water and nutrient requirements, at least as mature trees (Leak 1975, 1978, 1979).

Red maple's range and local physiographic distribution are greater than either 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. However, very little is known about red maple seedling survival, and the author has noted the existence of notable persistence (>15 years, with annual growth rates <1cm) by red maple seedlings in mature stands at the Harvard Forest (Sipe, unpublished data). 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 sub-canopy tree that is capable of

Table 2-3. Autecological and life historical traits of the three study species.

TRAIT	ACER PENSYLVANICUM	ACER RUBRUM	ACER SACCHARUM
Shade Tolerance	Tolerant to Very Tolerant	Tolerant	Very Tolerant
Longevity (yrs) Max, Mean	60+,25+	150+,90+	400+,150+
Mean Mature Size Height (m) Diameter (cm)	8+ 15-25	18+ 45-75	20+ 50-90
Minimum Fruiting Age	10	4	40-60
Seed Dispersal Time	Oct-Nov	Apr-Jul	Oct-Dec
Good Seed Year Periodicity (yrs)	?	1-2	3-7
Mean Seed Weight (mg)	40	20	74
Germinative Capacity Range (%)	?	1-74	16-68
Stratification Requirement (days)	90-180	0	60-90
Germination Time	Mar-May	Apr-Jul	Apr-May
Seedling Mortality In Understory First Two Years Subsequently	Moderate Very Low	Moderate Low?	Moderate Very Low
Maximum Growth Rate Seedling Sprout	Fast Very Fast	Fast Very Fast	Moderate Moderate
Sprout Occurrence	Profuse	Profuse	Common
Water Requirement	Moderate	Broad	High
Nutrient Requirement	Moderate	Broad	High

References: Baker (1949); Fowells (1965); Hibbs (1979); Leak (1975);
Solomon and Blum (1967); Trimble (1975); USFS (1974)

reproductive output in fairly deep shade. It's longevity and maximum size are well below that of the other two species, but it is quite successful at resprouting from the base of senesced individuals, potentially occupying the same microsite through several generations of mature stems. Opinions differ markedly on striped maple's shade tolerance, ranging from very tolerant (Hibbs 1979) to intermediate (Bormann and Likens 1979). Hibbs (1979) has produced the best data on suppressed survival and growth by seedlings, which would support its classification as very tolerant, at least through about 15 years. The author's field experience would agree with this assessment.

Wilson and Fischer (1977) studied striped maple response to step changes in irradiance that simulated canopy gap release. They concluded that it was capable of dramatic changes in shoot development and rapid leader growth when irradiances were increased from 5% to 18% full sun, corresponding to a small (single-tree) gap. On the other hand, Bicknell (1982) found that striped maple was one of the dominants 5 years after clearcutting on one of the watersheds at Hubbard Brook, far outpacing advance-regenerated sugar maple seedlings and beech sprouts in height growth. Thus striped maple seems to be the most opportunistic of the three species in responding to gaps of different size.

Germination and establishment in all of these species may occur after disturbance, especially by red maple, but advance regeneration is considered to be more important for canopy participation and/or reproductive maturity in all three species, and foresters manage maples on this principle (Zilgitt 1944; Gilbert and Jensen 1958; Leak and Wilson 1958; Leak et al. 1969; Tubbs and Metzger 1969; Godman and Tubbs 1973; Trimble 1973; Leak and Solomon 1975; Tubbs 1977; Barden 1983;

Canham 1985; Runkle 1985).

Scattered information is available on seedling growth in various experimental light environments. The best height growth is generally obtained for red and sugar maple in moderate shade (40-50% full sun). The data on total seedling biomass across light levels are not sufficient to distinguish clearly between species. Root:shoot (R:S) dry weight ratios increase monotonically but not proportionally for red and sugar maple as light intensity increases from 3% to 100% full sun (Logan 1965, Loach 1970).

Comparative physiological studies among these three species are limited to data on diffusive resistance versus xylem water potential in saplings (Federer 1976; Federer and Gee 1976; Pereira and Kozlowski 1977) and photosynthetic adaptation to light intensity in sugar maple seedlings (Logan and Krotkov 1968; Logan 1970). With the exception of Jurik et al. (1985), no studies have compared more than one of the maple species, and very little data exist for striped maple.

Red and sugar maple exhibit higher diffusive resistances to water loss than most other hardwood associates at both high and low light intensities. This is variously attributed to faster stomatal opening and closing, greater cuticular resistance, and stomatal closure that is more sensitive to vapor pressure deficits, light intensities, or leaf turgor pressure (Woods and Turner 1971; Davies and Kozlowski 1972, 1974; Federer 1976, 1977; Federer and Gee 1976; Pereira and Kozlowski 1977; Hinckley et al. 1978; Roberts et al. 1979, 1980; Wallace and Dunn 1980).

The relationships between stomatal closure versus light intensity and light required to saturate photosynthesis may result in sugar maple being less limited by carbon dioxide transfer than are red oak and black

oak at certain light intensities (Wuenschel and Kozlowski 1970). However, Wuenschel and Kozlowski (1971b) found that even though sugar maple began to close stomata before black oak as leaf temperature increased, black oak's rate of closure was greater; thus oak may lose less water than maple over a moderately high range of leaf temperatures. Lower thresholds for stomatal closure by maple may regulate water loss, but net carbon gain per longer unit of time may be reduced below that of less tolerant species. This has been suggested for sugar maple versus black oak during drought cycles (Hinckley et al. 1978a) and, especially relevant to this research, for sugar maple versus bur oak in canopy gaps (Geis et al. 1971).

Sugar and red maple usually have lower light compensation points than associated species due to lower respiration rates, under both sun and shade conditions (Kozlowski 1949; Loach 1967; Logan and Krotkov 1968; Wuenschel and Kozlowski 1970; Hinckley et al. 1978a). The maples also exhibit lower saturation irradiances in most cases. Light-saturated net photosynthetic rates per unit leaf area were about the same in sun-grown sugar maple and yellow birch, but sugar maple had rates three times higher than yellow birch in 13% full sun (Logan 1970).

In one study of sugar maple in Michigan, only 30% of the annual net photosynthate gained under normal understory irradiance was required for current year leaf construction and leaf maintenance; the remaining 70% was available for stem and root respiration as well as storage. In addition, though peak net photosynthetic rates were reached during sunflecks, the relative contribution of sunfleck-derived photosynthate to total diurnal and seasonal carbon gain was estimated to be no more than 12% (Weber et al. 1985).

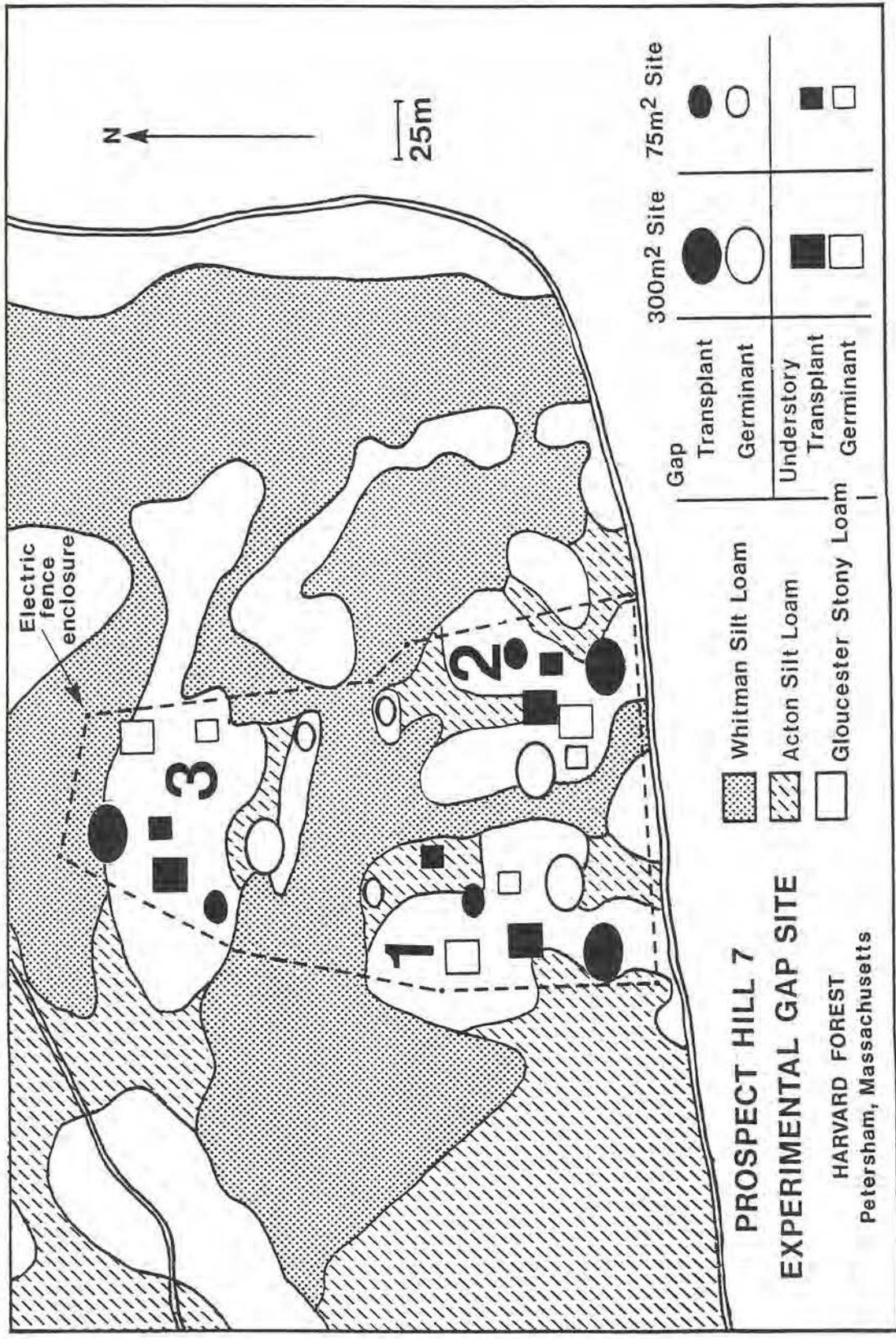
In summary, the three maple species tend to behave similarly in autecological terms in comparison to their common associates in mixed broadleaved forests. But even though they are all shade tolerant and typically employ advance regeneration, they appear to respond differentially to canopy gaps of varying size. Therefore, if these species do partition the microenvironmental gradient across the understory, single-tree (75m²) and small multiple-tree gaps (300m²) created in this study, then the prediction is that sugar maple will outperform the others in the understory, striped maple will dominate in the small gaps, and red maple will be superior in the larger gaps. As a corollary, the species should likewise partition different positions within the large and small gaps depending on the microenvironmental conditions specific to each location.

2.4. SITE SELECTION AND EXPERIMENTAL DESIGN

The Harvard Forest records were examined to select the best available site for experimental gap creation. Several criteria were used to identify suitable sites, and a 4-hectare portion in the Prospect Hill 7 compartment was chosen for the experiment (Figure 2-2).

The forest in this portion is not old-growth. It is, however, a relatively mature stand which originated after clearcutting in 1890. It incurred modest damage during the last severe hurricane in 1938, some minor stand improvement was done in 1947-49 to favor red oak (*Quercus rubra*) growth, and some defoliation occurred during the last gypsy moth outbreak in 1982. 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*,

Figure 2-2. Map of the Prospect Hill 7 experimental gap study area. The 12 transplant sites are shaded. The figure includes a matching set of 12 gap and understory sites in which the post-gap responses of seven maple and birch species from planted seed were studied. These germinant sites, part of a larger project that included both germinants and transplants, are not included in the discussion.



Fraxinus americana, *Pinus strobus*, and *Tsuga canadensis*. Striped maple is common in the understory. Sugar maple is not abundant in either the understory or overstory, but it is present.

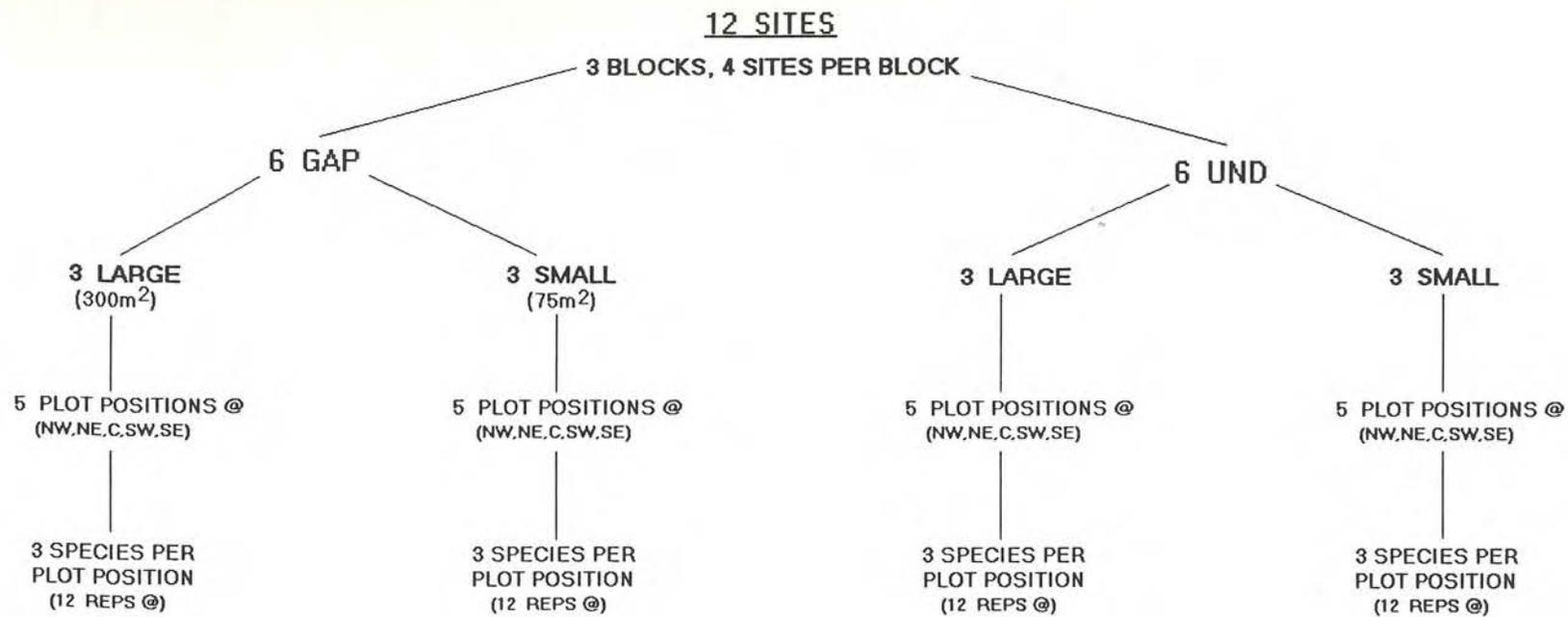
The study area shows marked physiographic variation. Three main portions of higher ground, on which the experimental gap and understory sites are located, are separated by shallow ravines with intermittent streams. Soils on the upland are primarily Gloucester stony loams, while Acton silt loams characterize the slopes and Whitman silt loam occupies the ravine bottoms. This soil catena is derived primarily from granitic glacial till. The Gloucester soils are well-drained, shallow, prone to drought and not fertile. The Acton soils are intermediate in all these respects, while the Whitman soil is more fertile but very stony and poorly drained.

The physiography and soils of the study site are representative of a large fraction of the Harvard Forest and surrounding landscape. The stand composition, although red oak has been favored somewhat by silvicultural activity, is also representative of much of the upland forests (based on Harvard Forest records).

In 1986, twelve gap and understory sites were positioned in the 4-hectare study area. These 12 sites represent a complete cross of two main factors (Gap versus Understory, Large versus Small) (Figure 2-3). The twelve sites are distributed throughout the study area such that each of these blocks contains a complete set of four site types (Figure 2-2). Each site type, such as Large Gap, thus has three block replicates.

The overall design used for analysis of variance (ANOVA) is a split-split-plot within the two main factors. The model actually applied

Figure 2-3. Hierarchical breakdown of the experimental gap design. Two levels of split-plot factors (plot positions and species) are nested within the two main factors (gap vs. understory, large vs. small). There are three block replicates of each site type.



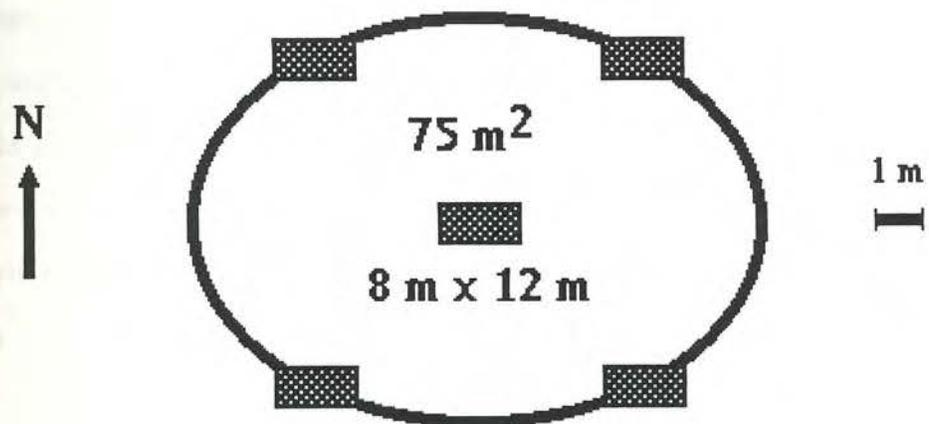
to the growth data combined the two main factors into one "Site" factor with four treatment levels (large gap, small gap, large understory, small understory). Plot positions are split within sites, and species are split within plot positions. The ANOVA model (Section 4.1.) excluded certain three- and four-way interactions of less interest to the interpretation.

The two gap sizes were chosen for several reasons (Figure 2-4). Gaps ranging up to 300m^2 in area typically represent 80-90+% of all gaps encountered randomly during surveys in old growth forests in the eastern U.S. (Barden 1979,1980,1981,1983; Runkle 1982,1984,1985). The median area of single-tree gaps in these systems ranges from 75m^2 to 130m^2 ; median multiple-tree gap areas are roughly $240\text{-}290\text{m}^2$. The two experimental sizes therefore encompass the most commonly encountered single-tree and multiple-tree gap sizes in eastern forests. However, since the average canopy height in the Prospect Hill 7 study area is lower (15-21m) than heights in the old-growth studies cited above, the effective sizes (gap area relative to surrounding forest height) of the experimental gaps are greater. The 75m^2 experimental gaps are still within the $75\text{-}130\text{m}^2$ median range for single-tree gaps, but the 300m^2 experimental gaps are larger than the $240\text{-}290\text{m}^2$ range for multiple-tree gaps. The significance of this difference in overstory height is that the effective gap sizes used here produce a broader gap-understory microenvironmental gradient than would occur for the same gap areas in taller old-growth forests, extending the conditions over which gap partitioning among the three maple study species may be detected.

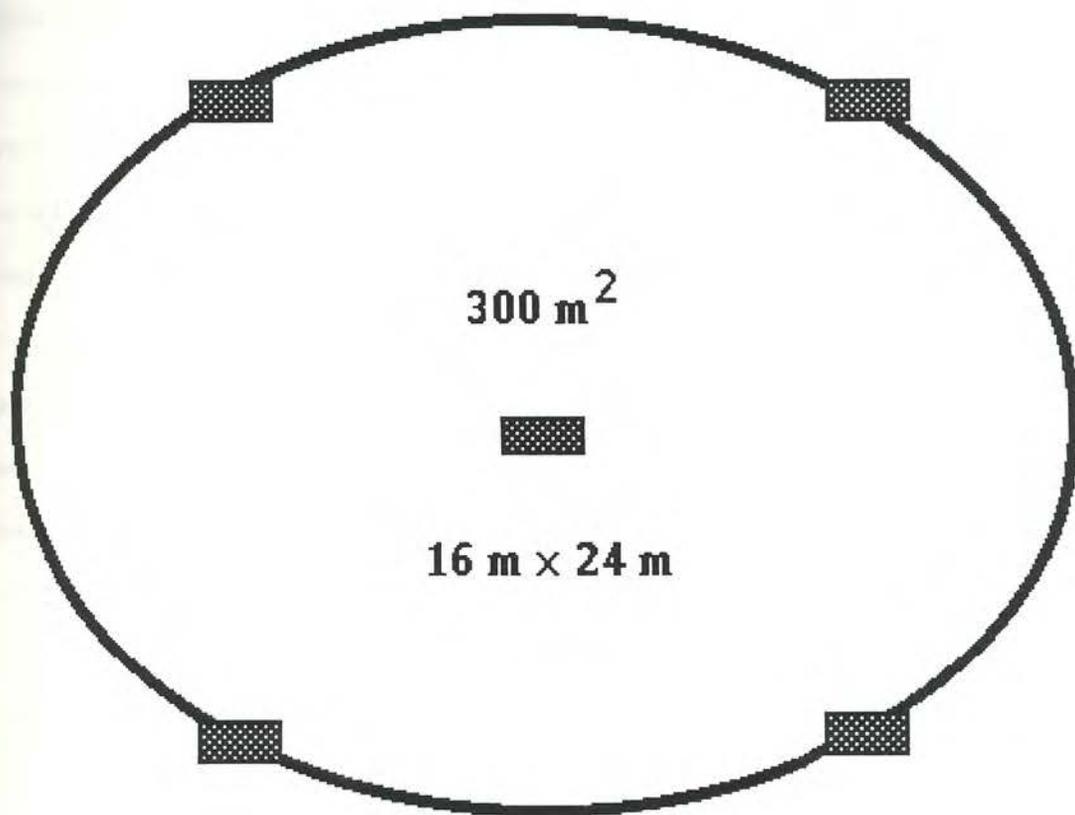
The experimental gap areas differ by a factor of four and their elliptical dimensions by a factor of two (8x12m versus 16x24m). The gaps

Figure 2-4. Dimensions, areas, and seedling plot positions for the two experimental gap sizes (all drawn to scale).

SMALL GAP



LARGE GAP



are elliptical since natural gaps themselves tend to be elongated and several authors (e.g., Barden 1979; Runkle 1982; Brokaw 1985a) have used elliptical functions on field measurements of gap dimensions to estimate gap area. The ratio of length to width is the same (1.5) for both gap sizes. Further control over gap geometry was achieved by orienting all gaps uniformly, with the long axis east-west. The sizes, shapes, and orientations of these twelve gaps were controlled through meticulous selection of overstory trees to be felled.

2.5. SEEDLING PLOT PREPARATION AND PLANTING

Five 1m x 1m seedling plots were laid out within each gap and understory site in August 1986, over a year before gap creation (Figure 2-4). Plot positions in future gaps were determined by calculating the distance from the estimated gap center to the vertically-projected canopy edge on the sub-cardinal axes (NW, NE, SW, SE). These five positions provided data on within-gap spatial patterns of microclimates and species responses. The same configurations of plots were used in the understory; hence the designations as large or small understory sites.

Since the goal of this experiment was to study non-competitive performances by the seedlings above- and belowground, all seedling plots were treated to remove root competition and rocks and homogenize the surface horizons (O and A). The plot margins were first sliced vertically to a depth of 25+cm with sharpened flat spades. Then mattocks and garden hoes were used to chop vertically through the soil profile down to approximately 25cm. Care was taken to minimize inversion of the soil profile. Small and large woody roots, herbaceous and shrubby perennials, and any rock fragments larger than 5cm in diameter were

removed. The surface layer (~5cm) was then purposely mixed and smoothed across the plots with garden rakes. The plot margins were re-spaded in the spring of each year, and the plots were weeded regularly within each season. 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 treatments clearly altered the belowground environment away from the surrounding forest floor in many ways, and therefore limit the extrapolation of the results to unmanipulated natural gaps. However, the significance of root competition and the enormous variability in physical and biological belowground conditions argued for such plot treatments so that seedling response to gap geometry would be less affected by non-geometric variables.

After plot preparations were finished, 2160 naturally-established seedlings were lifted from the understory in several other compartments of the Harvard Forest and transplanted into the 60 plots. These transplants (720 per species) were selected within a specified height range (15-30cm tall) in order to reduce initial variation. The age range was also restricted to 4-10 years, although determinations of ages after transplanting revealed that some seedlings were as old as 20 years. All seedlings were unbranched and undamaged with an intact terminal meristem (leader).

The seedlings were dug with a small soil ball in October 1986 after leaf senescence. They were stored outdoors for about three weeks until all 2160 were ready for planting. They were then transported to the field and bare-rooted into the prepared plots over a two-week period.

Each seedling plot contained 36 seedlings (12 per species),

randomized by position in 4 rows of 9 seedlings each. Seedlings were separated by 25cm in all directions to avoid aboveground competition. The plots had been spaded and prepared such that the edge seedlings also had 25cm of growing space on the plot margins. Seedlings from the various source locations in the were non-systematically randomized across the 60 plots. Leaf litter was scattered over the plots after planting to match litter depths outside the plots. An initial attempt was made to maintain leaf litter on all plots, particularly in the large gaps where it was regularly removed by wind. However, it was decided that this was part of the gap effect, and litter additions were discontinued.

Survival over the first year (Oct 1986-Sept 1987) was 95% across the study area (discussed further in Section 4.2.1.). Measurements of seedling height, age (via terminal bud scars), basal diameter (with dial calipers, one centimeter above the root collar), condition (subjective scale 1-5) and number of leaves were taken a year later (September 1987) to provide data on pre-gap (initial) status. These data are summarized in Section 4.3.1.1.

2.6. GAP CREATION AND SITE TREATMENT

The six gaps were created during September 25 through November 2, 1987. Members of the Harvard Forest woods crew felled the marked trees and cut the boles into sawlogs and the crowns into cordwood. The sawlogs were removed carefully with a small caterpillar and chain winch, resulting in remarkably little soil disruption. The cordwood was split by hand, stacked, and then transported from the site on a custom-built trailer with large tires, again minimizing soil disruption. The

remaining brush was spread in the understory 5-10 meters beyond the gap margins, well away from plot positions.

The transplanted seedlings, which were in the plots a year before gap creation, were protected from damage during felling in two principal ways. First, the skill of the woodsman allowed him to drop the overstory trees in precise positions, often in narrow confines between plots. Second, in cases where bole or crown contact with seedlings was likely, 20-30 cm thick cordwood sections were placed at strategic locations in and around plots to support the falling masses and keep them above seedling level. Together, these tactics resulted in no seedling being lost to the felling process. This measure of success was quite satisfying, given the fact that 61 stems => 15cm in diameter at the base were felled to create the 6 gaps (Table 2-4).

Understory saplings and tall shrubs were cut basally prior to felling the overstory trees. In addition, any remaining saplings or shrubs > 0.5m tall were removed after tree felling. All regrowth (especially stump sprouts) was cut back regularly every year in all gaps. These site treatments represent another important level of control in the experiment. The effects of downed biomass and remnant and regrowing plants are certainly critical factors in natural gap processes. However, these factors could have easily thwarted the attempt to understand the potential significance of non-competitive physiological specialization in response to gap geometry. The experimental gaps created here yielded the most exposed conditions possible for the two gap sizes and position within the gaps, and thus tested how the three species may sort themselves out on the high exposure end of the gap-understory gradient in this gap size range.

Table 2-4. Summary of the trees cut to make the 12 experimental gaps, by species and size class. Diameter classes are based on stump diameters, not breast height. Relative importance is the average of relative density and relative basal area.

SPECIES	NUMBER	RELATIVE DENSITY	BASAL AREA (sq cm)	RELATIVE BASAL AREA	RELATIVE IMPORT	BASAL DIAMETER CLASS (cm)					
						10.0-19.9	20.0-29.9	30.0-39.9	40.0-49.9	50.0-59.9	60.0+
<i>Acer rubrum</i>	19	31.1	6409	11.6	21.4	9	10				
<i>Betula allegheniensis</i>	3	4.9	1198	2.2	3.5		3				
<i>Betula lenta</i>	2	3.3	1218	2.2	2.7	1		1			
<i>Fagus grandifolia</i>	5	8.2	3823	6.9	7.6	1	1	2	1		
<i>Quercus alba</i>	1	1.6	881	1.6	1.6			1			
<i>Quercus rubra</i>	21	34.4	36922	66.7	50.6		4	2	8	5	2
<i>Tsuga canadensis</i>	9	14.8	4639	8.4	11.6	5	2	1	1		
(unknown)	1	1.6	227	0.4	1.0	1					
TOTAL	61	100.0	55317	100.0	100.0	17	20	7	10	5	2

A two-meter five-stranded electric fence was installed around the entire study area in December 1987 (Figure 2-2). The 800m spring-tension fence was powered by a deep-cycle auto battery and a specialized fence charger (Gallagher Systems, Inc.). The purpose was to exclude large herbivores, especially deer, and unwanted human traffic. There has been regular evidence of deer movement just outside the fence. However, no browsing on the transplanted maple seedlings occurred after fence erection, except for one plot in Block 3, where 5 seedlings suffered terminal leader loss in 1989 during a brief fence failure.

CHAPTER 3

MICROMETEOROLOGICAL PATTERNS IN GAPS AND UNDERSTORY

3.1. METHODS AND INSTRUMENTATION

3.1.1. HARVARD FOREST CLIMATE

Daily climate records from the NOAA weather station at the Harvard Forest headquarters were used to construct 20-year (1967-1986) summaries of the macroclimate for our study area. Daily precipitation (to the nearest 0.01 inch) and maximum and minimum temperature (to the nearest 0.1°F) were entered into computer files and converted to metric scales. Monthly and yearly means and standard errors were then calculated. The data for the main study seasons (1987-89) were plotted as differences from monthly means for the previous 20-year period to judge whether or not the study years deviated markedly from long-term averages.

3.1.2. GAP GEOMETRY

The three-dimensional structures of the six gaps were quantified in 1988. First, hemispherical photos (35mm color slides) were taken at the center plots of all gaps. These images were projected onto a flat surface and the gap outlines were traced on paper. This provided a visual judgment on the comparability of gap size replicates and a check for field measurements.

In the field, the distance to the vertically-projected canopy edge was measured from the center plot along the eight cardinal and sub-cardinal axes. The canopy height and the species responsible for the height were recorded along each axis as well. The distance and bearing to the center of each seedling plot were measured. For each of the eight

sectors formed by the axes, (i.e. $0-45^{\circ}$, $45-90^{\circ}$, ..., $330-360^{\circ}$), notes on sub-canopy vegetation were taken. Finally the shape of the gap and the occupation of crown space by different tree species were mapped along the entire canopy opening perimeter.

The field data were then used in the lab to draw accurate scale maps of each gap on gridded paper, with canopy outlines and precise plot positions. Gap areas were determined in two ways: (1) by applying the ellipse area formula to length and width dimensions, and (2) by counting grid cells on the scaled maps and converting to area in square meters. The ratio of gap diameter to canopy height was calculated as the N-S gap width divided by the mean canopy height ($n=3$: SE, S, and SW radii) on the south edge of the gap.

3.1.3. SEASONAL AND DIURNAL DIRECT BEAM ARCS

The patterns of direct beam exposure in the gaps were of particular interest in this study because of both their positive (enhanced PPFD) and negative (photorespiration and thermal stress) effects on seedlings. Seasonal changes in the positions of direct beam arcs were determined both theoretically and empirically, while diurnal arcs were measured in the field only. The goal in both cases was to describe more completely the dynamic nature of the light environment on different time scales and quantify these aspects of the spatial microclimatic gradient across gaps.

The gap geometry data were used to model the weekly positions of arcs at solar noon throughout the growing season. Solar altitude (angle above the horizon) changes at a constant rate ($0.2575^{\circ}/\text{day}$) throughout the year. Given canopy height on the south side of a gap, the position

of arcs at solar noon can be determined trigonometrically for any date. These calculations were done for each gap, and weekly arcs were plotted on scale maps. The number of weeks each of the five plot positions in each gap received potential direct beam radiation were then summed.

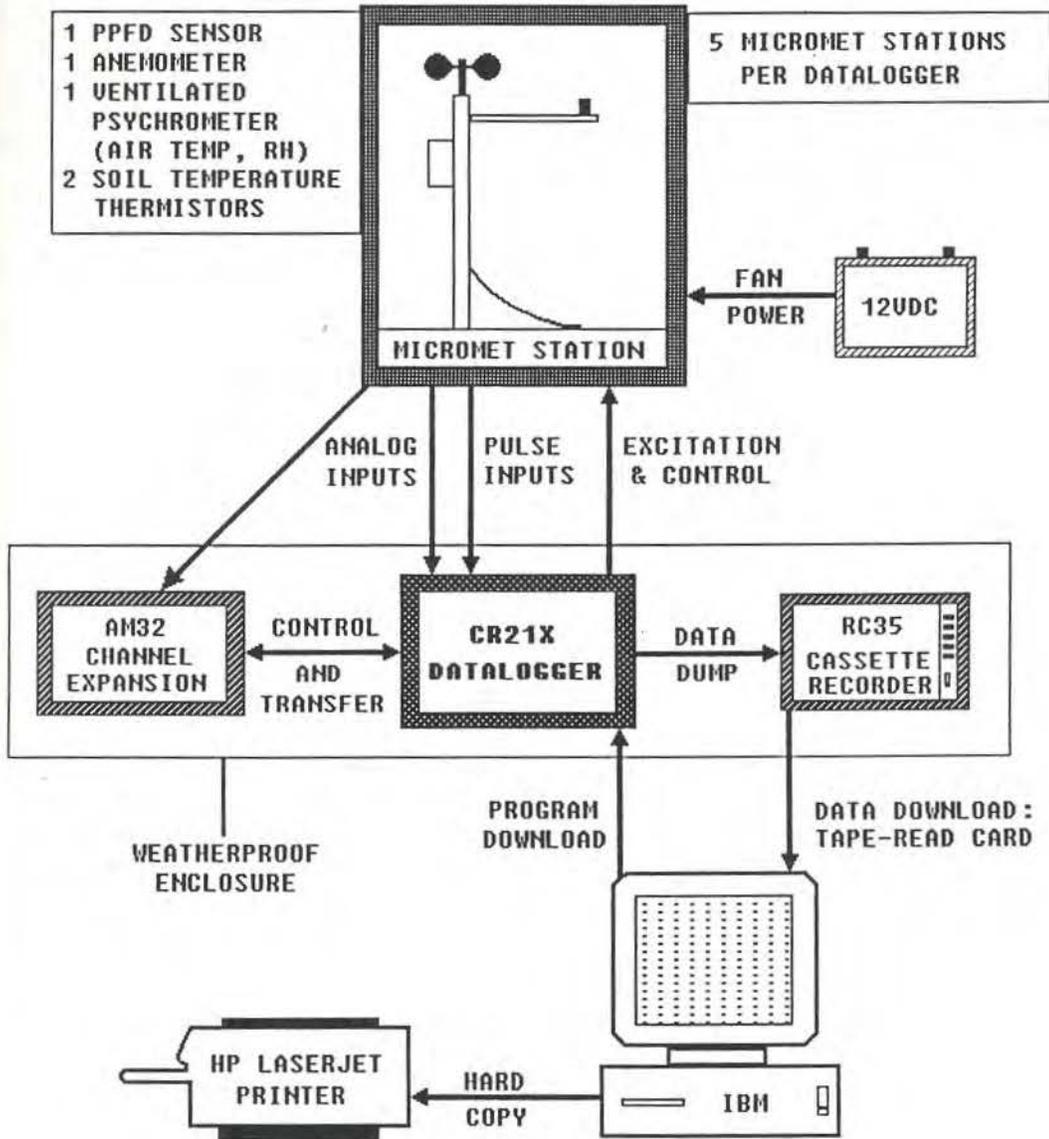
Since downed and remnant vegetation were removed from the gaps, direct beam arcs were easily observed and mapped in the field. Positions were recorded at solar noon on three dates (6/29, 7/11, 9/5) in 1989 to validate predicted positions.

Diurnal direct beam arcs were mapped directly in the field on these same three dates. Five arcs were plotted at two-hour intervals spaced symmetrically on either side of solar noon (i.e. 8am, 10am, noon, 2pm, 4pm). The number of hours each plot position received potential direct beam were then summed visually. The microclimatic data discussed below were then used as a check on diurnal timing and longevity of direct beam on clear days for each plot position.

3.1.4. MICROMETEOROLOGICAL SYSTEM AND SAMPLING REGIMES

In order to provide comprehensive data on microclimates, a set of fifteen portable microclimate stations was designed and used to quantify the physical aspects of the understory-gap gradient (Figure 3-1). Each of the stations had sensors for photosynthetic photon flux density (PPFD; home-built silicon photodiode quantum sensors, based on design by Biggs et al. 1971, modified by R. Pearcy and R. Chazdon, personal comm.), windspeed (Met-One 014A), air temperature and vapor pressure (Delta-T WVU-7 Ventilated Psychrometer), and soil temperature at two depths (Campbell Scientific 107B Thermistors), 1cm and 15cm. Five stations were connected to a field datalogger (Campbell Scientific

Figure 3-1. Diagram of the micrometeorological instrumentation and data management interfaces used during the study.



CR21X) housed in a picnic cooler. A channel expansion unit (Campbell Scientific AM32) extended the number of input signals beyond that of the CR21X. Sampling programs were downloaded from computer to the datalogger. Data were stored on cassette tapes in the field and downloaded to computer directly from tape.

The sensors for each station were mounted on lightweight angled aluminum support stands. All cable lead lengths were 15m. Transportation to the field site and set up for all 15 stations took one person 2-3 hours. The flexibility of this system made it possible to sample in various spatial configurations with relative ease.

The spatial and temporal characteristics of the sampling regimes are listed in Table 3-1. The three dataloggers and fifteen stations were designed to sample all five plot positions within three sites simultaneously. The primary comparison was among large gap, small gap, and understory sites. In order to achieve both diurnal and seasonal understanding of microclimatic patterns, the same trio of sites was sampled in Block 1 (LGAP1, SGAP1, LUND1) every other week throughout the growing season in both 1988 and 1989. Site type replicates were also sampled periodically (e.g., three large gaps), and on two occasions all fifteen stations were placed in a large gap to measure patterns at a finer resolution.

The standard sampling program scanned all the sensors on ten-second intervals and stored ten-minute means of both primary variables (PPFD, windspeed, temperature) and calculated variables (saturation vapor pressure, vapor pressure deficit, relative humidity). The ten-minute storage resolution was a compromise between the need for physical data on the time scales of leaf-level physiological processes (seconds to a

Table 3-1. Spatial and temporal micrometeorological sampling schemes used during the study.

SPATIAL SCALES

TEMPORAL SCALES

ACROSS SITES

Large Gap/Small Gap/Understory
3 Site Type Replicates
(e.g. 3 Large Gaps)

ANNUAL

1988, 1989

SEASONAL

Biweekly Sampling
in LG1, SG1 and LU1

WITHIN SITES - COARSE

5 Within-Site Plot
Positions Simultaneously

DIURNAL

10-sec Scan, 10-min Means,
Continuous, 4-5 Days

WITHIN SITE - FINE

(e.g. 15 Stations
in a Large Gap)

few minutes) and the ability to manage the large volumes of data output. The fifteen stations usually recorded in one field configuration for 3-5 days, logging continuously day and night. With the exception of electrical storms and infrequent equipment downtime, the stations were active nearly every week from May through September in both 1988 and 1989. Due to difficulties in the use of the ventilated psychrometers, data on relative humidity are less complete than for all other variables, and were not included in the micrometeorological analysis below.

3.1.5. MICROMETEOROLOGICAL DATA ANALYSIS

The goal of the micrometeorological analysis was to extract the data necessary to test the gap partitioning hypothesis. This involves several time scales, however, from photosynthetic performance (diurnal) to cumulative survival and growth (seasonal, annual).

The data used consisted of carefully-chosen sample days from the large gap/small gap/understory biweekly measurements. One clear and one overcast day from 1988 were selected to illustrate the most important features of diurnal microenvironmental patterns.

Seasonal summations were then derived by selecting an additional five clear and five overcast days from May through September 1988, spread as evenly as possible throughout the season. The diurnal courses of microclimatic variables were graphed for all plot positions in the three sites. Then several diurnal variables were calculated over a constant twelve-hour interval (six hours on either side of solar noon), including:

- (1) cumulative daily photosynthetic photon flux density (PPFD,

- mol/m²/12-hr day);
- (2) mean instantaneous PPFD (micromol/m²/s);
 - (3) cumulative duration of PPFD below 25 micromol/m²/s, defined operationally as the photosynthetic light compensation point for all three species (minutes);
 - (4) cumulative duration of PPFD in the 200-600 micromol/m²/s range, defined operationally as the optimal range for net photosynthesis (minutes);
 - (5) cumulative duration of PPFD above 800 micromol/m²/s, the approximate point beyond which all three species tended to show reduced net photosynthesis due to water deficits, stomatal closure, thermal stress, and/or significant photoinhibition (minutes);
 - (6) mean instantaneous air and soil temperatures (°C);
 - (7) cumulative duration of air temperature above 25°C, the general photosynthetic optimum for these species (minutes).

Mean values of these variables were calculated and graphed separately for the five clear days, five overcast days, and combined clear and overcast days.

A second strategy for condensing the seasonal data differed significantly from the first. It is difficult to relate long-term seedling performance to the microclimatic conditions of each site and plot position, given the temporal variability of macro- and microclimates and the asynchrony with which the several variables change over different time scales. What was needed was a condensed quantitative representation for each site/plot position that simultaneously takes several variables and sampling periods into account, so that the gap-understory gradient could be defined in a comprehensive way.

This is a classical problem for multivariate analysis. So variable means for each of the ten sampling days used above were also entered into discriminant analysis. Because we have known treatment groups (i.e., plot positions within sites), discriminant analysis can determine if there are significant multivariate differences among the groups and indicate, through loading coefficients, which of the original variables (e.g., cumulative diurnal PPF) are most responsible for distinguishing the groups. The success of the discriminant functions in classifying each sample into its original group (site or plot) provides another test of the distinctiveness of groups, plus insight into which groups are more variable than others. Scatterplots of centroids (group means) on discriminant axes display the n-dimensional relationships among groups and visually portray the statistical results.

The discriminant analysis was initially applied to the clear and overcast days separately. Spatial microclimatic variation among sites and plots is dampened considerably on overcast days. Analyzing all overcast and clear days simultaneously would obscure the significant plot differences that do occur on clear days. However, this obscuration is real. Plots do experience clear and overcast (and partly cloudy) conditions, and the bottom line measure of comprehensive microclimatic differences among sites/plots must consider all types of weather simultaneously. Therefore, the final discriminant analysis was done on the complete set of ten days.

Only clear and completely overcast days were used in the diurnal, seasonal univariate, and seasonal multivariate analyses presented here. Partly cloudy weather presents problems of sample day selection that are even more subjective than for clear and overcast weather. Until further

analysis of the data is completed, the assumption here is that mean daily values of microclimate variables on partly cloudy days are approximately the average of values on clear and overcast days.

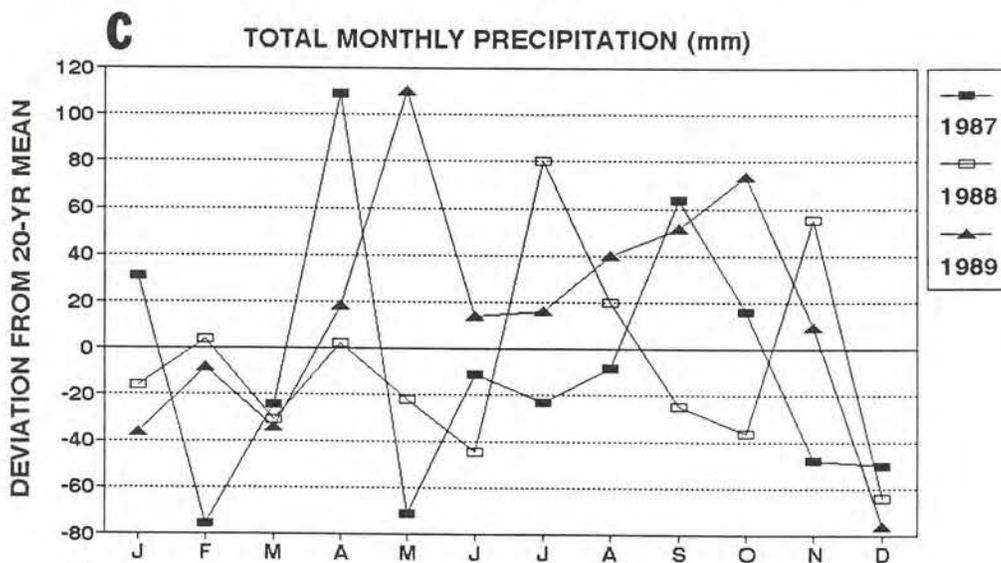
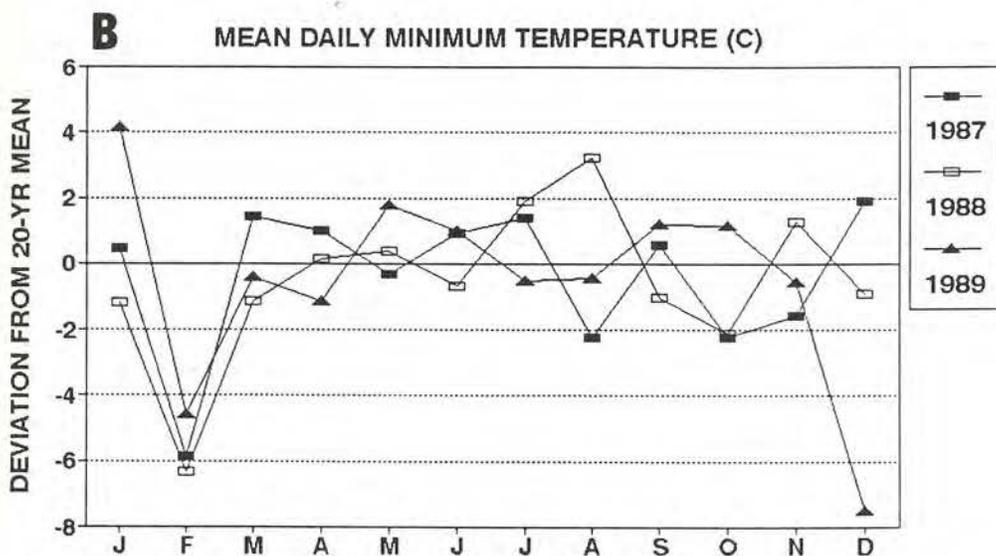
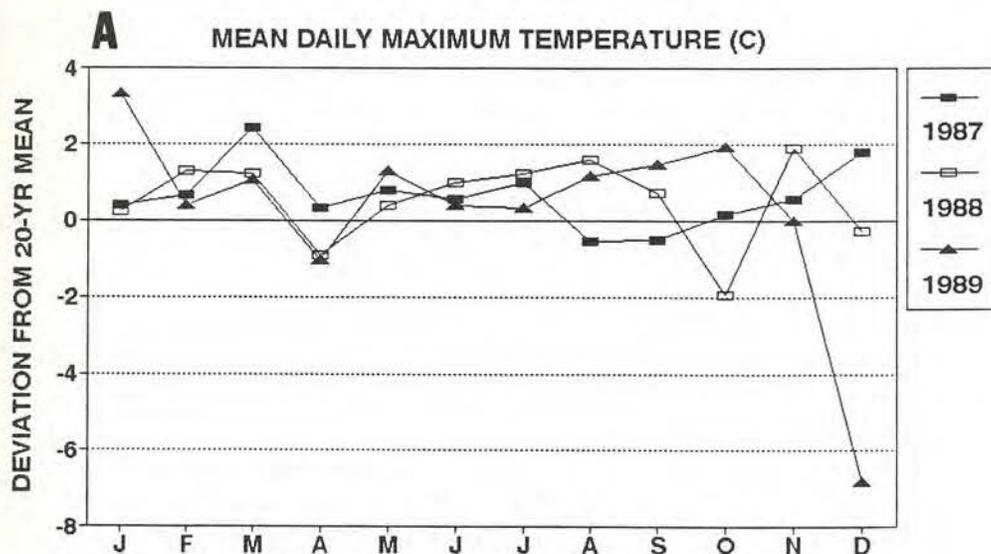
3.2. HARVARD FOREST CLIMATE VERSUS 1987-1989

Figure 3-2 summarizes temperature and precipitation deviations for the 1987-89 seasons as compared to the previous 20 years. Several points are suggested. First, there are few agreements from month to month among years. Each year displays its own pattern. The striking exception to this is the convergence on very cold minimum daily temperatures in February in all three years. This fact will play a role in later discussions about seedling dieback (Section 4.5.)

Second, mean maximum daily temperatures were slightly warmer during the May-September growing season in all three years, while minimum daily temperatures showed no such trend. In general the minimums showed greater month-to-month variability than the maximums.

Precipitation showed large year-to-year differences within several months, especially during the growing season. Some of these deviations, such as April 1987, May 1989, and July 1988, exceed the average monthly precipitation (which ranges from 8.0 to 11.0cm), and in this sense may be considered unusually high. The 1987 season was drier than average during May-August. The following year was variable, with a dry May-June followed by a wetter July-August. This surge in precipitation in July 1988 will be related below to suspected pathogen-caused mortality (Section 4.2.3.). The 1989 season was wetter than average for April-November. Finally, the December-March winter months showed an overall deficit of precipitation in all three years. The lack of snow cover will

Figure 3-2. Monthly deviations of temperature and precipitation from 20-year averages during the three study years 1987-89, based on the NOAA weather station located at the Harvard Forest headquarters. (A) Mean daily maximum temperatures, (B) Mean daily minimum temperatures, (C) Total monthly precipitation.



also figure into the discussion of seedling dieback, along with the low daily minimum temperatures in February mentioned above.

3.3. GAP GEOMETRY

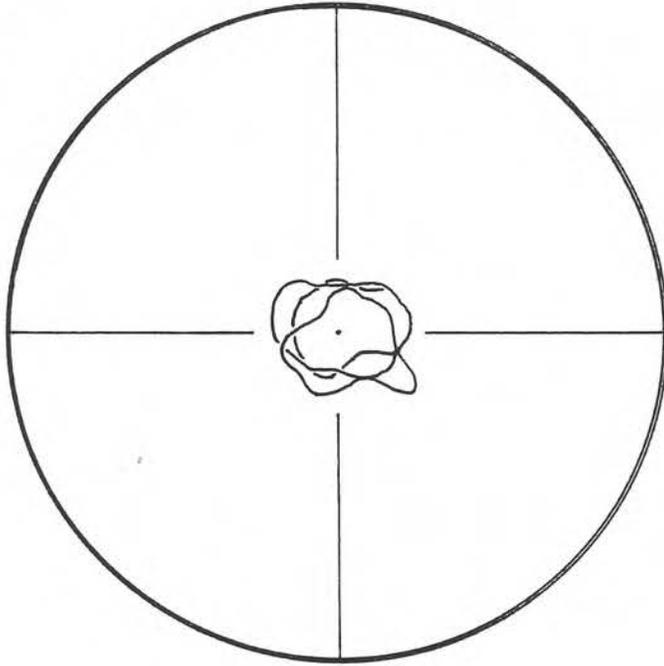
The effort to control gap size, shape, and orientation produced satisfying results and confidence in data interpretation. Figure 3-3 shows the canopy gap outlines traced from projections of hemispherical photographs. There is some variation among replicates of a size. For example, LGAP2 is narrower on the north-south axis than the other large gaps. But given the fact that plot centers were established before tree felling, the agreement among replicates is generally good.

Geometric results for these gaps are presented in Table 3-2. The variation among gap size replicates is clear. However, the mean dimensions, areas, and length:width ratios of the large gaps are very close to the planned values. The small gap areas are larger than desired by about 27%, due to the difficulty in tailoring the canopy opening when only 1-2 overstory canopy trees were removed. The mean area of 95m^2 is still within the range for median sizes of single-tree gaps in old-growth forests of the eastern U.S. ($75\text{-}130\text{m}^2$), and is thus considered representative.

Given a relatively uniform canopy height in the surrounding forest matrix, the diameter:height ratios of the large gaps should have been exactly twice that of the small gaps. Canopy heights were not uniform, however, with the small gap edges being noticeably taller. But due to the larger-than-intended N-S dimensions of the small gaps, these two factors cancelled each other, producing diameter:height ratios of 1.00 for the large gaps and 0.46 for the small. These ratios differ by a

Figure 3-3. Canopy gap outlines for the three small (A) and large (B) gaps. The outlines were traced from projections of hemispherical photos taken at the center plot of each gap.

A



B

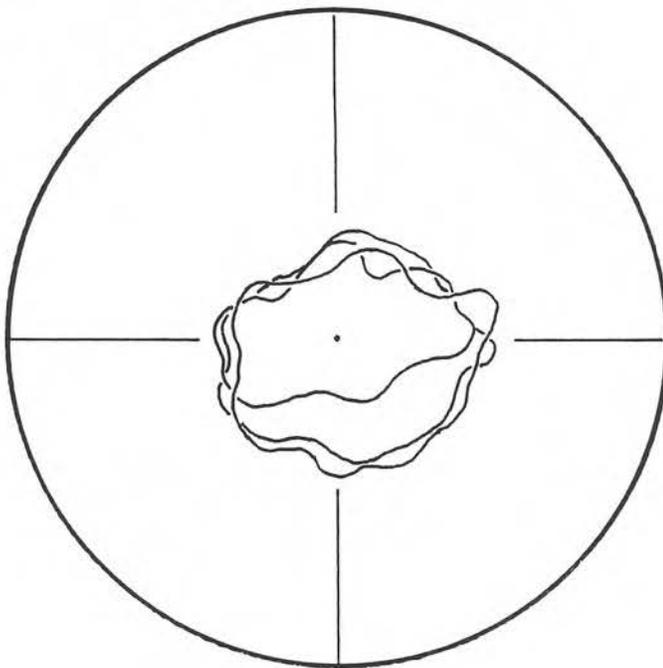


Table 3-2. Geometric data for the six experimental gaps, plus the number of trees cut to create each gap.

GAP CODE	N-S WIDTH (m)	E-W LENGTH (m)	AREA(1) (sqr m)	AREA(2) (sqr m)	LENGTH: WIDTH RATIO	CANOPY HT (m) (SOUTH)	DIAM/HT RATIO (N-S)	NUMBER TREES CUT >=15cm BASE	NUMBER TREES CUT >=30cm BASE
LG1	17.8	21.9	306	291	1.23	15.4	1.16	17	9
LG2	12.6	25.7	254	240	2.04	17.7	0.71	16	5
LG3	19.7	23.5	364	370	1.19	17.4	1.13	15	5
SG1	9.5	11.9	89	74	1.25	19.6	0.48	3	1
SG2	7.5	12.6	74	106	1.68	20.2	0.37	4	3
SG3	10.9	13.9	119	107	1.28	21.3	0.51	6	1
LG MEAN	16.7	23.7	308	300	1.49	16.8	1.00	16.0	6.3
GOAL	16.0	24.0	300	300	1.50				
SG MEAN	9.3	12.8	94	96	1.40	20.4	0.46	4.3	1.7
GOAL	8.0	12.0	75	75	1.50				

NOTES: AREA(1) was calculated using the ellipse formula $AREA = 0.25(3.14159)(WIDTH)(LENGTH)$.
 AREA(2) was derived from field drawings of gap openings on gridded graph sheets.
 Canopy height is the average of three measurements taken along SE, S, and SW bearings from gap centers.
 Cut tree diameters are the average of maximum and minimum basal (stump) diameters.

factor of 2.17, close to the desired 2.0.

On average, it required the felling of 1.7 canopy trees >30cm diameter at the base to create small gaps, and 4.3 trees to create large gaps, a 2.5-fold difference. The same ratio also applies to the lower size cutoff of 15cm diameter for felled trees.

While the average geometries of the large and small gaps were controlled with suitable accuracy, there were non-trivial variations in individual gap dimensions and areas which could affect microclimatic patterns and species performance. The more important variations will be discussed below where appropriate.

3.4. SEASONAL AND DIURNAL DIRECT BEAM ARCS

The movements of direct beam radiation arcs in gaps on diurnal and seasonal time scales were one of the most striking results of this study. Figures 3-4 and 3-5 and Table 3-3 summarize these movements.

Seasonal positions of arcs are portrayed in Figure 3-4. The NW, NE, and C plots of large gaps receive direct beam, while only the NW and NE plots receive it in small gaps. The large gap north plots receive potential direct beam for up to seven months, including the entire growing season, from March 22 through September 20 on average (Table 3-3). This varies from 24 to 34 weeks among the large gap replicates. Large gap centers receive direct beam for about 18 weeks, from the beginning of the growing season (May 1) to mid-August. This number is higher than the actual average of 12.7 weeks because LGAP2 was narrower than desired (see Figure 3-3), such that its center plot barely received direct beam (2 weeks). LGAP1 and LGAP3 are considered to be more representative.

MAY
MAY
JUN 14

Figure 3-4. Seasonal movement of direct beam arcs at solar noon in the small and large gaps, based on trigonometric calculations and field mapping. The drawings are idealized somewhat to represent the average pattern for gaps of each size.

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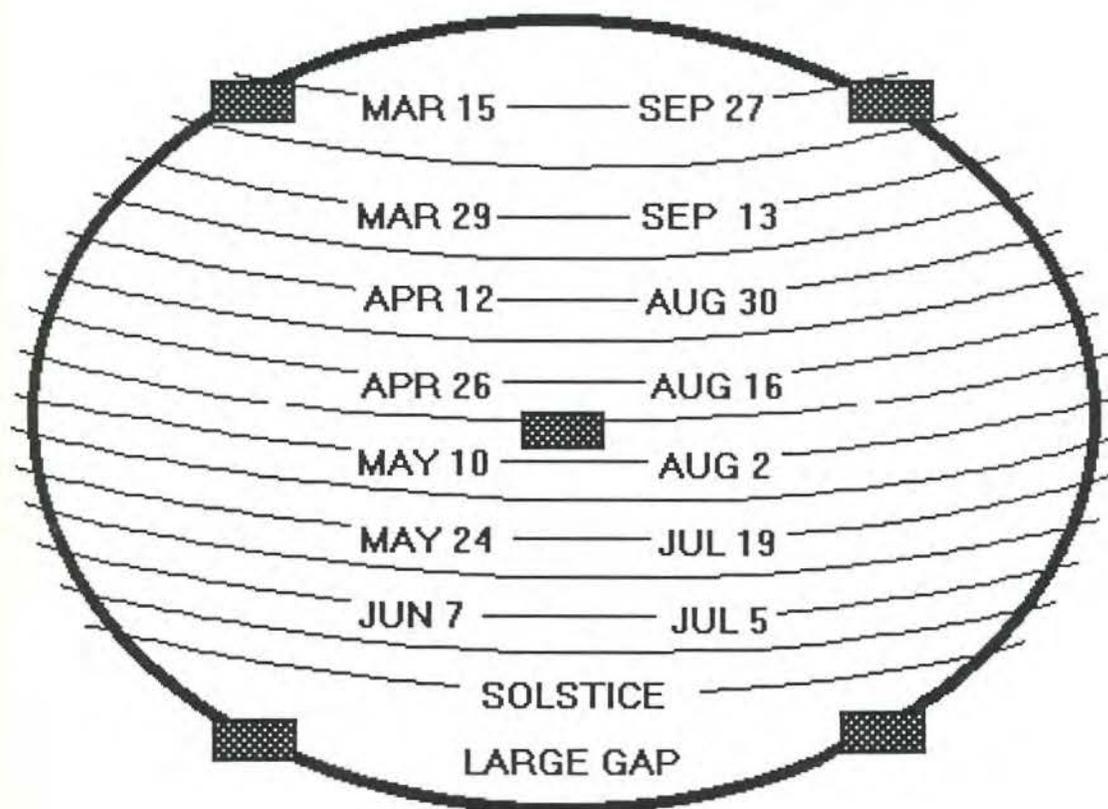
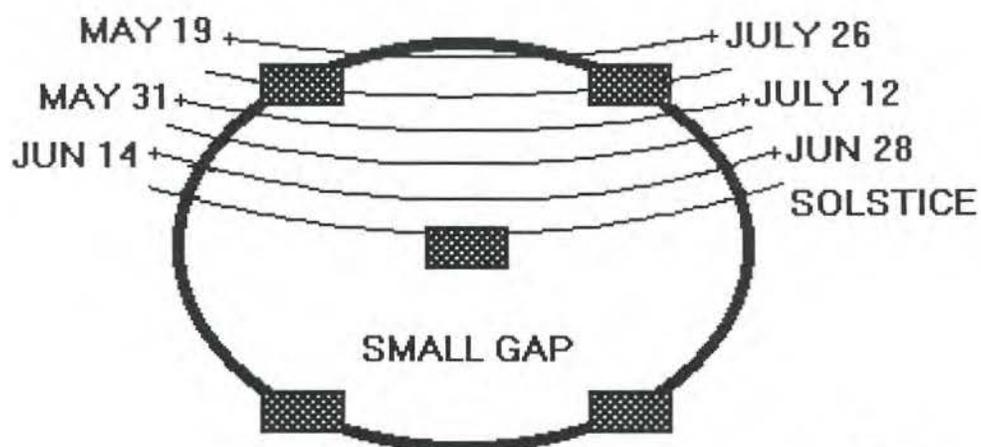


Figure 3-5. Diurnal movement of direct beam arcs near summer solstice for the small and large gaps. As with the seasonal movement of arcs (Figure 3-3), the drawings are idealized to represent the average for gaps of each size. Hours are solar time.

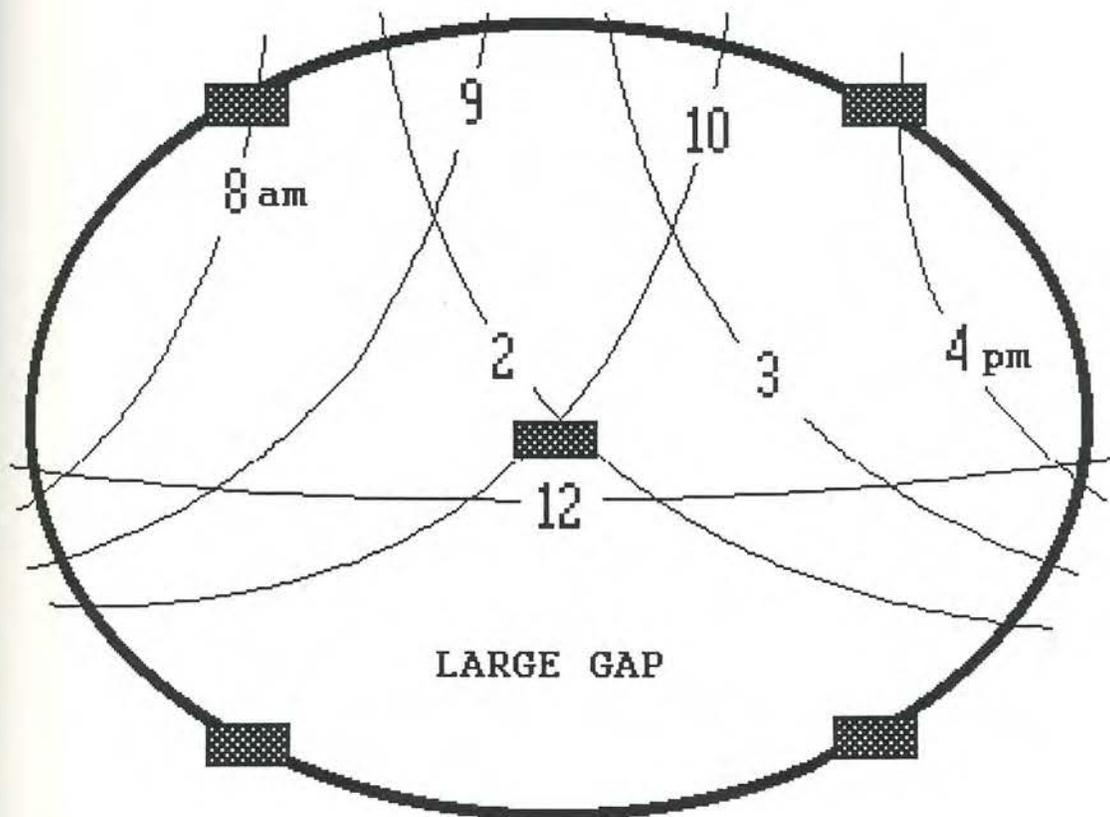
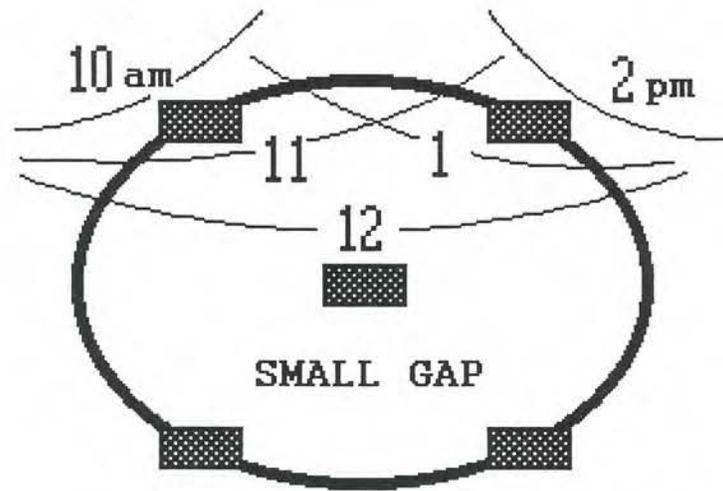


Table 3-3. Seasonal and diurnal durations and timings of direct beam arcs by plot position for each large and small gap.

GAP CODE	PLOT POSITION					GAP CODE	PLOT POSITION		
	NW	NE	C	SW	SE		NW	NE	C
SEASONAL DIRECT BEAM DURATION (WEEKS)						SEASONAL DIRECT BEAM TIMING (SOLAR TIME)			
LGAP1	34	24	18	1	0	LGAP1	Feb 21-Oct 18	Mar 22-Sep 20	Apr 12-Aug 30
LGAP2	24	24	2	0	0	LGAP2	Mar 29-Sep 13	Mar 29-Sep 13	Jun 7-Jul 5
LGAP3	32	28	18	0	0	LGAP3	Mar 1-Oct 11	Mar 8-Oct 4	Apr 19-Aug 23
SGAP1	8	7	1	0	0	SGAP1	May 24-Jul 19	May 24-Jul 19	Jun 18-Jun 24
SGAP2	6	6	0	0	0	SGAP2	May 24-Jul 12	May 24-Jul 12	
SGAP3	4	2	0	0	0	SGAP3	Jun 7-Jul 5	Jun 14-Jun 28	
LGAP MEAN	30.0	25.3	12.7	0.3	0				
SGAP MEAN	6.0	5.0	0.3	0	0				
DIURNAL DIRECT BEAM DURATION (HOURS)						DIURNAL DIRECT BEAM TIMING (SOLAR TIME)			
LGAP1	6.0	5.5	4.0	0	0	LGAP1	7:30 - 13:30	10:00 - 15:30	10:30 - 14:30
LGAP2	5.0	3.5	3.0	0	0	LGAP2	8:30 - 13:30	10:30 - 14:00	11:30 - 14:30
LGAP3	5.0	5.0	4.5	0	0	LGAP3	8:30 - 13:30	10:30 - 15:30	10:00 - 14:30
SGAP1	3.0	1.5	0	0	0	SGAP1	9:30 - 12:30	11:30 - 13:00	
SGAP2	1.5	2.0	0	0	0	SGAP2	11:00 - 12:30	11:00 - 13:00	
SGAP3	3.0	1.5	0	0	0	SGAP3	9:30 - 12:30	11:30 - 13:00	
LGAP MEAN	5.3	4.7	3.8	0	0				
SGAP MEAN	2.5	1.7	0	0	0				

- NOTES: 1. Seasonal direct beam timings are based on weekly intervals, not daily. Thus they may encompass a slightly longer period than the actual numbers of weeks listed, which are weighted sums of full and partial weeks of exposure for plot positions.
2. Diurnal beam durations are based on microclimate data near summer solstice.

The small gap north plots receive direct beam for only the 3-4 weeks just before and after summer solstice (total = 6-8 weeks). This represents about 20% of the duration of comparable positions in the large gaps. Again, site variation is present, with SGAP3 possessing a significantly smaller diameter:height ratio and a narrower window in time for the sun to shine over the south canopy edge.

Superimposed on seasonal direct beam movements are diurnal patterns. Figure 3-5 displays diurnal arcs near summer solstice (June 21). The overall differences between gap sizes are analogous to seasonal differences, in that the large gap durations are amplified, receiving direct beam 2-3 times longer than comparable small gap plots (Table 3-3). Large gap plots experience direct beam from early morning (8am solar time) to late afternoon (4pm) while small gap windows are compressed toward the middle of the day (9:30am-1:00 pm). The same differences in replicate gap geometry that affected seasonal patterns (i.e., LGAP2 and SGAP3) also operate on the diurnal scale, causing notable site-to-site variation for comparable plot positions.

There are significant east-west phase shifts for the NW, NE, and C plots in the actual timing of direct beam. The large gap NE plots experience direct beam 2.0-2.5 hours later than the NW plots as the sun moves diurnally. The phase shift for the small gaps is smaller, averaging 1.5-2.0 hours. Since air and soil temperatures increase steadily while vapor pressure declines on clear days, the NW and NE plots will experience different combinations of irradiance, temperature, and relative humidity, which may prove significant in gas-exchange responses. More subtle, but important to the south plots of large gaps, is the fact that diffuse irradiance background levels also show a

diurnal phase shift among plot positions. This is because the relatively brighter portion of the sky emitting diffuse radiation moves with the sun, and even though the south plots may not receive significant direct beam, they are exposed to changing diffuse levels as the day progresses. The result is an east-west diffuse crossover at solar noon similar to the direct beam crossover.

These diurnal arcs change dramatically over the course of the season. For example, all small gap plots receive direct beam only as sunflecks before and after seasonal sun altitude rises above the south canopy edge, which includes the majority of the growing season. Likewise, the large gap centers experience significant direct beam only through late August, unlike the north plots. The overall effect of this interaction between seasonal and diurnal solar movements is multiplicative, stretching the microenvironmental gradient and amplifying the differences among plots even more than they would be in the absence of the seasonal/diurnal interaction.

The seasonal and diurnal diagrams illustrate two important points about solar movement and gap effects in temperate latitudes. First, the potential for significant microenvironmental differences among gap sizes and within individual gaps is greater due to oblique solar altitudes. Put simply, the sun never shines directly on the south sides of gaps with extended duration, and all points along the north-south axis, even in gaps as small as the large gaps used here (16m N-S), therefore exist on a continuum of exposure determined primarily by gap geometry and secondarily by seasonal solar movement. With the exception of increased diffuse radiation levels, the south sides of large gaps are essentially like the understory, whereas the north plots are exposed the entire

growing season. This is not true for equatorial latitudes, where irradiance zones are more concentric, radiating outward from the gap center (Lee 1978, Chazdon 1986; Canham 1988a; Torquebiau 1988).

Second, the oblique solar angles displace the effect of the canopy opening beyond the north edge, since direct beam and enhanced diffuse radiation penetrate well into the understory on the north side. While this may not prove sufficient to support the growth of light-demanding pioneer tree species, its effect on intermediately tolerant, advance-regenerating shade-tolerant, and permanent understory species may be marked (Chazdon 1986; Canham 1988b).

On the basis of seasonal and diurnal variation in direct beam irradiance, the microenvironmental gradient, in terms of site/plot positions, is as follows:

LGNW...LGNE...LGC...SGNW...SGNE...[SGC=LGSW]...[LGSE=SGW=SGSE]

3.5. MICROMETEOROLOGICAL DATA

3.5.1. DIURNAL PATTERNS

Micrometeorological conditions vary with macroclimate so much on a daily basis that it is neither practical nor helpful to present a barrage of graphs from more than a few days. Consequently, it is necessary to select representative days, which is unavoidably subjective. The seasonal micrometeorological summary in Section 3.5.2, will provide some idea of mean conditions on the longer time scale. This section will draw on one clear (6.15.88) and one overcast day (8.25.88) to illustrate a number of points about gap and understory microenvironments. Obviously, the results for two days do not encompass seasonal variations for clear or overcast conditions. The purpose here

is to understand the extremes of gap-understory microclimatic gradient expression. Clear days near solstice maximize gradient breadth by producing the highest irradiance levels and the greatest distinctions among sites and plots, while overcast days minimize gradient breadth.

The graphs in Figures 3-6 through 3-14 include photosynthetic photon flux density (PPFD), air temperature, and surface and deep soil temperature. Throughout this section, the standard for full sun on a horizontal surface on the clearest days near solstice in the study area is 2000 micromol/m²/s. Thus 20 micromol/m²/s is 1% full sun. This level is not reached often, but it serves as a convenient reference point.

Clear day PPFD (Figures 3-6, 3-7) shows striking variability among sites and plots. After variable lengths of diffuse conditions in the morning, irradiance rises sharply to peak values in the north and center plots of large gaps and the north plots of small gaps. PPFD values reach 1650 micromol/m²/s in the large gap and 1550 micromol/m²/s in the small gap at solar noon. Understory levels never exceed 750 micromol/m²/s on the basis of 10-minute means. The rapid increase in direct beam of the exposed gap plots takes place within 10-20 minutes as the sun crests the canopy edge. So there is little acclimation time for seedlings as they go from diffuse background levels of less than 200 to more than 1200 micromol/m²/s.

There are noticeable phase shifts among the north and center plots of large gaps and north plots of small gaps, shifts which are more clearly portrayed in the smoothed curves (n=9) in Figure 3-7. The smoothed traces neatly show how the large gap NW and NE plots are phase-shifted by approximately 2 hours in the morning and about 1 hour in the afternoon, while the center plot is sandwiched between them on both

Figure 3-6. Clear day diurnal patterns of PPF_D for the large gap (A), small gap (B), and large understory site (C) in Block 1 near summer solstice (6.15.88). Each figure shows PPF_D traces for all five plot positions.

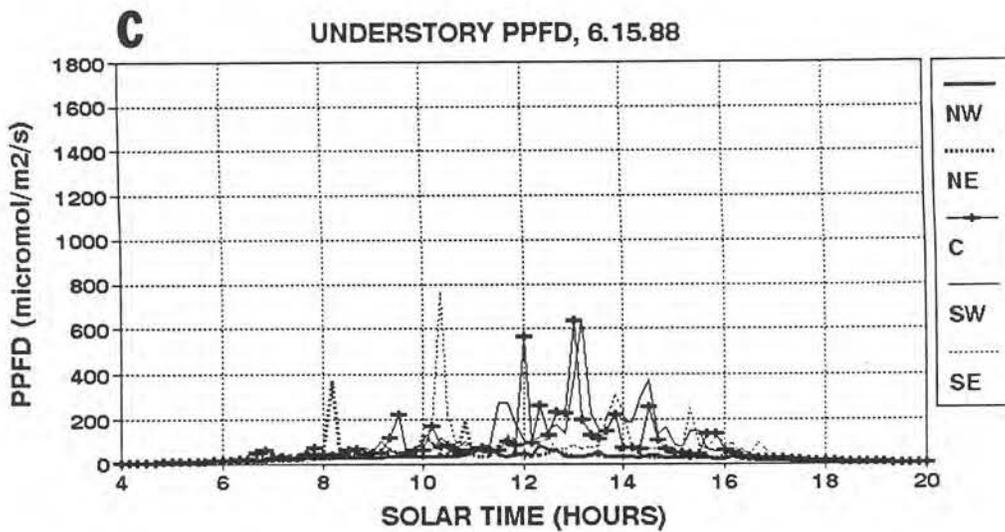
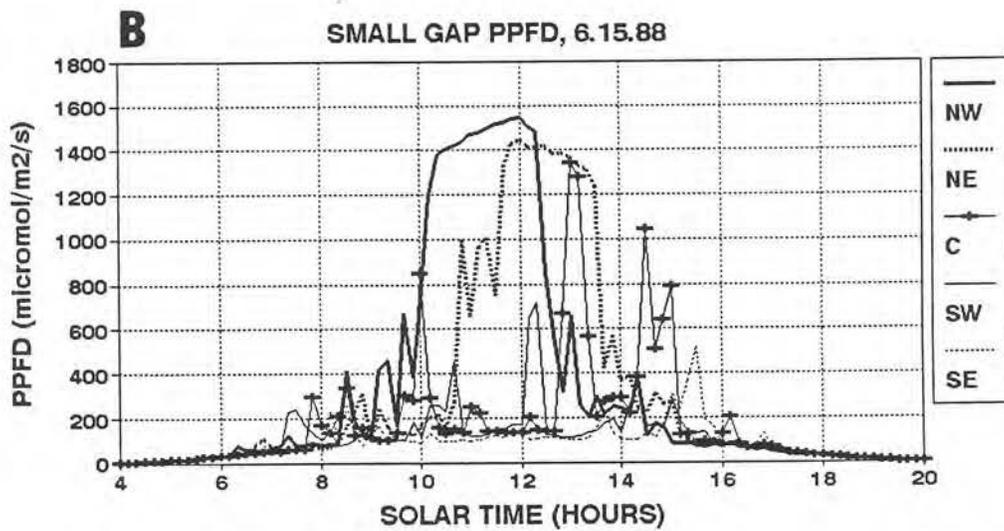
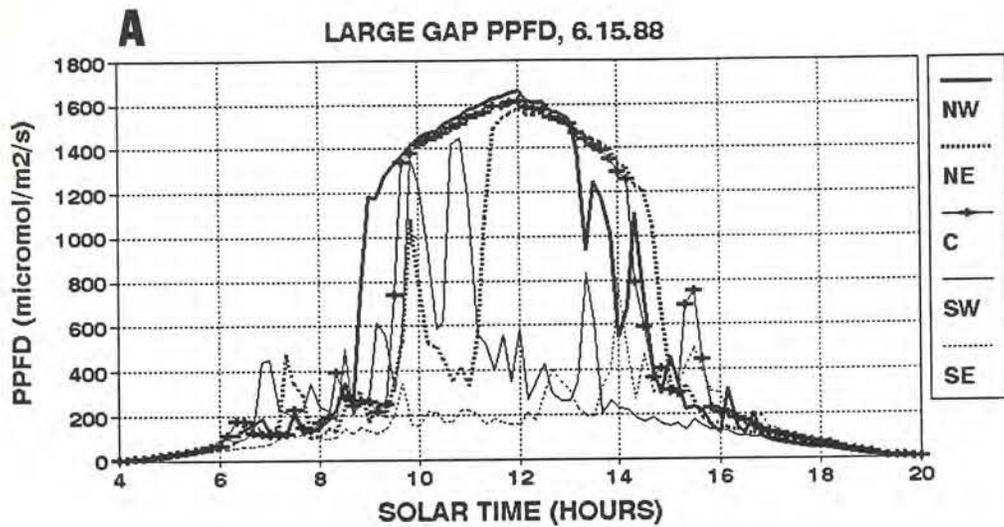
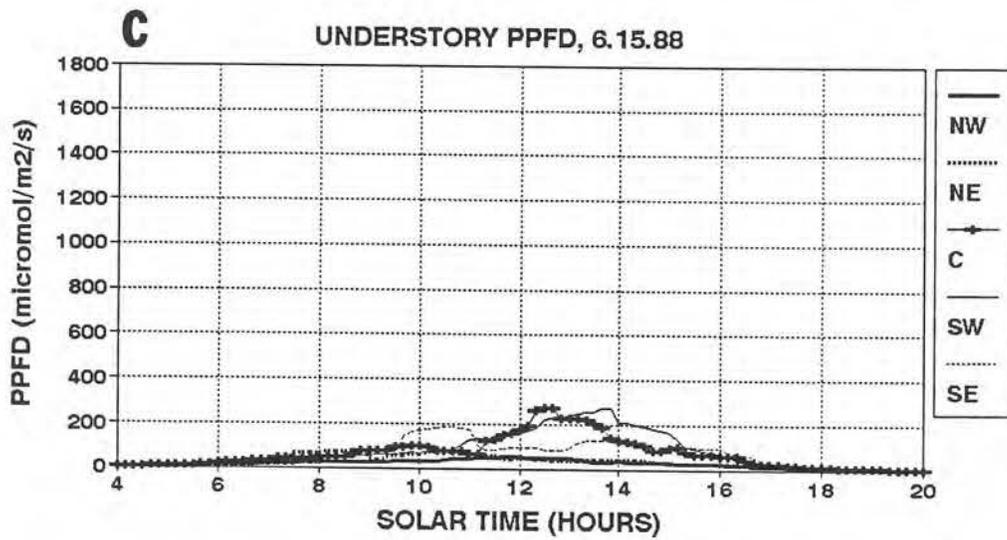
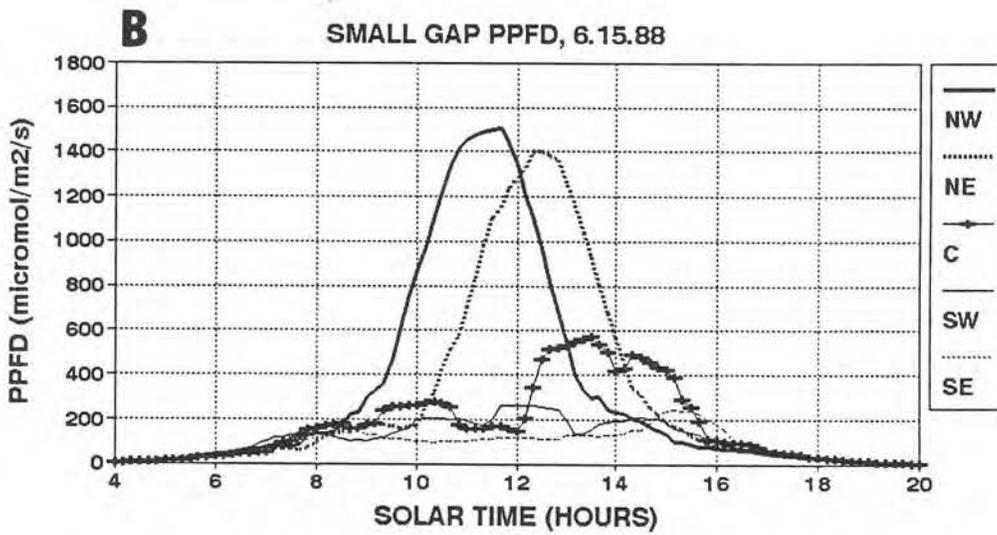
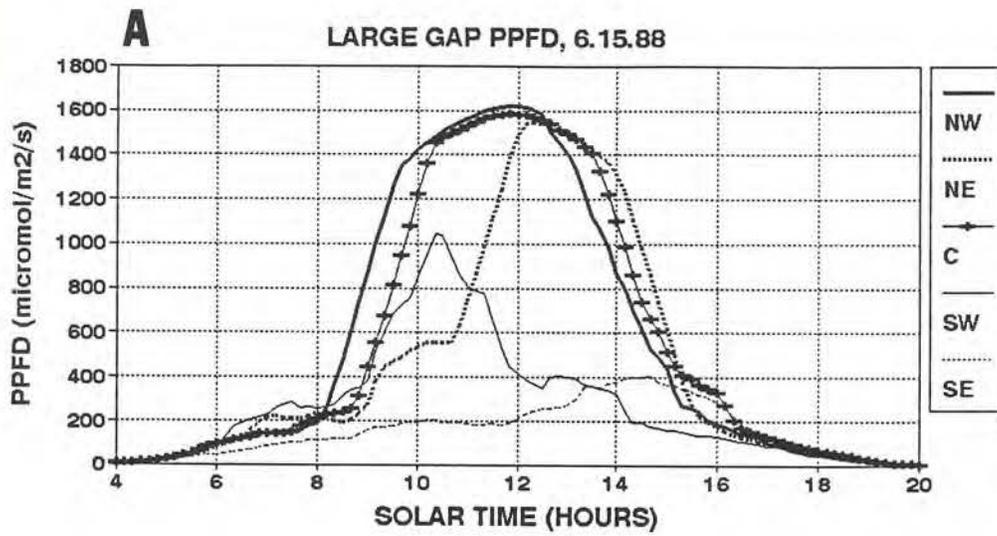


Figure 3-7. Smoothed curves (n=9) for the diurnal traces in Figure 3-6, to clarify the patterns at each plot position, particularly the phase shifts between NW and NE plots.



sides of solar noon. The phase shift between small gap NW and NE plots is very clear.

Two anomalies relative to idealized predictions about diurnal patterns occur on this day that illustrate the importance of even seemingly small variability in gap geometry and the surrounding forest structure. First, the canopy structure of the small gap yields an unusual period of high PPFD for the center plot in the late afternoon. This is probably due to a narrow swath unavoidably cut into the southwest corner of the canopy edge by a falling crown during gap creation. Such swaths, although created experimentally in this case, will occur in natural gaps as well, and may alter spatial radiation patterns considerably, particularly when they occur on the south canopy edge.

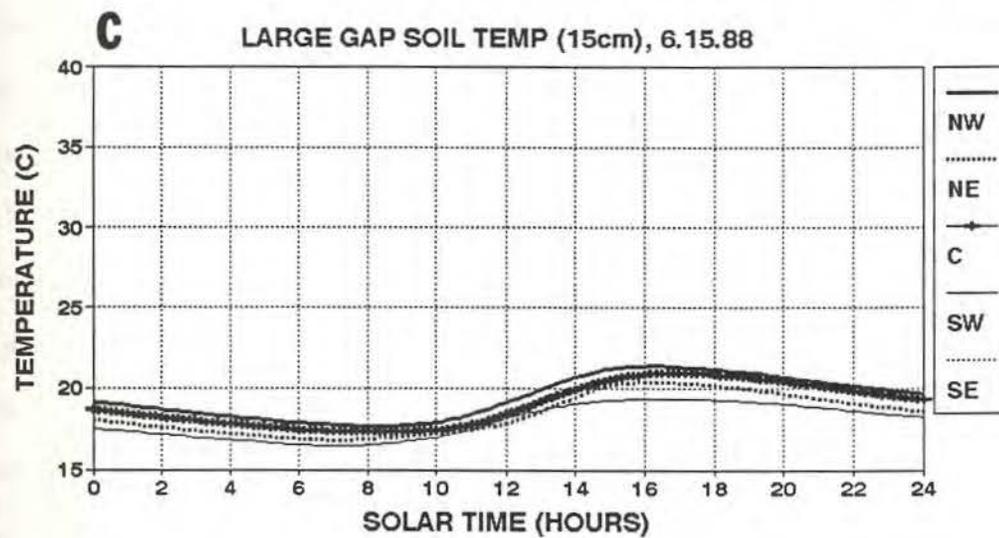
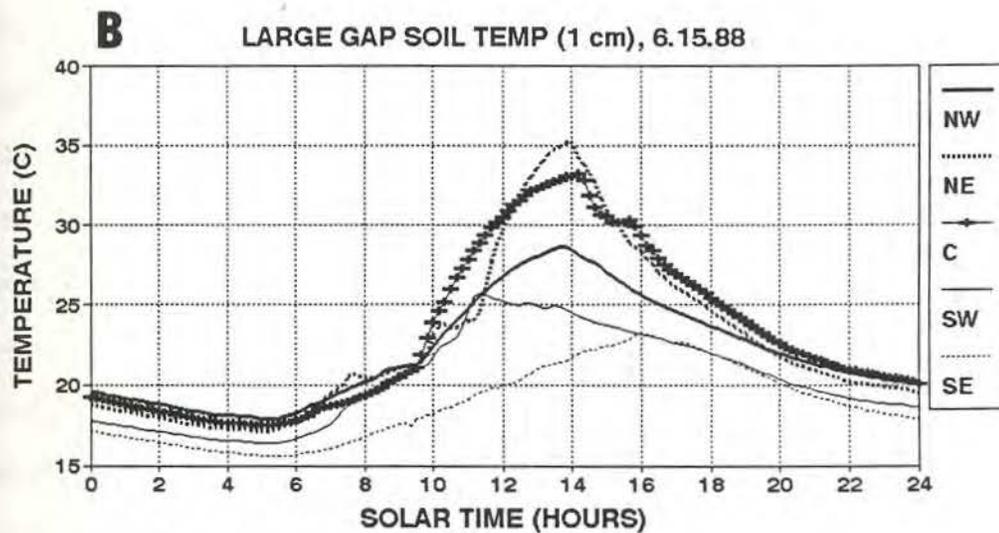
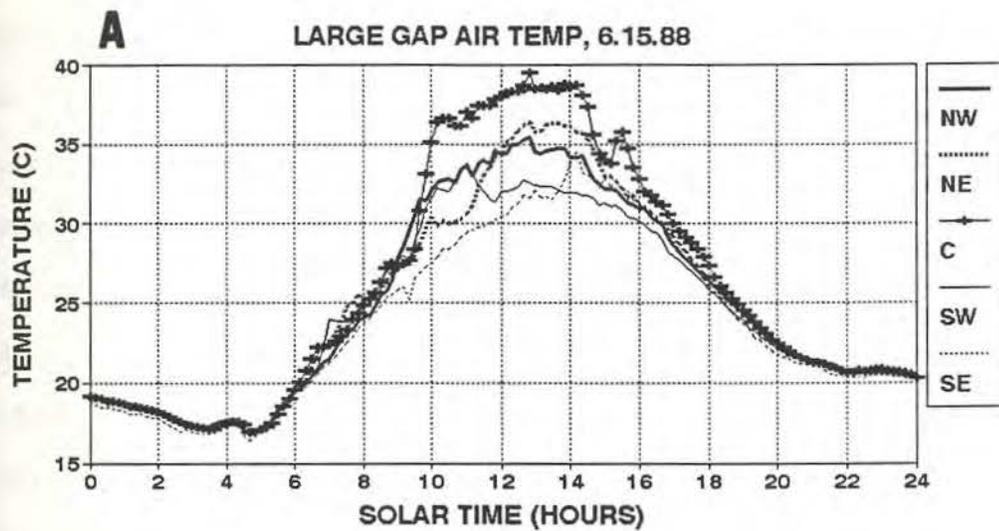
Second, the large gap SW plot shows much higher PPFD than the SE, especially during the period 9:30 to 11:30. Two factors contribute to this. The sun actually rises to the north of true east and sets to the north of true west due to the latitude and the earth's spherical rotation on a tilted axis (Lee 1978). This northward displacement of rising and setting azimuths increases with latitude, and is the least at solstice and the greatest at equinox within any given latitude. Consequently, if the N-S gap width is great enough relative to canopy height, the sun may rise above the eastern edge soon enough (or drop below the western edge late enough) for even the south plots to receive a brief period of direct beam radiation. Then if either the east or west canopy edge is significantly asymmetric with respect to the other side, the SW and SE plots may receive unequal amounts of radiation, as happens in this case.

Due to the greater opening in the canopy and the larger window of sky, diffuse background levels are higher in the large gap (approximately 200-250 micromol/m²/s at midday) than in the small gap (100-150 micromol/m²/s) or the understory (50 micromol/m²/s). Furthermore, as mentioned in Section 3.4., there is an east-west crossover in diffuse irradiance in the large gap not long after solar noon, as the bright region of the sky moves diurnally with the sun. In this large gap, the crossover does not occur at solar noon for the SW and SE plots as it ideally should, possibly due the canopy asymmetry discussed above.

Understory irradiances vary considerably from plot to plot. In this particular site, the north plots receive significantly less light than the remaining three plots. This is due to compositional differences in the overstory across the 13 meters between the north and south plots. The north plots are heavily shaded by several mature and large sapling beech trees, with dense crowns extending nearly to ground level, while the center and south plots are under more open red oak and birch canopy. This kind of variation should not be regarded as anomalous or as experimental error. Such compositional and structural variation occurs in varying degrees throughout the mixed broadleaved forests of eastern North America, even in mature stands, heterogenizing understory light environments. In this case, the result is a three-fold difference in total daily PPFD between the north and south plots, which may have significant impact on understory survival and/or growth.

The large gap temperature profile is shown in Figure 3-8. Air temperatures are greater than soil surface temperatures (1cm), which are in turn greater than deep soil temperatures (15cm), for the entire 24-

Figure 3-8. Diurnal temperature profile for the large gap on the same clear day (6.15.88) portrayed in Figures 3-6 and 3-7. (A) Air temperature (at 25cm), (B) Surface soil temperature (1cm), (C) Deep soil temperature (15cm).



hour period for all plot positions. On average, air temperatures show a greater diurnal range (21°C) than the soil surface (16°C) or deep soil (4°C). All plot positions tend to converge to near equal air temperatures at night (approximately 20°C).

Significant differences occur along the N-S axis among plot positions for air and soil surface temperature, but not for the deep soil. Soil surface shows greater difference among plots (up to 13°C) than air temperature (approximately 9°C), since long-wave reradiation to sky and convective air movement allow greater diffusion of localized heating during the day. For the same reasons, plot differences converge at night for air temperature as reradiation to space and air movement quickly reestablish spatial uniformity. The plot differences in soil surface temperature last longer during the day and don't completely converge at night, possibly due to a number of factors (local heat conduction in the soil profile, litter and vegetative cover, etc.). It is notable that even in the exposed conditions of the large gaps, where the north plots differ so greatly from the south plots in total PPF, soil temperatures at 15cm show remarkable diurnal dampening and do not vary spatially by more than $1-2^{\circ}\text{C}$. The conclusion is that the temperature contribution to the gap-understory gradient is limited primarily to aboveground and surface zones, even for seedlings.

It is interesting that the large gap center plot shows higher air and soil surface temperatures than the NW and NE plots for most of the day. The soil difference may be due to factors such as differential litter cover, although this is unlikely. The reason for greater air temperature may be that, although horizontal and vertical mixing may reduce spatial variation in air temperatures more than soil surface

temperatures, the center plot is surrounded by a substantial area of exposed surface where temperatures are higher than in the understory. Unlike the north plots, which are on the forest edge and may benefit from advective exchange with air masses in the cooler understory, the center plot's ability to dissipate heat may be reduced, especially on a calm day.

The relative shapes of the diurnal air and soil surface curves among plots tend to mirror the traces for PPF_D in some ways. For example, both the north and south plots show an air temperature crossover that corresponds to PPF_D crossover. In other respects, the traces differ substantially from PPF_D patterns. The relative differences among plots (as a percentage of the lowest value) are not as great for air temperature (20% difference at midday for north vs. south plots), soil surface temperature (approximately 60% difference at 2:00pm), or deep soil temperature as they are for PPF_D (400-800% difference at solar noon). Thus in absolute terms the temperature gradient is not as broad as the PPF_D gradient.

Peak air temperatures tend to occur at or shortly after peak PPF_D in all plot positions. This is not true for soil surface temperatures, which peak on average about an hour after air temperatures. Finally, deep soil temperature traces do not mirror PPF_D patterns, and peak values show an even greater lag (3-4 hours) behind peak PPF_D than do soil surface temperatures.

The increased dampening and phase shifts from air to soil surface to deep soil temperatures are a widely recognized phenomenon (Geiger 1965), but they have been observed primarily in quite different systems (typically cultivated agricultural fields). The virtue of the data

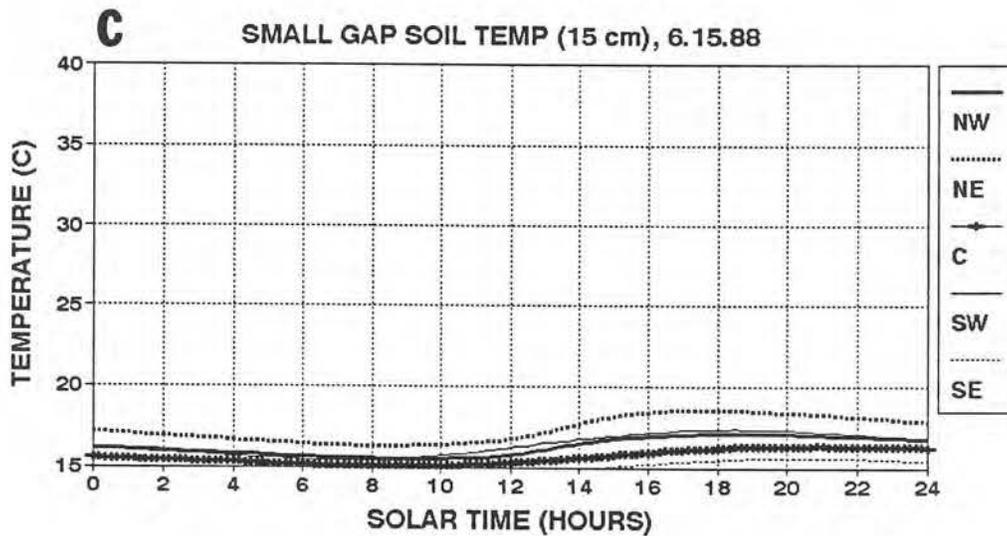
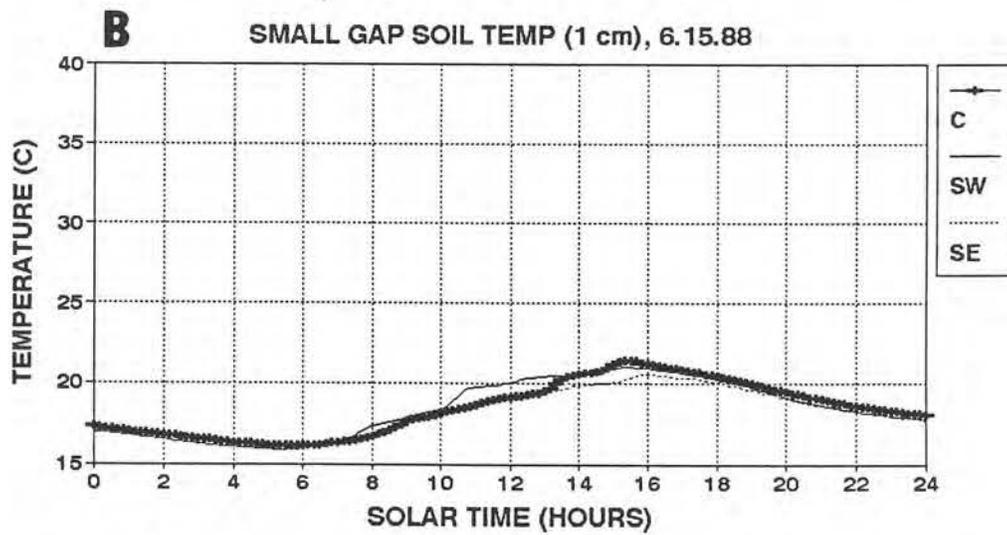
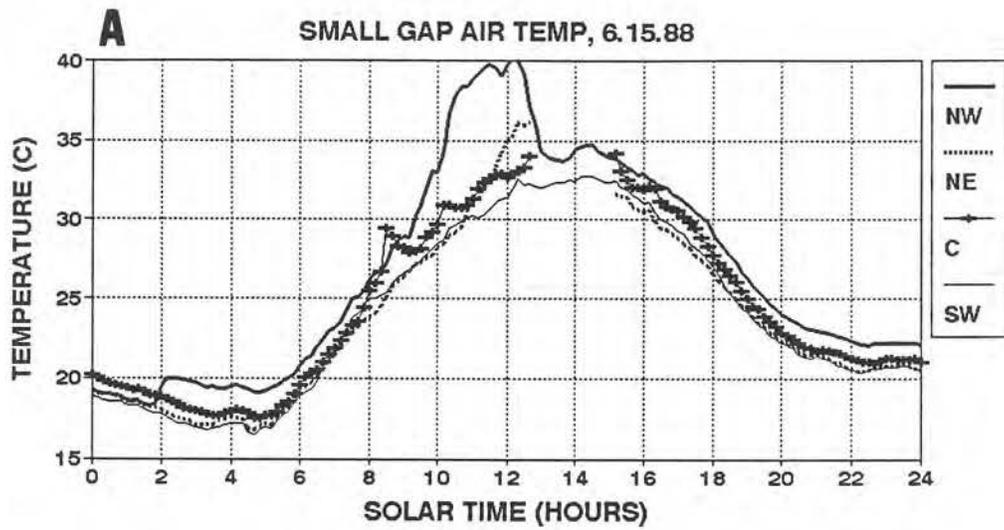
presented here is that no comparable information exists for gap environments in temperate forests.

It is worth noting that both air and soil surface temperatures reach considerable levels on this day (38°C and $33\text{-}35^{\circ}\text{C}$, respectively). These values are above the general physiological optima for the study species. Thus the duration of high temperatures at various plot positions may prove more important to species success than mean daily values. This point will resurface in Section 3.5.3., where it will be shown that mean daily air and soil temperatures do not differ much among sites and plots.

The small gap temperature profile is shown in Figure 3-9. Several points already made for the large gap apply equally to the small gap, so the following discussion will emphasize the contrasts between the two sites. First, air temperatures reach levels in the small gap comparable to that for the large gap, but both surface and deep soil peak temperatures are reduced by several degrees.

Second, as with the large gap, the diurnal range decreases moving downward through the temperature profile (21°C , 6°C , and 1°C , respectively). But the difference between the surface and deep soil ranges is not nearly as great as in the large gap. Also in contrast to the large gap, air temperature is greater than surface soil temperature, which is in turn greater than deep soil temperature, for all plot positions during the entire 24-hour period. Thus there is no 3-dimensional convergence of temperatures comparable to the large gap at night. Since nighttime air temperatures are about the same in the two gap sizes, the difference is due to the small gap soil temperatures, which are lower because of substantially less diffuse and especially

Figure 3-9. Diurnal temperature profile for the small gap on the same clear day (6.15.88) portrayed in Figures 3-6 and 3-7. (A) Air temperature (at 25cm), (B) Surface soil temperature (1cm), (C) Deep soil temperature (15cm).



direct beam radiation.

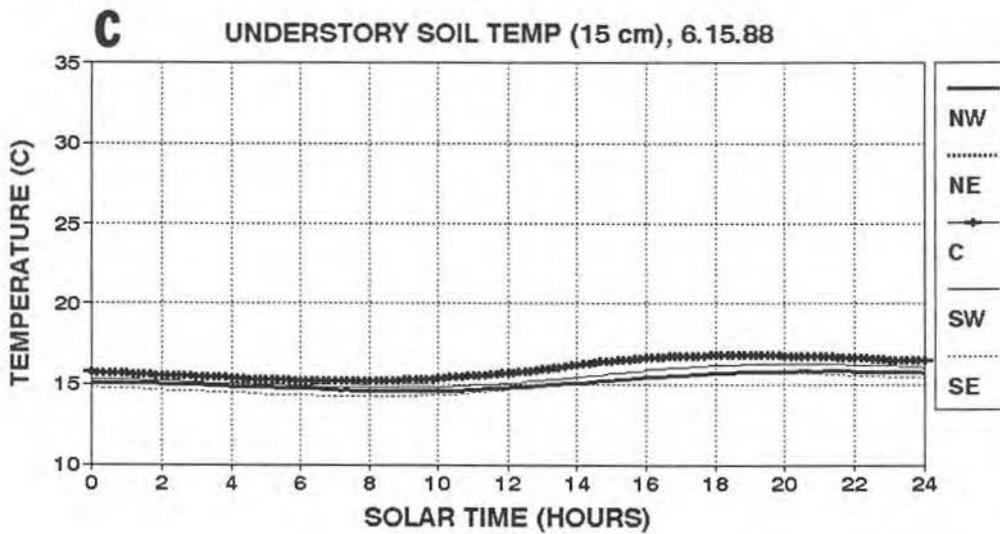
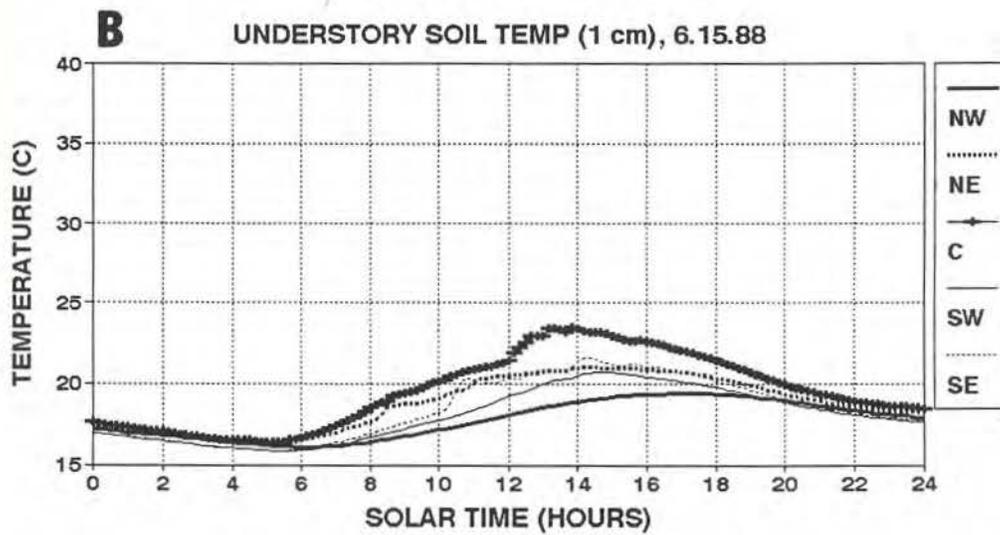
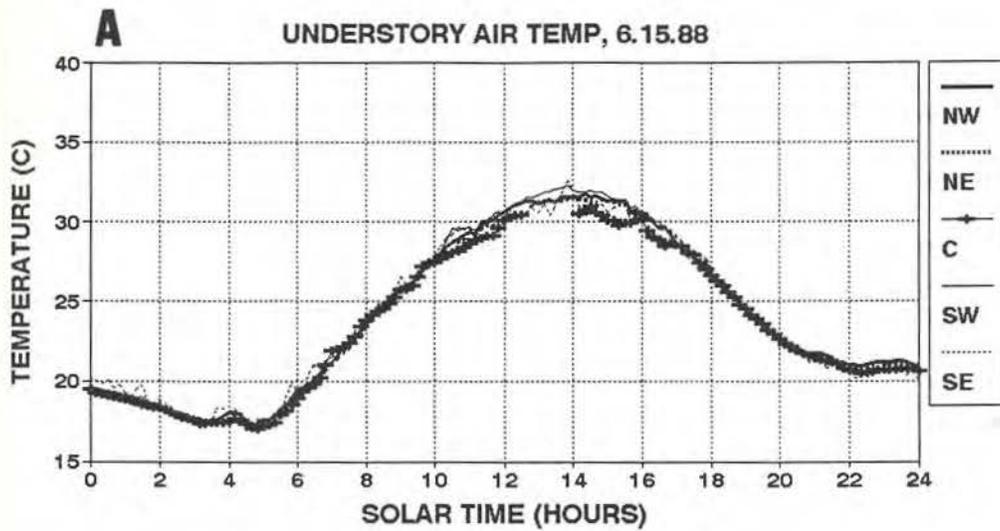
There is a NW to NE phase shift in air temperature that mirrors PPF_D patterns. But since the other three plots receive mostly or only low-level diffuse radiation, their air and soil temperatures are relative uniform.

Large understory temperatures are graphed in Figure 3-10. In most respects, the diurnal profile is similar to that for small gaps, particularly the south side. The diurnal ranges, peak values, and plot-to-plot variation are nearly identical, with the exception of air temperatures on the north side of the small gaps.

The most important point to be gleaned from Figure 3-10 is that the temperature background at all points in the profile is spatially uniform among plot positions. This is true in spite of a three-fold difference in total daily PPF_D between the north and south plots. Apparently, the slightly higher diffuse levels and more frequent sunflecks on the south side do not yield marked differences in temperatures. From other sampling days, we know that relative humidities and windspeeds also do not differ greatly among understory plots. Hence in a generalized fashion, it could be said that on clear days, the physical understory environment is a comparatively uniform backdrop against which the interplay of diffuse and direct beam light availability plays the decisive role in determining species success. This statement includes the south sides of small gaps as well. Note that this applies only to the physical environment, and that spatial variation in other resources (water, nutrients) may frequently override the effects of variable PPF_D.

Unlike the clear day just discussed, all spatial and temporal variations in light and temperature are reduced substantially on

Figure 3-10. Diurnal temperature profile for the understory on the same clear day (6.15.88) portrayed in Figures 3-6 and 3-7. (A) Air temperature (at 25cm), (B) Surface soil temperature (1cm), (C) Deep soil temperature (15cm).



overcast days. In fact, as Figures 3-11 through 3-14 indicate, there are relatively few differences among sites and plots, particularly for temperature.

PPFD values do not differ greatly among plot positions in any of the three sites. Since spatial variation in the understory is dampened even on clear days, the relative increase in uniformity caused by overcast conditions is greater for both gap sizes than for the understory.

Peak PPFD values are only 3-10% of what they are on clear days for all sites and plot positions. There is an overall diurnal increase and fall in the diffuse PPFD values, but all sites and plot positions show parallel rises and falls from one 10-minute sample interval to the next as cloud density varies. The only difference is in the actual diffuse values - 40-120, 20-60, and 10-25 micromol/m²/s for large gaps, small gaps, and understory, respectively. This is due to the difference in the window of exposed sky among sites. In fact, the only noticeable plot position difference is that the centers of both large and small gaps receive consistently higher PPFD than the other four plots. On overcast days such as this, PPFD apparently varies in more of a concentric fashion, with the highest values in the centers, since the perceived window is greater there than on gap edges (Nakashizuka 1985).

The ratio of values across the sites is relative constant with time, at LG:SG:LU = 2:1:0.5. This is approximately the same ratio as the diffuse background levels for the three sites on clear days.

The large gap plots spend most of the day above photosynthetic compensation, defined here as 25 micromol/m²/s for all three study species. But the small gap plots hover near this critical value, and the

Figure 3-11. Overcast day diurnal patterns of PPF_D for the large gap (A), small gap (B), and large understory site (C) in Block 1 on 8.25.88. Each figure shows PPF_D traces for all five plot positions.

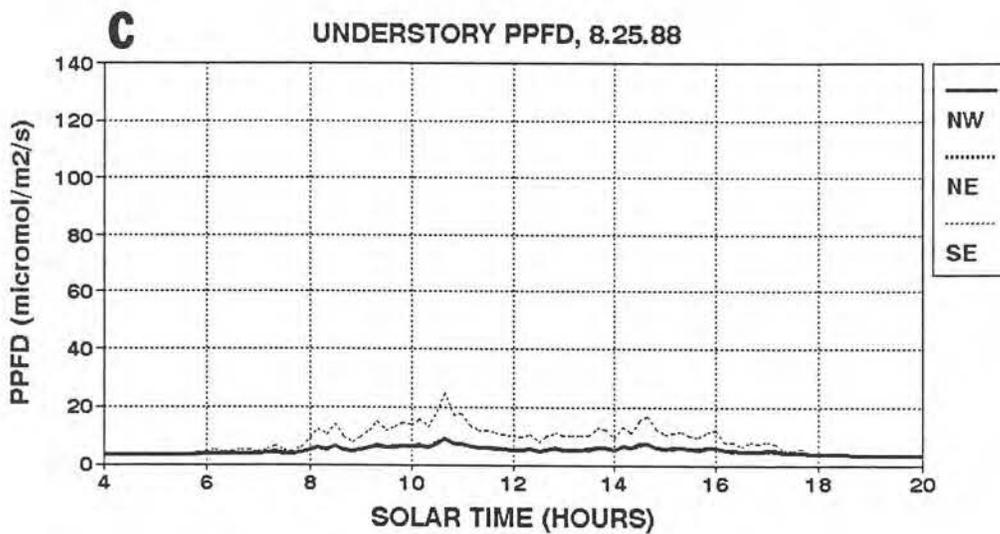
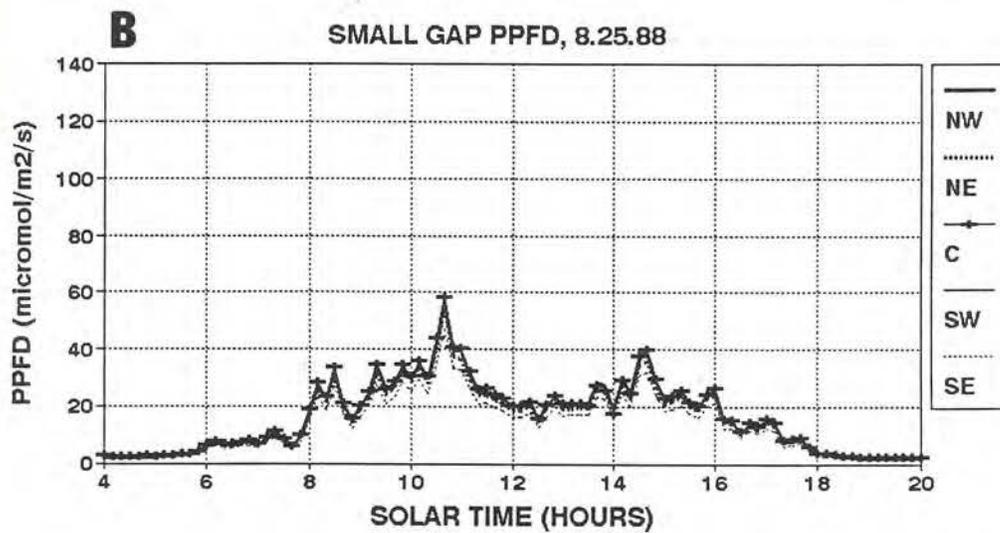
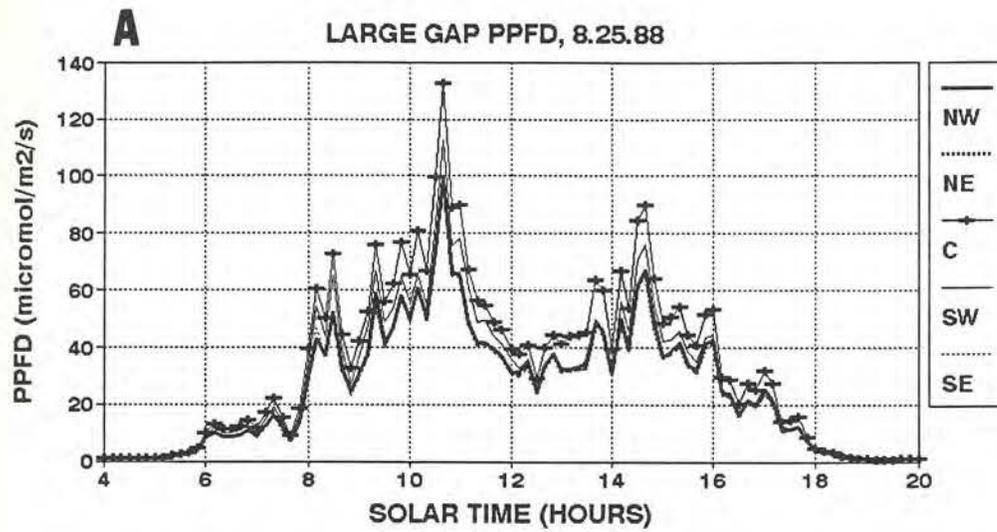


Figure 3-12. Diurnal temperature profile for the large gap on the same overcast day (8.25.88) portrayed in Figure 3-11. (A) Air temperature (at 25cm), (B) Surface soil temperature (1cm), (C) Deep soil temperature (15cm).

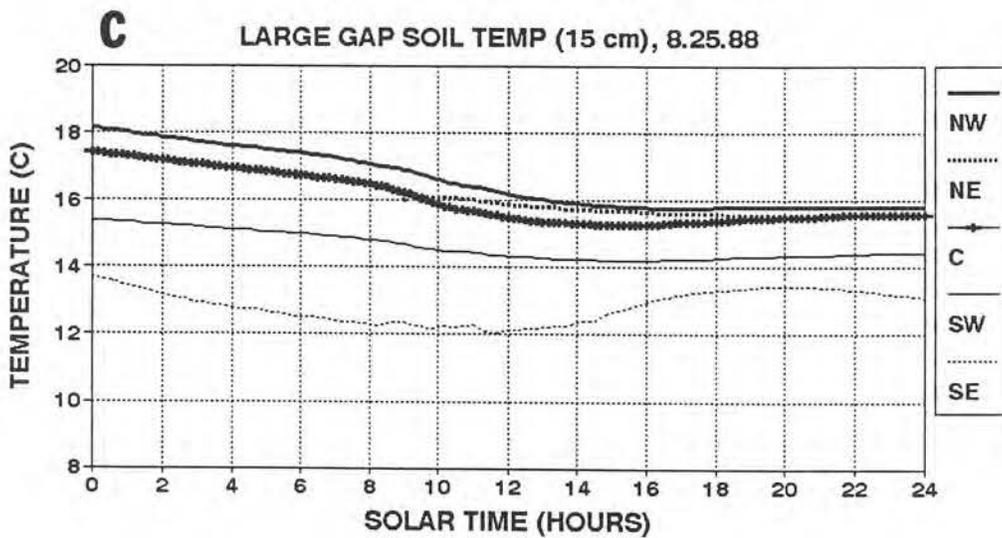
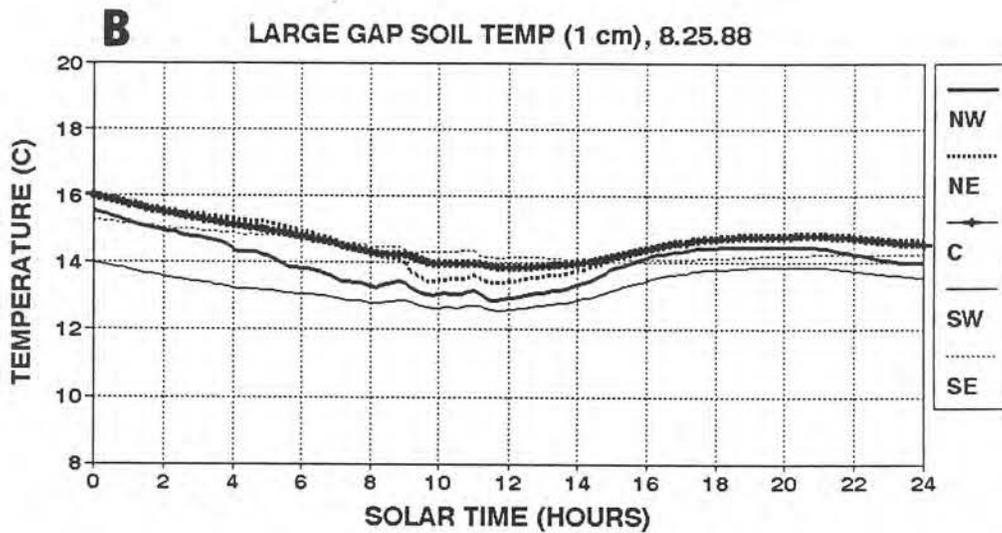
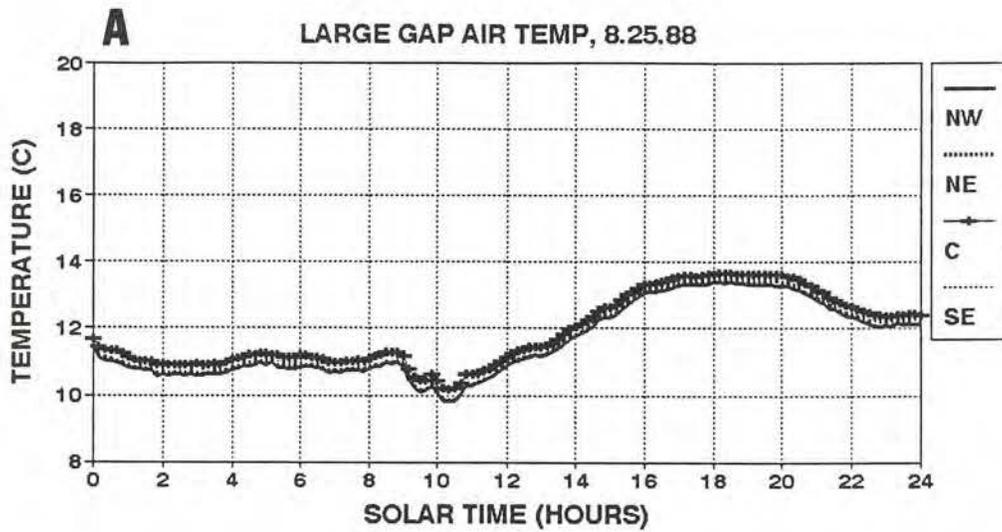


Figure 3-13. Diurnal temperature profile for the small gap on the same overcast day (8.25.88) portrayed in Figure 3-11. (A) Air temperature (at 25cm), (B) Surface soil temperature (1cm), (C) Deep soil temperature (15cm).

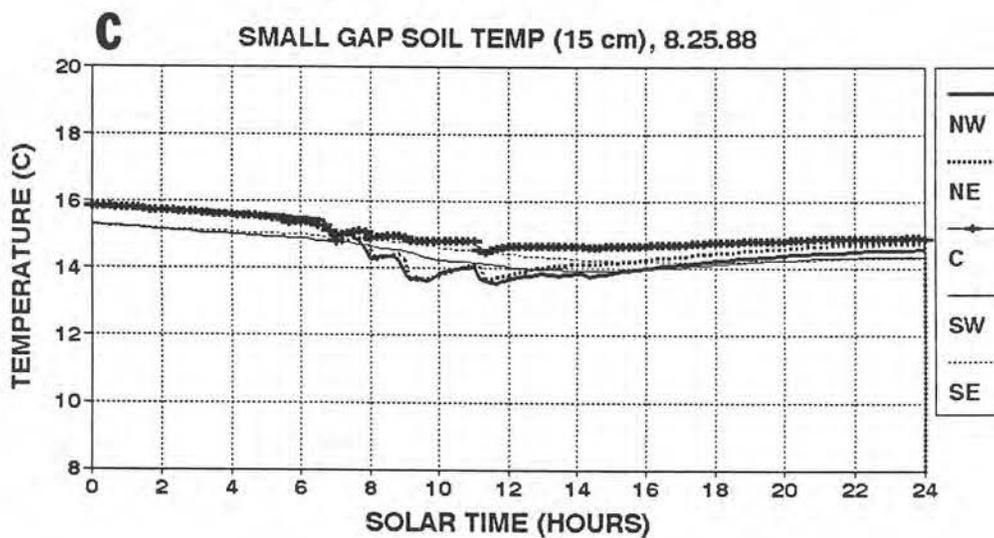
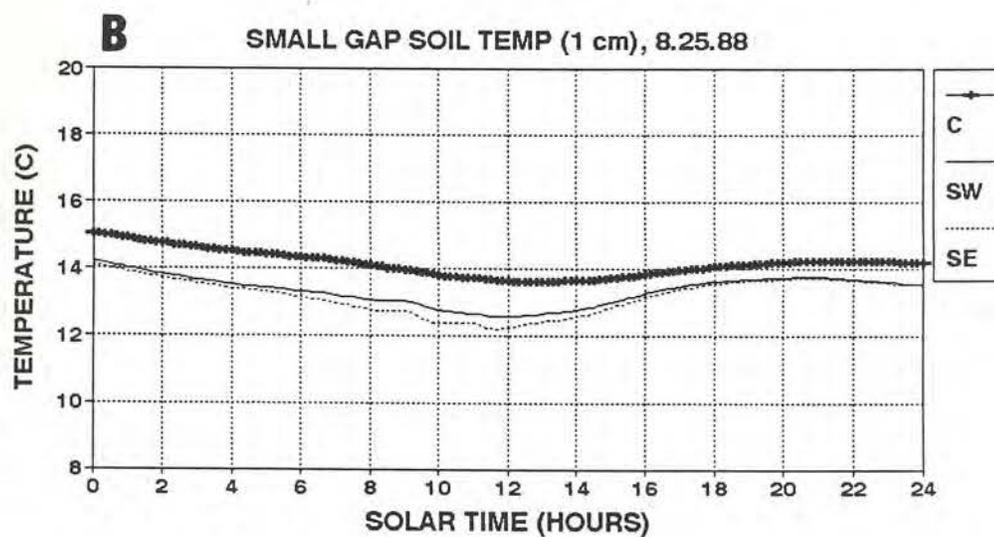
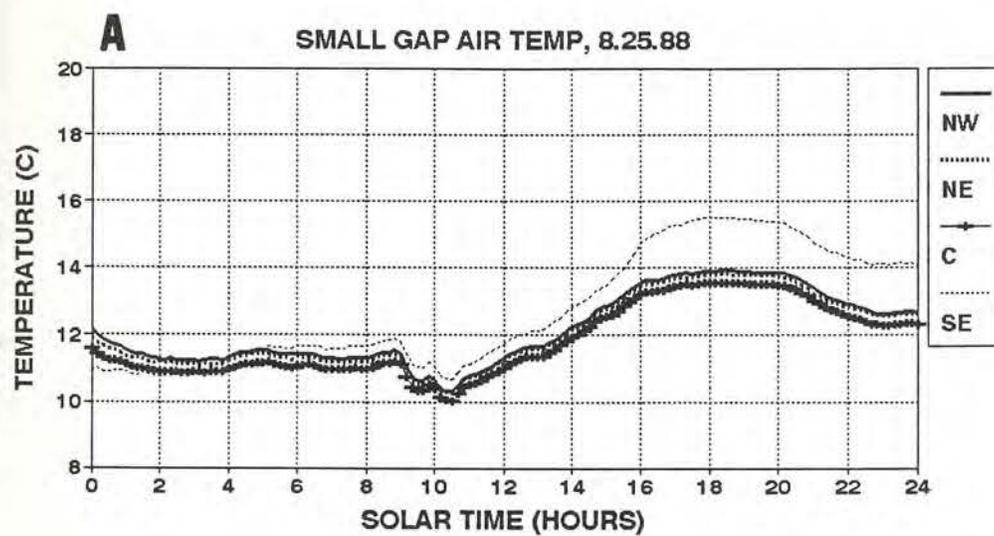
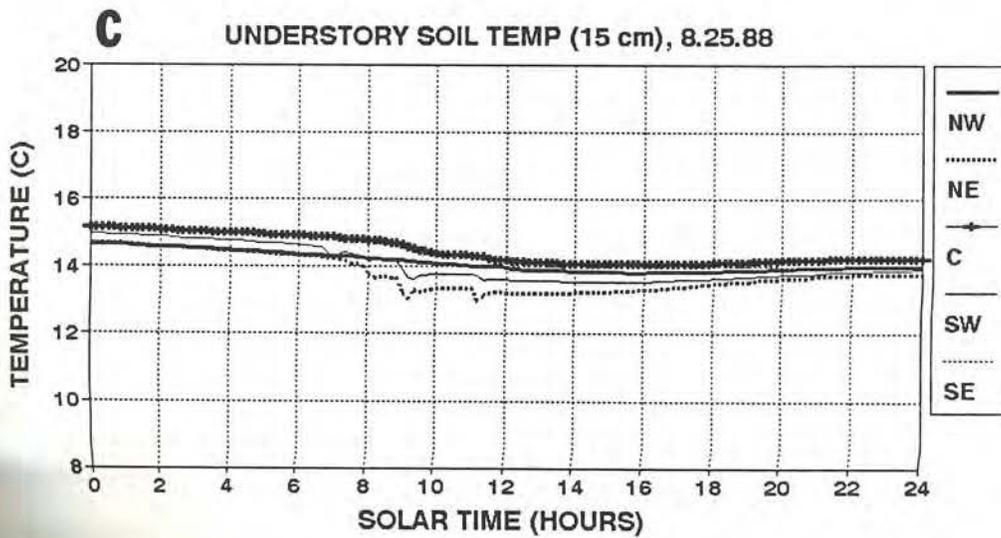
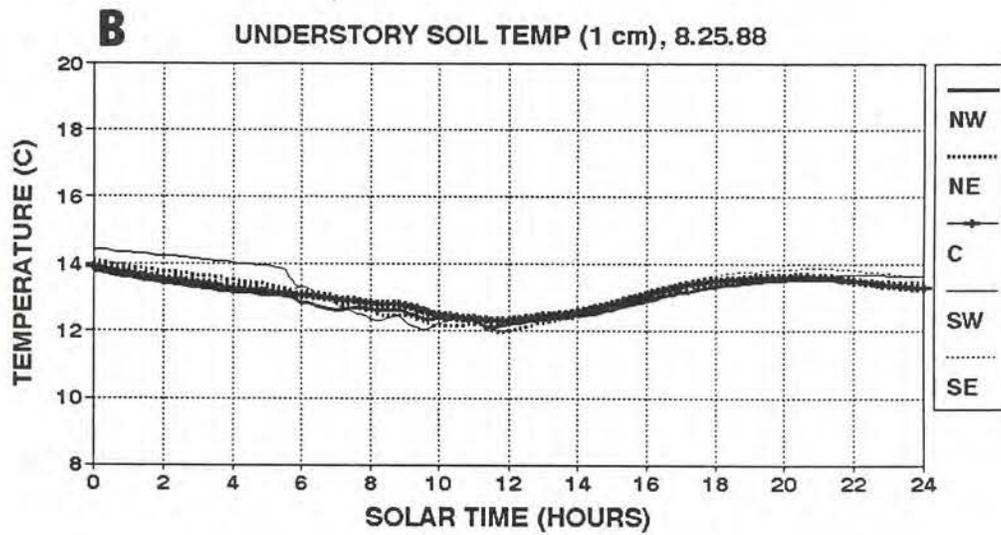
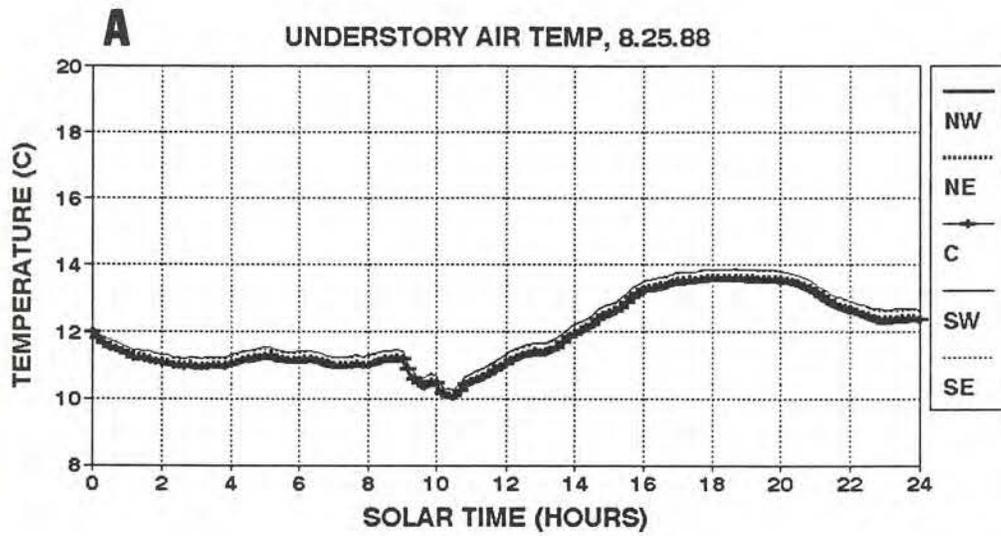


Figure 3-14. Diurnal temperature profile for the understory on the same overcast day (8.25.88) portrayed in Figure 3-11. (A) Air temperature (at 25cm), (B) Surface soil temperature (1cm), (C) Deep soil temperature (15cm).



understory plots are well below this value the entire day. Thus any photosynthetic differences in species success that overcast days may induce will occur in the compensation ($0-25 \text{ micromol/m}^2/\text{s}$) and quantum yield ($25-100 \text{ micromol/m}^2/\text{s}$) portions of light response curves.

There is considerable uniformity across sites and plot positions at all points in the temperature profile, especially for air temperature (Figures 3-12, 3-13, 3-14). Soil surface temperatures show minor differences due to both reduction of incoming radiation by the surrounding canopy and localized soil conditions.

Interestingly, the deep soil temperatures differ more than surface or air. This may be due to lag effects from the previous clear day. If conditions became overcast by midnight, then deep soil temperatures may not have been able to dissipate as completely as air and surface temperatures by the next day. Then, since the absence of direct beam radiation would minimize divergence among plots on the current day, it would appear that the deep soil temperatures were inherently more variable. We know that deep soil temperatures are less variable than air or surface on clear days (Figure 3-10), so this may be the most likely explanation. Supporting evidence comes from the fact that air temperatures are consistently below surface and deep soil temperatures during the entire 24 hours, especially in the large gap.

Alternatively, this sample day may simply represent a relatively cold overcast event, in which case season-long buildup of average temperatures in the soil profile may result in higher soil than air temperatures on such a day. This kind of asynchrony provides a good example of the difficulty of selecting "representative days" from an entire growing season.

It is important to note the scale differences between the clear (15-40°C) versus overcast day (8-20°C) temperature profiles. Had the overcast graphs been plotted on the same scale as the clear, the differences just discussed would have been hardly noticeable. And the overall temperatures are not above physiological optima at any point in the profile. In fact, they may be well below optima for many processes.

The conclusion from overcast data is that the micrometeorological gradient across the large gap, small gap, and understory is compressed considerably on such days, yielding few significant site and plot differences. The most important point is that PPFD values, which vary more than air temperature among sites, are in the critical range near photosynthetic compensation, and thus relative small differences (e.g., $\pm 25-50$ micromol/m²/s) may play an amplified role.

3.5.2. SEASONAL PATTERNS

The results of averaging daily values of light and temperature across the five clear, five overcast, and ten total (clear + overcast) days are shown in Tables 3-4 through 3-6 and Figures 3-15 through 3-22. Many relationships among sites and plot positions just established for diurnal patterns on two illustrative sample days hold across the season, producing supportive conclusions on the microenvironmental gradient. All the graphs presented are broken out by site type and plot position for the three categories of sample days (clear, overcast, combined), so this discussion will begin with differences at the level of the entire study area ("total") and site types.

For clear days mean PPFD is 218 micromol/m²/s, well above the compensation point and on the edge of the optimal range for

photosynthesis, defined here as 200-600 micromol/m²/s. The sites do differ considerably. The large gap mean PPFD (434) is 2.5 times that of the small gap (171) and over eight times as great as the understory (50) (Table 3-4).

Even more dramatic are the differences in compensation PPFD (0-25 micromol/m²/s) duration. The large gap is below compensation for only 26 minutes of the 12-hour day (<4%), the small gap for 138 minutes (19%), and the understory for 394 minutes (55%). This represents a 15-fold difference between the understory and large gap. The divergence is just as impressive for superoptimal PPFD (>800) duration, where the large gap is 147 minutes (20%), the small gap 41 minutes (6%), and the understory essentially 0. The important point here is that mean daily PPFD alone does not provide comprehensive information about site differences, and especially on low and high portions of the photosynthetic light response curve that are crucial to seedling performance.

Surprisingly, mean daily air temperatures differ among sites by no more than 1.5°C, in spite of the fact that air temperatures show vastly different diurnal patterns (Section 3.5.1.). As with PPFD, the durations of air temperatures above physiological optimum (25°C) describe the site differences more accurately. Large gap duration (287 minutes, 40%) is almost twice that of small gaps (155 minutes, 22%) and over twice that of the understory (128 minutes, 18%).

Also in keeping with the diurnal interpretation is the fact that mean daily soil surface and deep temperatures show greater differences than air temperatures at the site level. Large gap surface temperatures are 6.3°C (35%) higher than small gaps and 7.3°C (42%) higher than the understory. Deep soil temperatures differ by 3.2-3.5°C. Overall, the

Table 3-4. Average clear day micrometeorological conditions across the season: [min] = number of minutes, from a total of 720 (12-hour day).

SITE	PLOT	PPFD TOTAL [mol/m ² /S]	PPFD MEAN [mmol/m ² /s]	PPFD 0-25 [min]	PPFD 200-600 [min]	PPFD >800 [min]	TAIR MEAN	TAIR >25 C [min]	TSOIL 1 cm MEAN	TSOIL 15 cm MEAN
MEANS										
	TOTAL	9.42	218	186	84	63	22.37	195	19.51	16.92
	LGAP	18.73	434	26	154	147	23.68	287	24.43	19.16
	SGAP	7.38	171	138	65	41	22.22	155	18.16	15.93
	UND	2.16	50	394	33	1	21.22	128	17.17	15.66
LGAP	C	24.39	565	8	166	216	24.75	314	25.19	20.31
	NE	23.79	551	32	162	204	24.55	330	23.70	18.05
	NW	29.02	672	24	118	270	24.88	352	24.64	19.15
	SE	6.29	146	42	132	4	21.94	214	22.74	18.05
	SW	10.17	235	24	194	42	22.30	224	24.11	20.25
SGAP	C	6.24	144	74	92	16	22.39	157	19.14	15.88
	NE	11.53	267	164	66	86	22.88	163	19.33	16.61
	NW	12.67	293	106	80	100	22.84	180	19.42	16.26
	SE	3.14	73	156	32	2	21.52	133	15.50	15.27
	SW	3.28	76	188	54	0	21.46	143	17.05	15.63
UND	C	2.72	63	266	36	2	21.15	138	21.37	15.55
	NE	0.95	22	592	8	0	21.21	116	17.63	15.66
	NW	0.91	21	576	4	0	20.89	112	16.52	15.23
	SE	3.16	73	258	60	2	21.47	138	16.14	16.21
	SW	3.08	71	276	58	2	21.40	134	16.31	15.66
STDERRS										
	TOTAL	0.13	3.1	3.0	1.1	1.3	0.05	2.5	0.09	0.04
	LGAP	0.42	9.8	1.8	3.2	4.7	0.14	6.0	0.22	0.14
	SGAP	0.25	5.7	6.6	2.4	2.3	0.14	10.2	0.15	0.10
	UND	0.08	2.0	9.3	2.3	0.1	0.11	5.5	0.20	0.10
LGAP	C	1.88	43.4	2.2	9.8	19.0	0.82	33.1	0.42	0.87
	NE	0.95	22.0	10.4	9.7	5.8	0.62	20.4		0.65
	NW	1.33	30.9	8.7	8.9	12.1	0.69	21.2		0.68
	SE	0.58	13.4	13.1	23.0	1.1	0.65	29.9		0.62
	SW	0.97	22.3	8.7	24.5	6.1	0.80	42.0	0.84	0.84
SGAP	C	0.66	15.3	16.8	14.8	3.0	0.78	55.2	1.05	0.58
	NE	1.52	35.1	39.7	9.4	12.0	0.79	47.2	0.65	0.58
	NW	1.43	33.0	25.0	9.3	13.6	0.78	60.0	0.70	0.55
	SE	0.31	7.2	20.8	7.3	0.9	0.68	63.1	0.46	0.55
	SW	0.50	11.7	56.5	17.8	0.0	0.75	71.5	0.67	0.55
UND	C	2.04	25.6	44.6	10.2	9.6	2.40	22.0		2.08
	NE	0.20	4.6	39.9	3.6	0.0	0.59	27.6	0.74	0.57
	NW	0.15	3.5	48.8	1.8	0.0	0.61	29.8	0.68	0.58
	SE	0.51	11.7	29.0	16.9	0.9	0.61	33.4		0.58
	SW	0.53	12.2	30.0	16.0	0.9	0.59	29.0	0.61	0.56

small gap and understory temperature profiles are much more like each other than either is to the large gap. Also worth noting is the fact that soil temperatures exceed air temperatures only in the large gap, and are significantly lower (4°C) than air temperatures in both small gap and understory.

As expected, these patterns are quite different on overcast days (Table 3-5). Total mean daily PPF_D is only 69 micromol/m²/s, in the region where the three species do not differ greatly in net photosynthesis across sites (discussed in Chapter 5). This value is only 32% of that for clear day mean PPF_D. Among the sites, the large gap is well above compensation but also well below optimal irradiances. The small gap is in the initial linear portion of the light response curve (25-100 micromol/m²/s; the apparent quantum yield region) and the understory is below compensation. Again, the durations of suboptimal PPF_D enforce the site differences more than just mean daily PPF_D. The large gap is below compensation for only 39 minutes (5%) of the 12-hour period, while the small gap is at 177 minutes (25%) and the understory is 570 minutes (79%).

An unexpected result is that the ratios among the three site types are approximately the same on clear and overcast days for both mean daily PPF_D and suboptimal PPF_D duration. For example, mean PPF_D ratios for LGAP:SGAP, SGAP:LUND, and LGAP:LUND are 2.5, 3.4, and 8.7 on clear days and 2.5, 3.2, and 7.9 on overcast days. Likewise, the suboptimal PPF_D duration ratios are 5.3, 2.9, and 15.2 on clear days and 4.5, 3.2, and 14.6 overcast days. This crucial fact means that site differences defined by mean PPF_D and suboptimal PPF_D are maintained across different cloud conditions not only in absolute terms, but in relative terms as

Table 3-5. Average overcast day micrometeorological conditions across the season: [min] = number of minutes, from a total of 720 (12-hour day).

SITE	PLOT	PPFD TOTAL [mol/m ² /S]	PPFD MEAN [mmol/m ² /s]	PPFD 0-25 [min]	PPFD 200-600 [min]	PPFD >800 [min]	TAIR MEAN	TAIR >25 C [min]	TSOIL 1 cm MEAN	TSOIL 15 cm MEAN
MEANS										
	TOTAL	2.98	69	262	43	1	20.05	171	18.55	17.41
	LGAP	5.85	135	39	128	2	20.68	198	20.46	18.49
	SGAP	2.35	54	177	0	0	19.84	172	17.97	17.02
	UND	0.73	17	570	0	0	19.62	143	16.72	16.72
LGAP	C	7.13	165	30	186	4	21.22	198	20.45	20.52
	NE	5.84	135	32	128	2	20.55	196	20.83	18.15
	NW	6.18	143	24	134	2	20.45	202	21.68	18.70
	SE	4.57	106	66	64	0	20.96	200	20.33	16.35
	SW	5.52	128	42	130	0	20.24	196	19.76	18.71
SGAP	C	2.89	67	116	0	0	19.79	174	18.23	17.05
	NE	1.94	45	190	0	0	19.63	120	18.87	17.32
	NW	2.25	52	214	0	0	20.29	192	18.07	17.32
	SE	2.00	46	246	0	0	19.59	186	16.46	16.63
	SW	2.67	62	118	0	0	19.90	190	17.91	16.81
UND	C	0.90	21	498	0	0	19.29	140	19.08	16.83
	NE	0.32	7	700	0	0	19.54	78	16.73	16.24
	NW	0.46	11	682	0	0	19.94	140	14.04	15.74
	SE	1.00	23	482	0	0	19.58	180		17.20
	SW	0.98	23	486	0	0	19.75	176	16.93	17.60
STDERRS										
	TOTAL	0.03	0.8	3.4	1.3	0.0	0.07	3.0	0.10	0.04
	LGAP	0.10	2.3	1.3	5.1	0.2	0.21	9.9	0.24	0.14
	SGAP	0.03	0.7	4.8	0.0	0.0	0.20	9.0	0.23	0.11
	UND	0.02	0.3	6.1	0.0	0.0	0.20	7.9	0.40	0.11
LGAP	C	0.73	16.9	6.6	32.2	1.8	1.00	54.3	0.99	0.79
	NE	0.39	9.1	6.7	22.0	0.9	1.25	53.7		0.75
	NW	0.63	14.5	4.6	32.4	0.9	1.23	55.4		0.66
	SE	0.23	5.4	8.2	15.2	0.0	0.97	54.9		0.61
	SW	0.40	9.3	6.4	26.0	0.0	1.19	53.8	1.06	0.74
SGAP	C	0.14	3.3	18.6	0.0	0.0	1.10	48.1	1.85	0.60
	NE	0.10	2.3	30.2	0.0	0.0	0.91	35.2	1.11	0.59
	NW	0.15	3.5	27.9	0.0	0.0	1.16	53.8	1.18	0.58
	SE	0.11	2.6	23.0	0.0	0.0	1.18	52.3	1.52	0.58
	SW	0.18	4.1	16.0	0.0	0.0	1.21	53.7	1.16	0.59
UND	C	1.86	7.2	55.4	0.0	0.0	2.30	25.6		2.12
	NE	0.02	0.6	8.9	0.0	0.0	0.89	34.9	1.66	0.52
	NW	0.03	0.7	14.9	0.0	0.0	1.06	39.0	1.76	0.52
	SE	0.07	1.6	32.2	0.0	0.0	1.16	49.5		0.59
	SW	0.06	1.4	29.7	0.0	0.0	1.16	48.5	1.74	0.63

well. So the light gradient shrinks on overcast days, but proportionally, such that sites retain their comparative differences.

Overcast temperature differences among sites are not as marked as PPF. On average, the soil temperatures are lower than air temperatures, but by smaller differences than on clear days. The small gap and understory profiles are very similar. Large gaps still tend to have a greater duration of air temperature above 25°C, but the maximum difference among sites, between large gap and understory, is only 38%.

Unlike PPF, the ratios among sites for temperature variables are not maintained as well across clear and overcast days. Mean daily air temperature ratios are fairly comparable, but the ratios for durations above 25°C are not. So the high temperature contribution to the complex gradient is not constant across different cloud conditions.

The results for combined days logically tend to be intermediate between clear and overcast values (Table 3-6). In terms of mean daily PPF, the large gaps are in the optimal range (285 micromol/m²/s), the small gaps are in the quantum yield region (113) and the understory is slightly above compensation (33). The divergence among sites is made quite clear in the data for compensation, optimal, and superoptimal PPF durations. The large gaps spend 4% of the day in the compensation range and 11% in the superoptimal range. Comparative data are 22% and 3% for the small gaps and 67% and 0% for the understory.

Temperature differences among sites are ≤1.2°C for air, ≤5.3°C for soil surface, and ≤2.6°C for deep soil. Again, the small gap and understory profiles are very similar and both are different from the large gap.

In summary, the microenvironmental gradient does exist at the site

Table 3-6. Average combined day (clear + overcast) micrometeorological conditions across the season: [min] = number of minutes, from a total of 720 (12-hour day).

SITE	PLOT	PPFD TOTAL [mol/m ² /s]	PPFD MEAN [mmol/m ² /s]	PPFD 0-25 [min]	PPFD 200-600 [min]	PPFD >800 [min]	TAIR MEAN	TAIR >25 C [min]	TSOIL 1 cm MEAN	TSOIL 15 cm MEAN
MEANS										
	TOTAL	6.20	144	224	63	32	21.2	182	19.1	17.2
	LGAP	12.29	285	32	141	74	22.2	243	22.3	18.8
	SGAP	4.86	113	157	32	20	21.0	166	18.1	16.5
	UND	1.45	33	482	17	1	20.4	135	17.0	16.2
LGAP	C	15.76	365	19	176	110	23.0	256	22.8	20.4
	NE	14.82	343	32	145	103	22.6	263	21.8	18.1
	NW	17.60	407	24	126	136	22.7	277	22.7	18.9
	SE	5.43	126	54	98	2	21.4	207	21.1	17.2
	SW	7.85	182	33	162	21	21.3	210	22.2	19.5
SGAP	C	4.56	106	95	46	8	21.1	168	18.8	16.5
	NE	6.74	156	177	33	43	21.3	136	19.1	17.0
	NW	7.46	173	160	40	50	21.6	188	18.8	16.8
	SE	2.57	60	201	16	1	20.6	166	15.9	15.9
	SW	2.98	69	153	27	0	20.7	173	17.4	16.2
UND	C	1.81	42	382	18	1	20.2	139	19.8	16.2
	NE	0.63	15	646	4	0	20.4	97	17.3	15.9
	NW	0.68	16	629	2	0	20.4	126	15.5	15.5
	SE	2.08	48	370	30	1	20.5	159	16.1	16.7
	SW	2.03	47	381	29	1	20.6	155	16.6	16.6
STDERRS										
	TOTAL	0.65	15.0	19.8	7.5	6.1	0.36	16.6	0.44	0.26
	LGAP	1.04	24.1	34.3	12.9	9.9	0.63	27.8	0.79	0.45
	SGAP	1.02	23.6	34.3	12.9	9.5	0.62	31.0	0.65	0.44
	UND	1.01	23.3	34.3	12.8	9.3	0.67	27.7	0.92	0.48
LGAP	C	3.57	82.7	8.2	35.6	40.7	1.48	69.7	1.38	1.24
	NE	3.18	73.7	13.1	26.0	34.2	1.61	64.5	1.24	1.05
	NW	4.11	95.2	10.3	35.5	46.5	1.66	67.3	1.24	1.00
	SE	0.72	16.6	16.8	31.2	1.3	1.24	65.9	1.55	0.96
	SW	1.35	31.2	11.7	39.2	9.5	1.55	72.1	1.52	1.20
SGAP	C	0.91	21.0	27.3	21.9	4.2	1.49	71.5	1.66	0.90
	NE	2.26	52.4	52.8	14.8	19.2	1.38	54.7	1.19	0.88
	NW	2.30	53.3	43.4	16.5	22.0	1.54	79.5	1.29	0.86
	SE	0.40	9.2	35.9	9.3	1.0	1.47	79.1	1.12	0.87
	SW	0.57	13.2	63.0	20.8	0.0	1.52	82.9	1.24	0.87
UND	C	0.59	13.6	63.0	12.9	1.0	1.39	51.4	1.05	0.90
	NE	0.24	5.5	46.7	4.0	0.0	1.16	47.3	1.37	0.82
	NW	0.18	4.1	56.6	2.0	0.0	1.30	51.9	1.19	0.83
	SE	0.65	15.0	59.0	20.4	1.0	1.42	63.3	1.32	0.89
	SW	0.66	15.2	56.6	19.4	1.0	1.40	60.0	1.32	0.95

level. It is most pronounced on clear days, when temperature differences are greater and superoptimal PPF_D, implying heavy radiation loads and likely thermal stress, may play a significant role. However, the influence of overcast days may be considerable, depending on the physiological responses of the study species.

It is now important to consider the microenvironmental gradient at the finer resolution of plots positions within sites. Tables 3-4 through 3-6 provide the mean values while Figures 3-15 through 3-22 graph the results.

The patterns for total daily PPF_D and mean daily PPF_D are the same, since they differ only by a constant scaling factor. For large gap plots, there is a five-fold difference in mean PPF_D on clear days, but only 10-20% difference on overcast days (Figure 3-16). Small gap plots differ by a smaller degree, while understory plots differ noticeably only on clear days. This is in absolute terms, however, and it is worth noting that the understory plots do differ from each other by up to three-fold. Figure 3-16 clearly shows a continuous gradient in mean PPF_D across the three site types on both clear and combined days. The gradient is dampened, though still present, on overcast days.

Mean PPF_D exceeds 30% full sun ($600 \text{ micromol/m}^2/\text{s}$) for only the large gap NW plot on clear days. The range across all plots is 1-34% full sun on clear days, 0.4-8.0% on overcast days, and 1-20% on combined days. These data provide striking evidence that experimental glasshouse or garden growth treatments subjecting tree seedlings to more than 50% full sun all day are not applicable to the vast majority of real natural gaps.

The gradient across the large gap on clear and combined days is not

Figure 3-15. Total daily photosynthetic photon flux (PPFD) by site and plot position for clear (A), overcast (B), and combined (C) sample days across the 1988 season. The totals are based on a 12-hour sample period symmetric around solar noon.

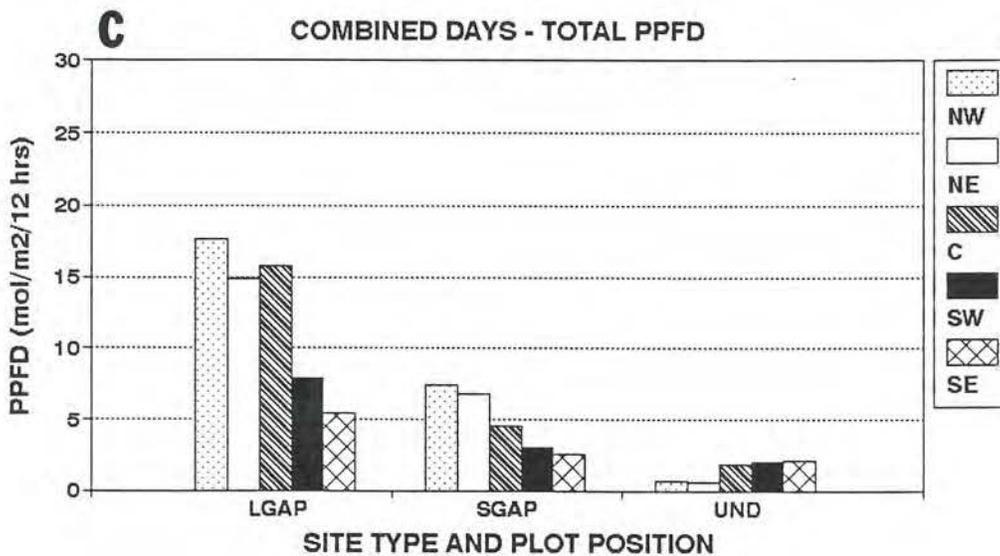
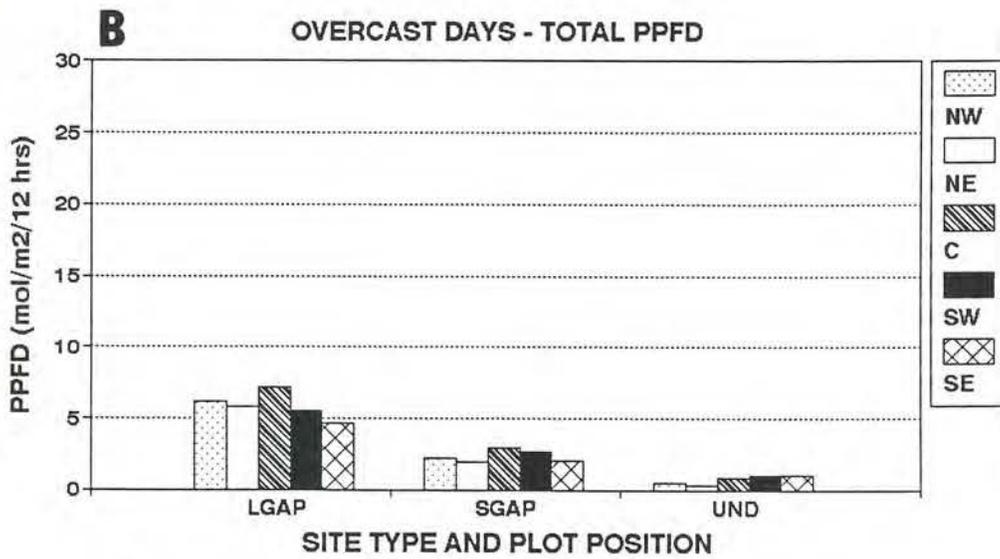
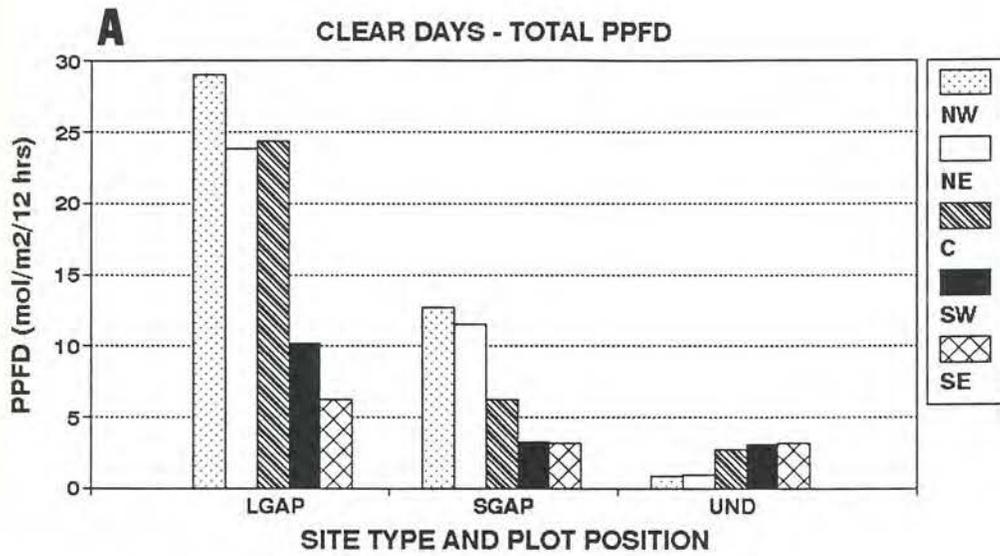
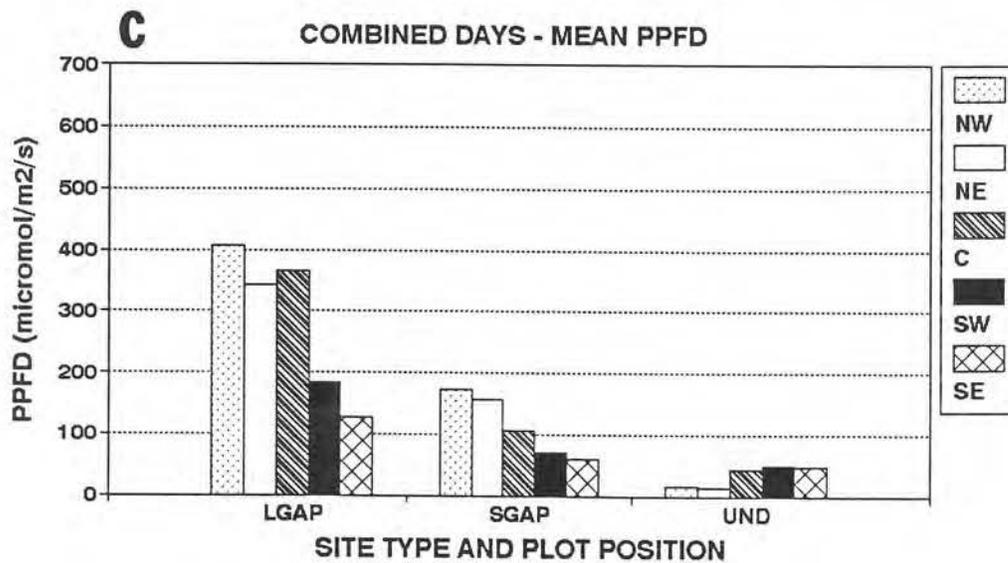
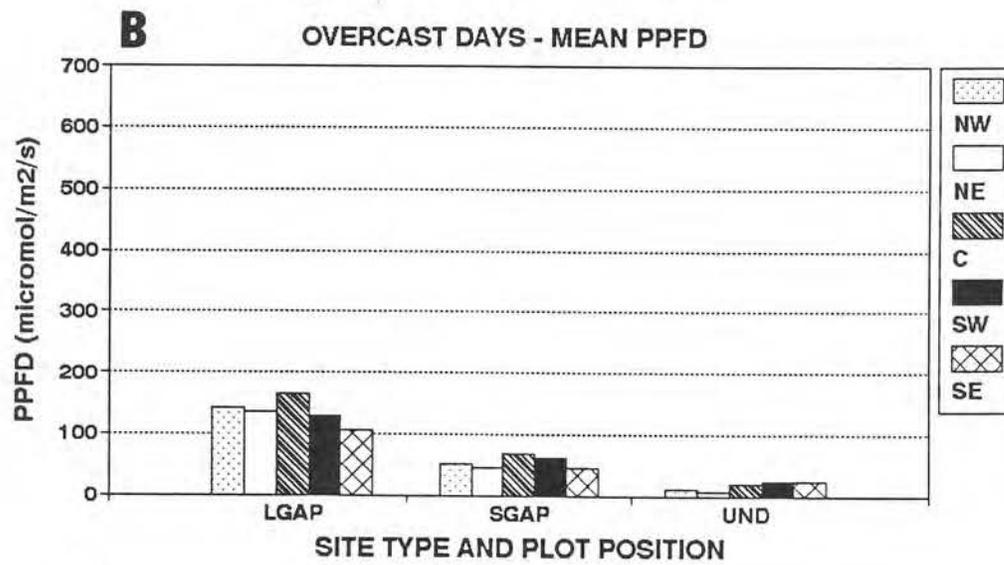
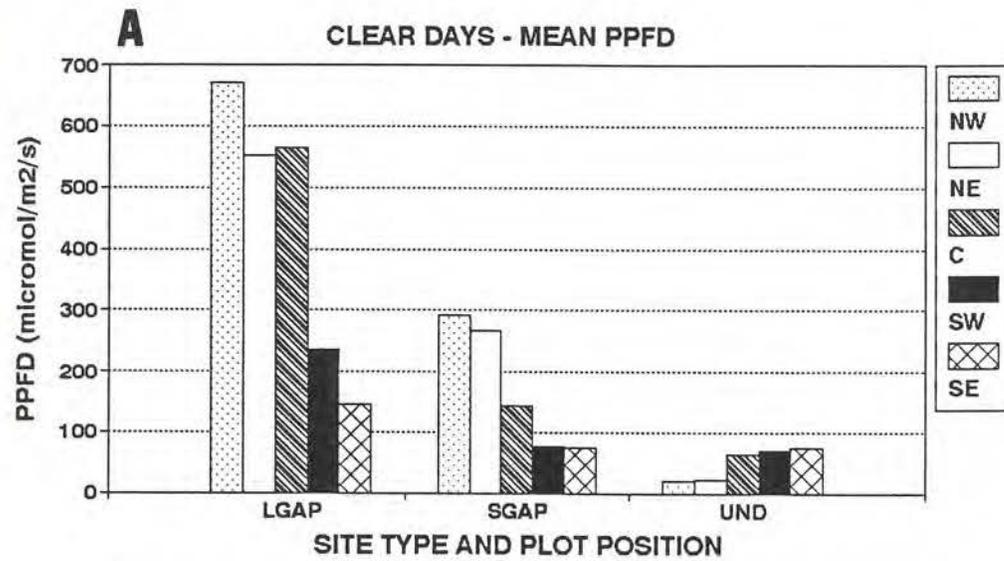


Figure 3-16. Mean daily PPF_D by site and plot position for clear (A), overcast (B), and combined (C) sample days across the 1988 season. The means are based on a 12-hour sample period symmetric around solar noon.



linear, rising steeply from south to center, and then changing very little toward the north plots. This pattern was confirmed during the occasional sampling regimes where all 15 micrometeorological stations were placed in the large gap. The diurnal traces (Figures 3-6, 3-7) showed that the center plot was sandwiched between the rising and falling of the NW and NE plots, but its total direct beam window was actually greater than either north plot. This yields mean daily PPF_D and total daily PPF_D values close to the NW and NE.

A gradient exists across the small gap as well, although it is not as broad as in the large gap. Mean PPF_D values in the north plots are about half that of the large gap north plots on clear and combined days. The small gap center is like the large gap south plots, and the small gap south plots are essentially understory.

The gradient due to PPF_D duration below 25 micromol/m²/s is a dramatic mirror image of the gradient produced by mean PPF_D (Figure 3-17). The large gap plots spend only 5-8% of the day below compensation, typically before 7am and after 5pm. The small gap plots are near compensation for 12-27% of the day. In both gaps, the center plot has the lowest duration, confirming the conclusion from the diurnal traces that the center plot receives greater diffuse irradiances, maintaining PPF_D levels above compensation. The understory plots spend 50-90% of the day below compensation for combined days, and there is a marked step change between the north versus the center and south plots.

The patterns for optimal PPF_D duration (200-600 micromol/m²/s; Figure 3-18) also show a site/plot gradient but one that is distinct from mean PPF_D and compensation PPF_D in several ways. First, the north plots are less divergent from the south plots in both the large and

Figure 3-17. Percentage of 12-hour day that PPFD is at or below average photosynthetic compensation point ($25 \text{ micromol/m}^2/\text{s}$), by site and plot position, for clear (A), overcast (B), and combined (C) sample days across the 1988 season.

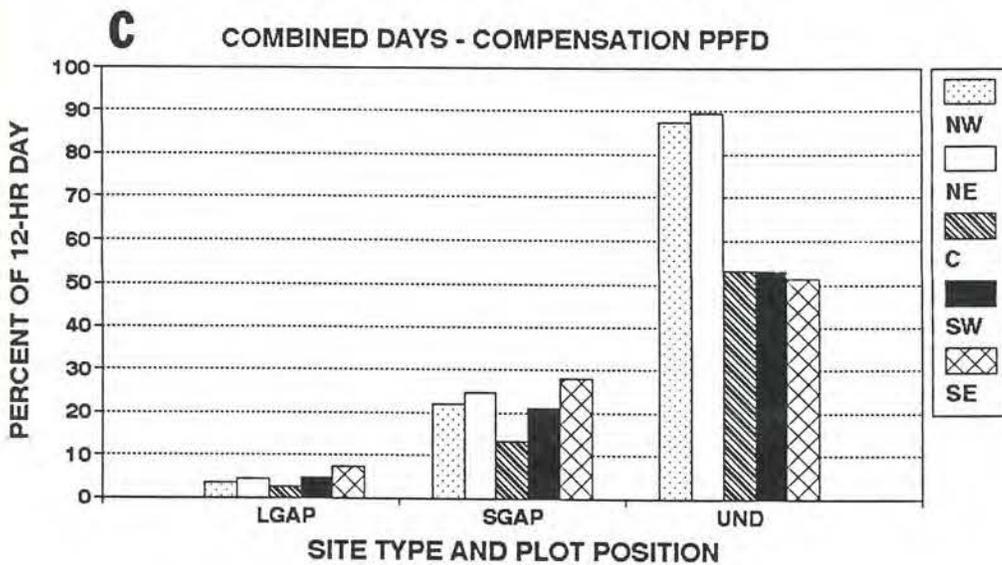
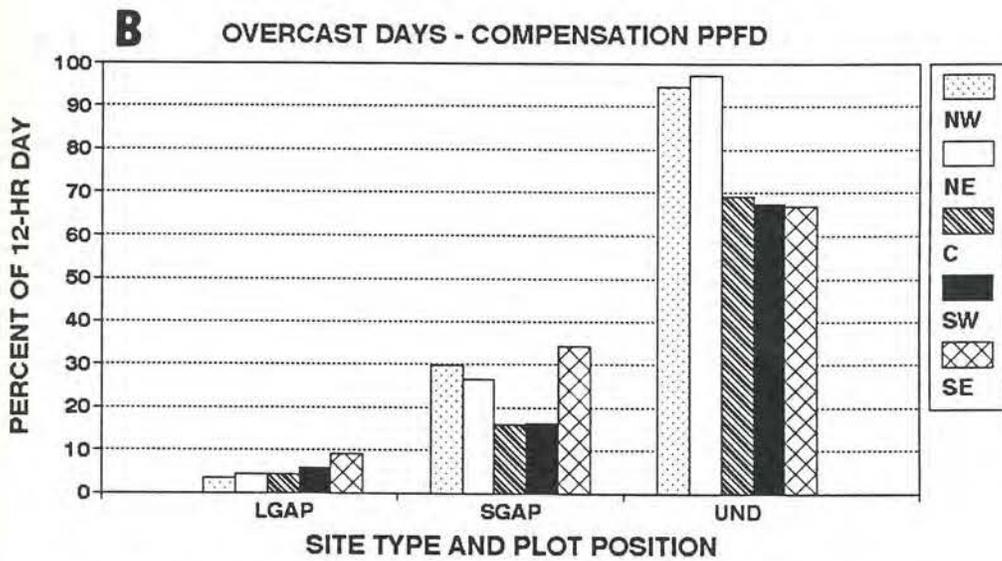
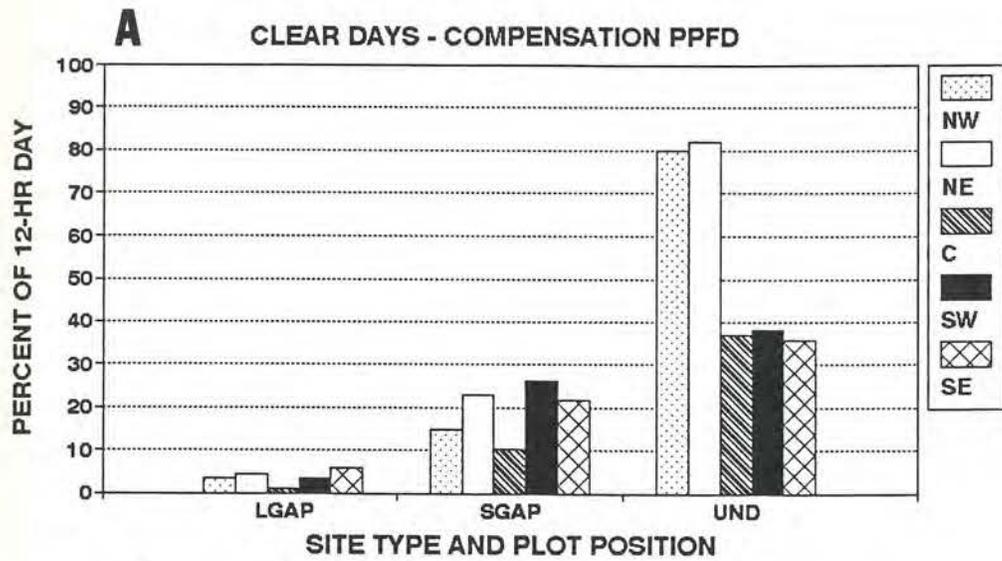
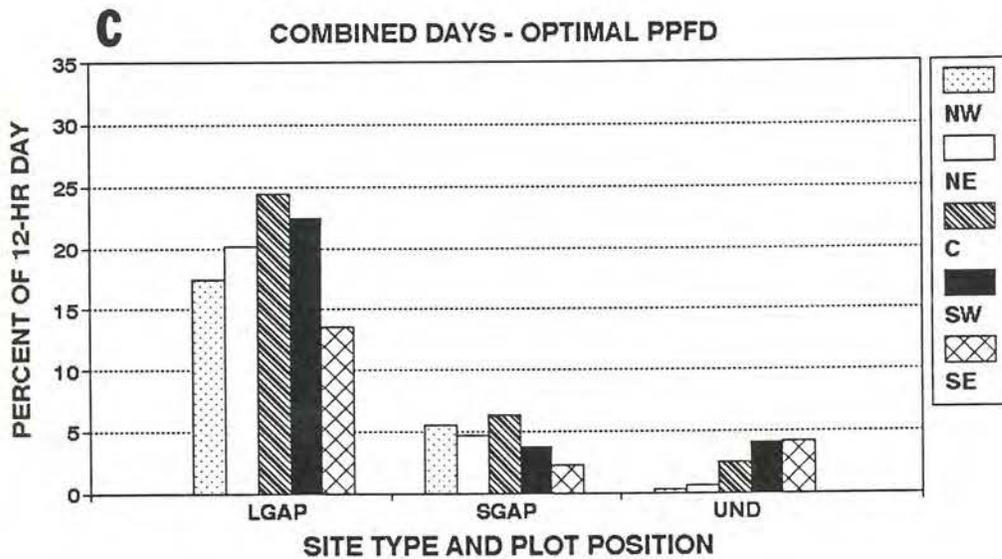
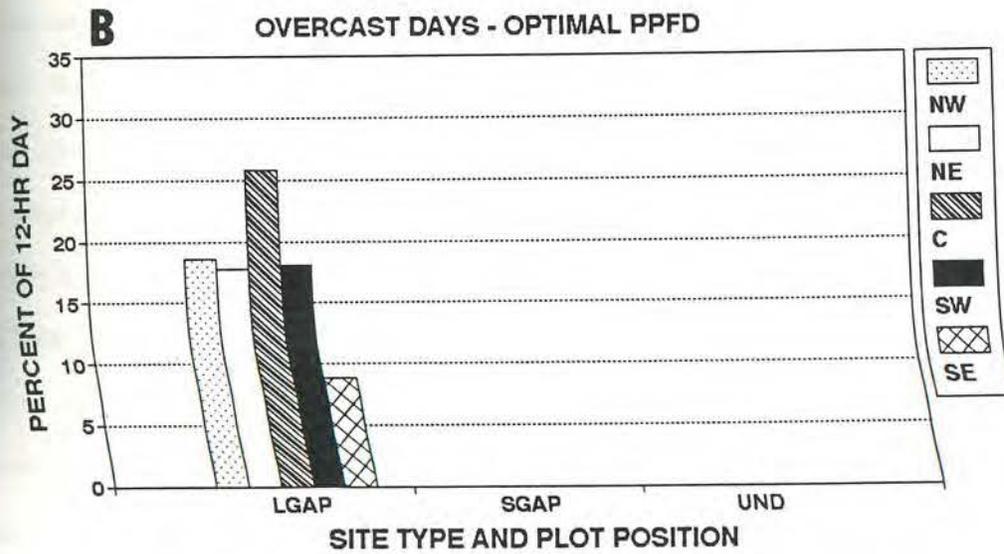
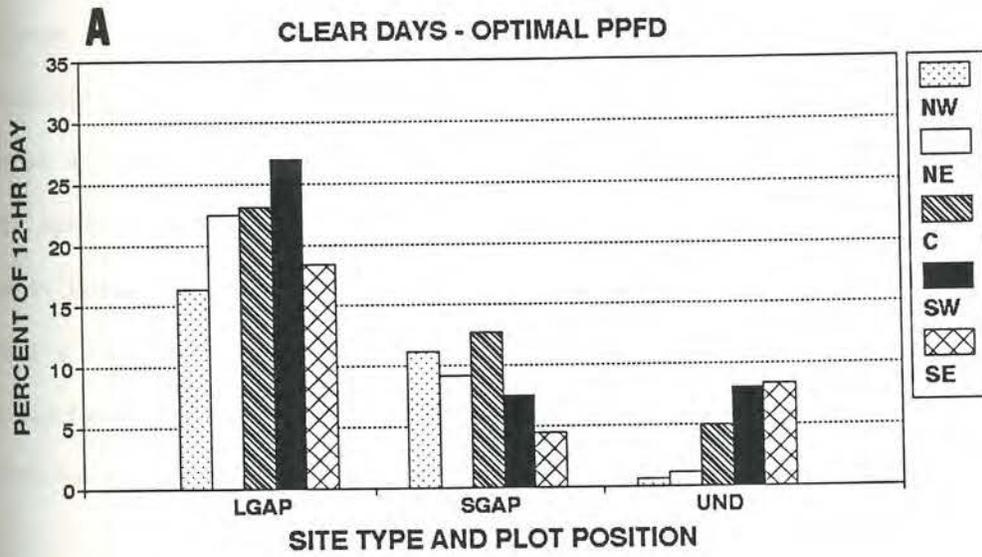


Figure 3-18. Percentage of 12-hour day that PPFD is in the photosynthetically optimal range (200-600 micromol/m²/s), by site and plot position, for clear (A), overcast (B), and combined (C) sample days across the 1988 season.



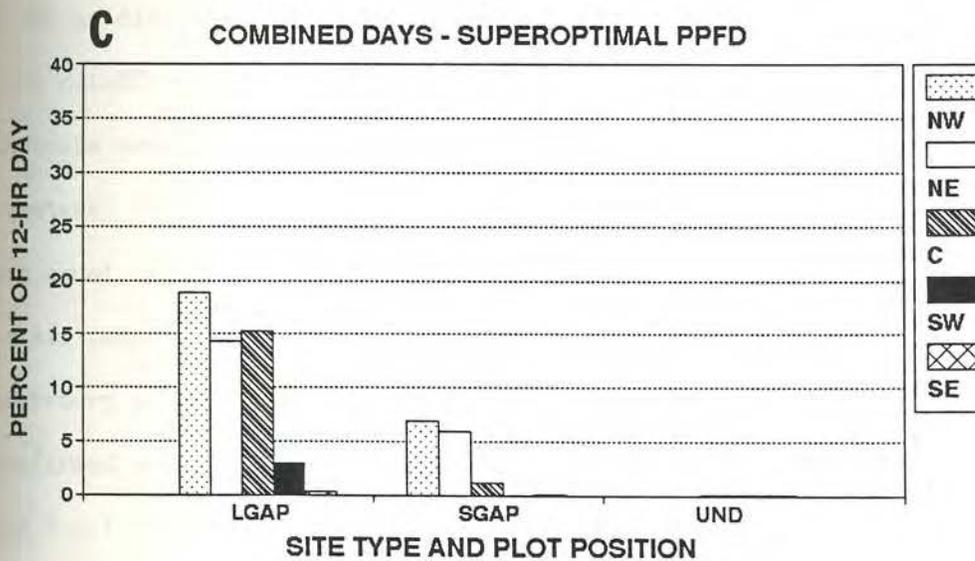
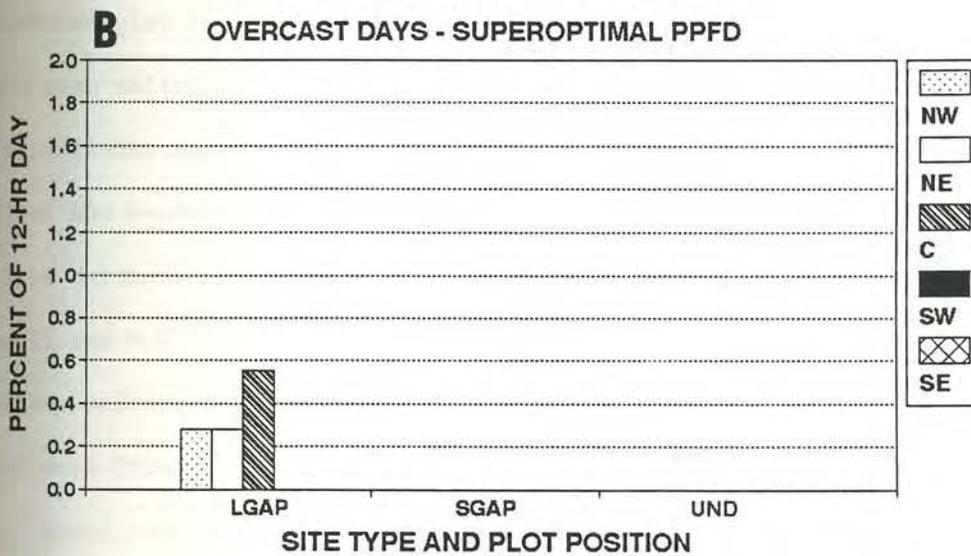
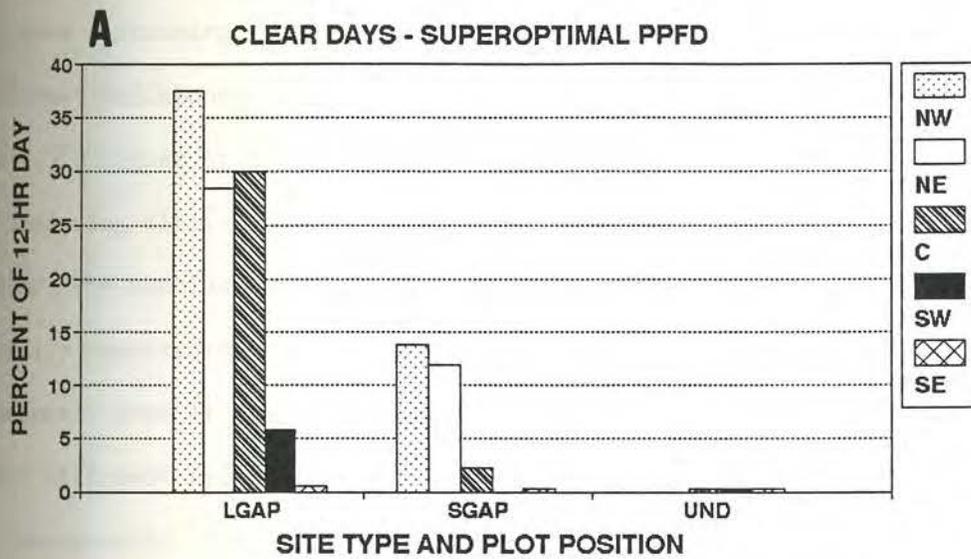
small gaps. Second, the overall gradient extremes are compressed, due to the reduction in the large gap north plots. Finally, the gradient does not exist across sites on overcast days; only the large gap plots exhibit optimal PPFD values. The importance of this depends on the degree to which each species depends on the optimal PPFD range for cumulative net photosynthesis, but in any case it is clear that the large gap has a more favorable light environment on overcast days.

Conversely, the large gap center and north plots show the greatest exposure as defined by superoptimal PPFD (>800 micromol/m²/s; Figure 3-19). The small gap north plots also experience superoptimal PPFD $>10\%$ of the day. On average, the large gap north percentages are about 3 times that of the small gap, and the small gap south and all understory plots never experience significant durations.

The gradient defined by superoptimal PPFD represents variation in two kinds of potentially detrimental effects. First, net photosynthesis in this range is substantially reduced as compared to irradiances between 100 and 600 micromol/m²/s (discussed in chapter 5), due to stomatal closure and possibly elevated photoinhibition. Second, such irradiances (typically >1500 micromol/m²/s on clear days) can have an enormous effect on leaf temperature balance, particularly if stomates are forced to close because of excessive vapor pressure deficits and tissue water loss. It was not unusual during gas-exchange measurements for leaf temperatures to exceed 40°C on clear days in the large gap north plots. It is likely that the three study species experienced thermal stress in non-trivial ways, particularly on clear days that were also hot and calm.

Unlike PPFD variables, mean daily air temperatures across sites and

Figure 3-19. Percentage of 12-hour day that PPFD is above the photosynthetically optimal range (>800 micromol/m²/s), by site and plot position, for clear (A), overcast (B), and combined (C) sample days across the 1988 season.



plots show a stunning lack of variation (Figure 3-20). The only significant differences are in the large gap NW, NE, and C, which tend to be 2-3°C higher on clear days. Overcast days are even more uniform, thus dampening clear day differences when the two types of days are combined. The conclusion is that there is no effective gradient based on mean daily temperatures, since it is unlikely that such small differences, even if held constant throughout the day, would elicit notably different responses among species.

Consequently, it is necessary to emphasize again that if air temperatures play any role at all, it is due to divergent diurnal ranges and not mean daily values. Figure 3-21 portrays the durations that each plot experiences greater than 25°C, and indeed a modest gradient emerges for clear and combined days. The overall pattern is a nearly monotonic drop from north to south across the large gap that continues on through the small gap N-S axis until the small gap south plots arrive at understory values. For combined data, all plots experience superoptimal temperatures from 14-38% of the day. The differences on overcast days are not great, except for the NE of both small gap and understory, and hence the gradient of extreme temperatures does not exist on such days.

Any cutoff such as 25°C is a subjective watershed divide that does not indicate how data values on either side of the cutoff may vary. In this context, it is important to remember that temperatures above 25°C are not equal, and that the large gap north and center plots experienced higher air temperatures for longer periods than in any of the small gap or understory plots (Section 3.5.1., Figures 3-12 through 3-14). This was confirmed on many other clear day samples beyond those presented in Section 3.5.1.

Figure 3-20. Mean daily air temperature by site and plot position for clear (A), overcast (B), and combined (C) sample days across the 1988 season. The means are based on a 12-hour sample period symmetric around solar noon.

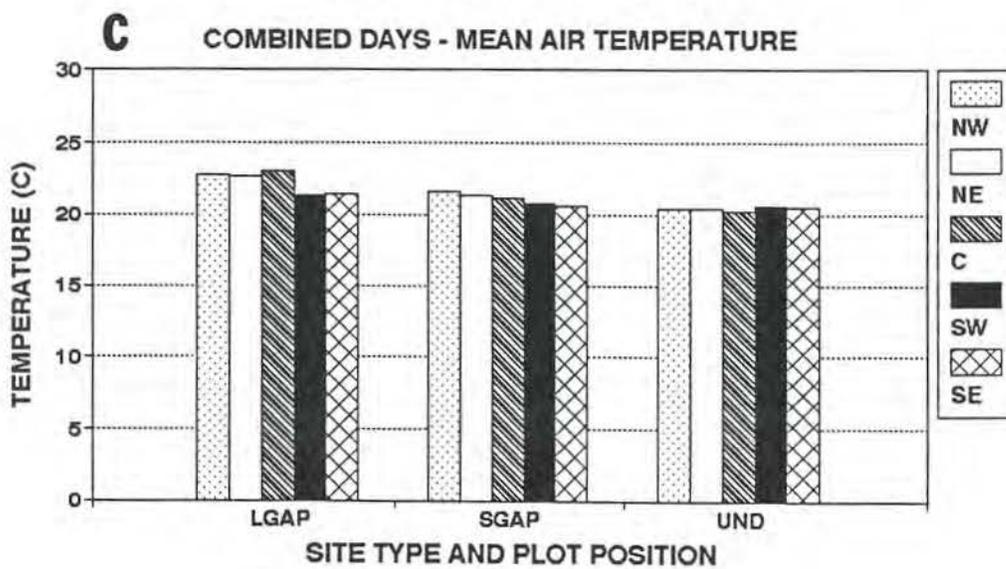
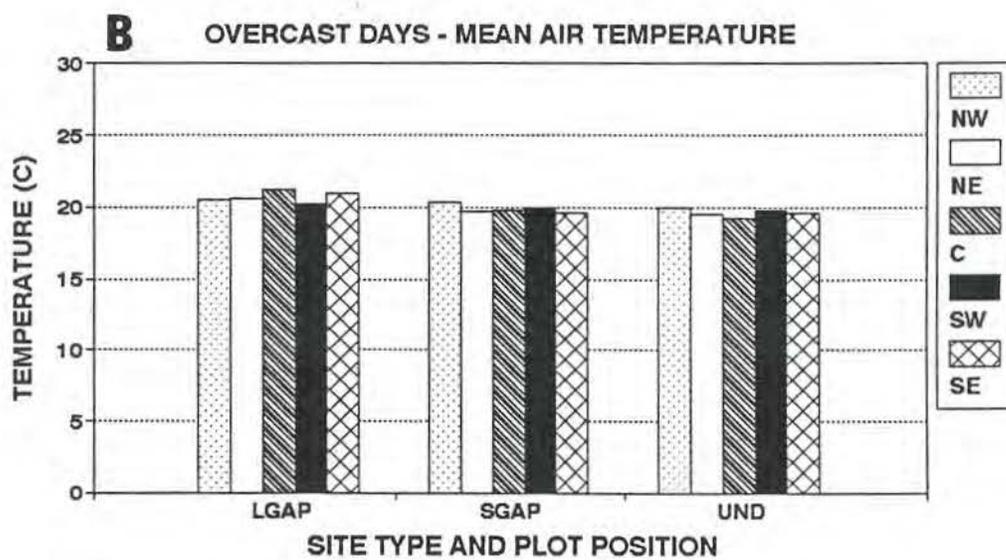
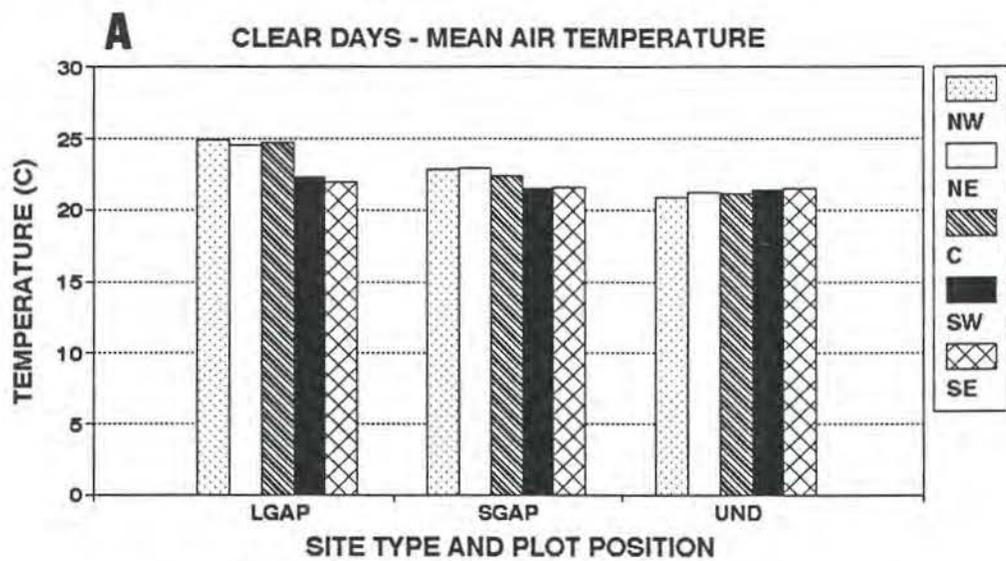
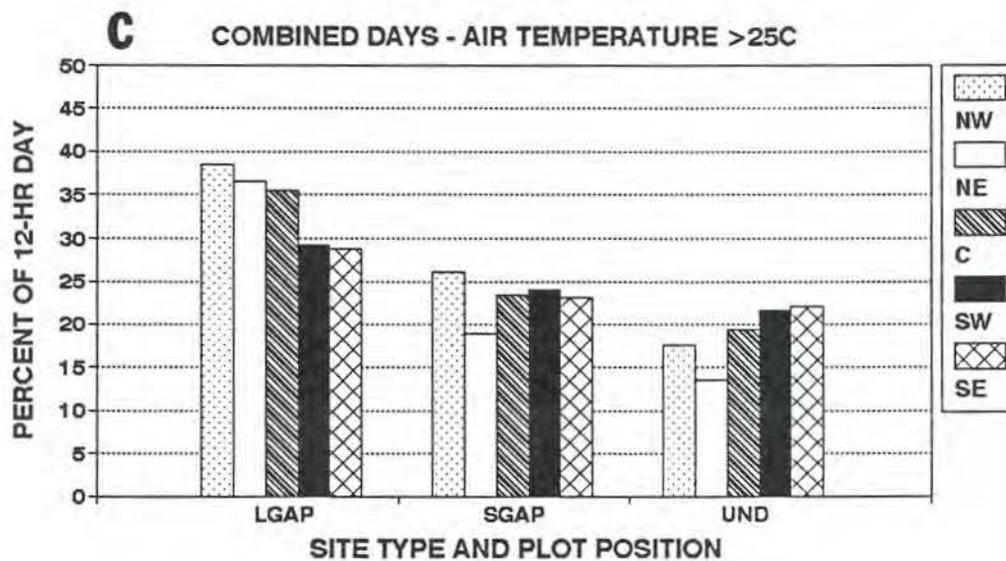
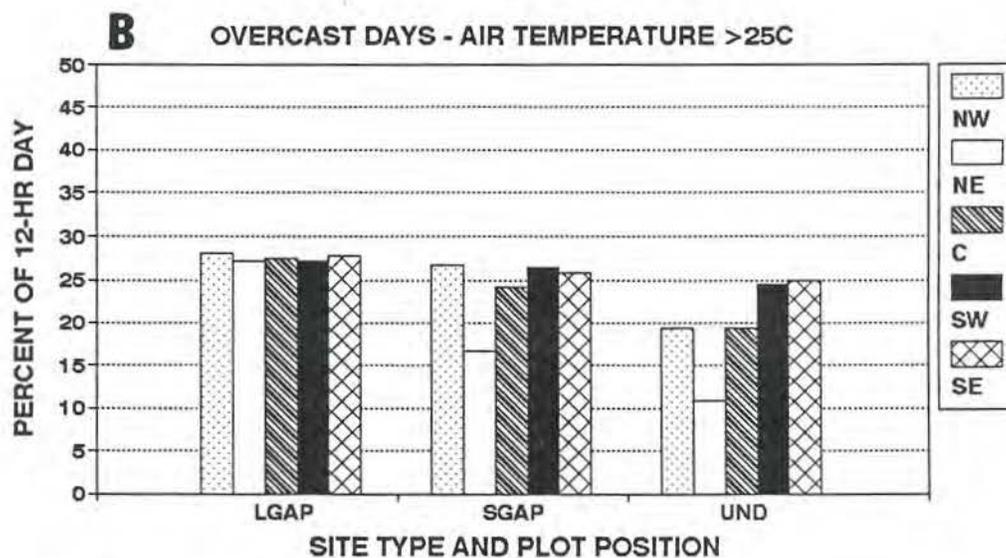
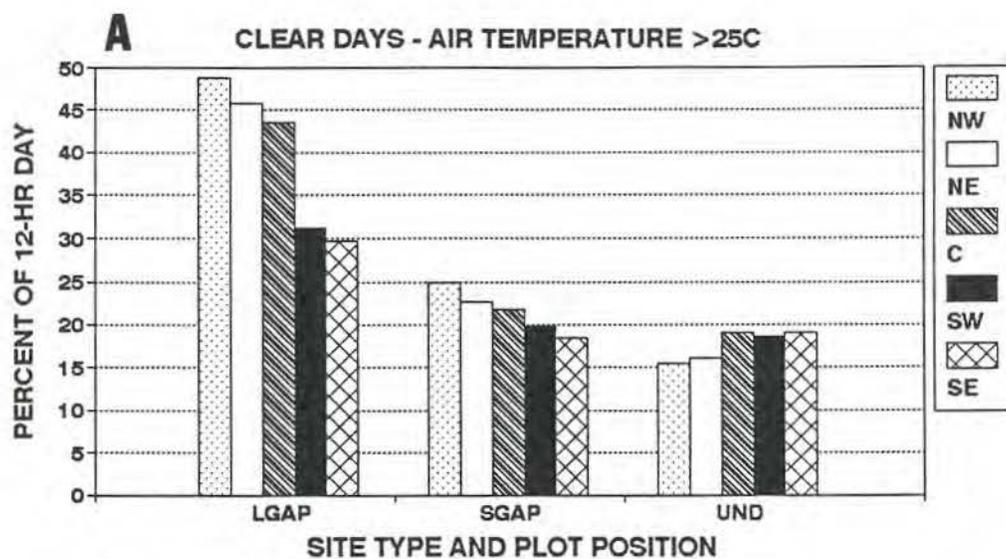


Figure 3-21. Percentage of 12-hour day that air temperature is above the photosynthetic optimum (25°C), by site and plot position, for clear (A), overcast (B), and combined (C) sample days across the 1988 season.



Soil surface temperatures are not graphed due to missing data from the five sample days. However, Figure 3-22 displays the deep soil temperatures. Like air temperatures, there are few differences among sites and plots. The large gap plots are 2-3°C higher than the small gap and understory plots on clear days, and 0-2°C higher on overcast days. As discussed below in Section 3.6., these differences may be more important than the 2-3°C differences in air temperature because of the lessened ability of roots versus leaves to adjust their own temperature in response to the microenvironment.

3.5.2. MULTIVARIATE ANALYSIS OF THE GAP-UNDERSTORY GRADIENT

The results of the discriminant analysis on irradiance and temperature data are shown in Table 3-7 and Figures 3-23 through 3-25. The discussion will proceed through clear, overcast, and combined days sequentially.

The multivariate F-test (Wilks' lambda) for clear days is highly significant, with $p < 0.000$, indicating strong differences among the 15 site/plot positions. The univariate tests on the input variables reveals that all the PPFD variables are individually significant at $p < 0.000$, but neither temperature variable is significant.

The classification success at the site level is very good (84% overall) and declines monotonically from large gap (92%) to small gap (84%) and large understory (76%). Plot level success is lower (52%), also declining monotonically through the three sites (72%, 52% and 32%, respectively). Thus the discrimination among sites is better than among plots within sites, suggesting that the gradient is not continuous, but clustered into recognizable plot groupings within sites. Furthermore,

Figure 3-22. Mean daily deep soil temperature (15cm) by site and plot position for clear (A), overcast (B), and combined (C) sample days across the 1988 season. The means are based on a 12-hour sample period symmetric around solar noon.

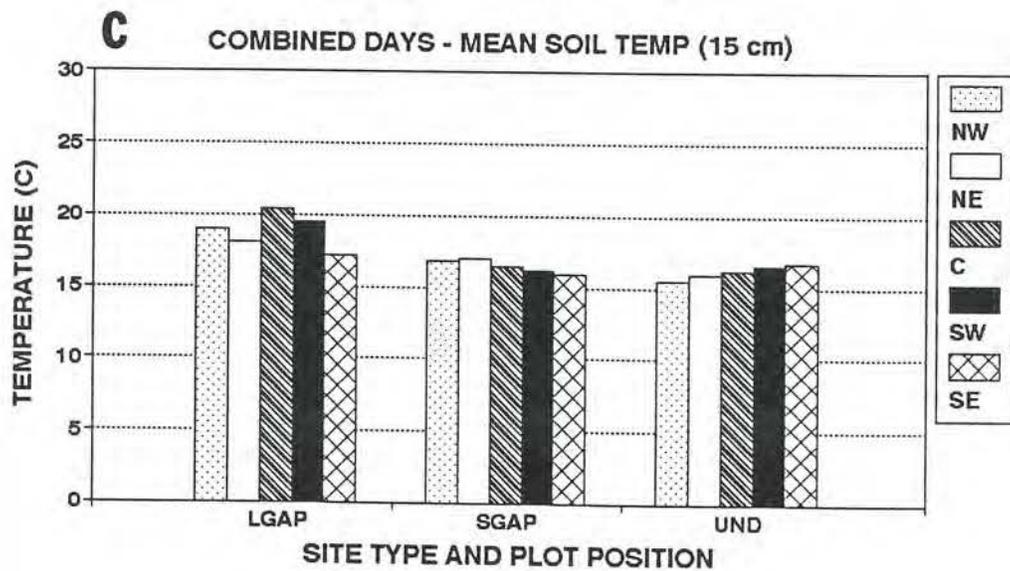
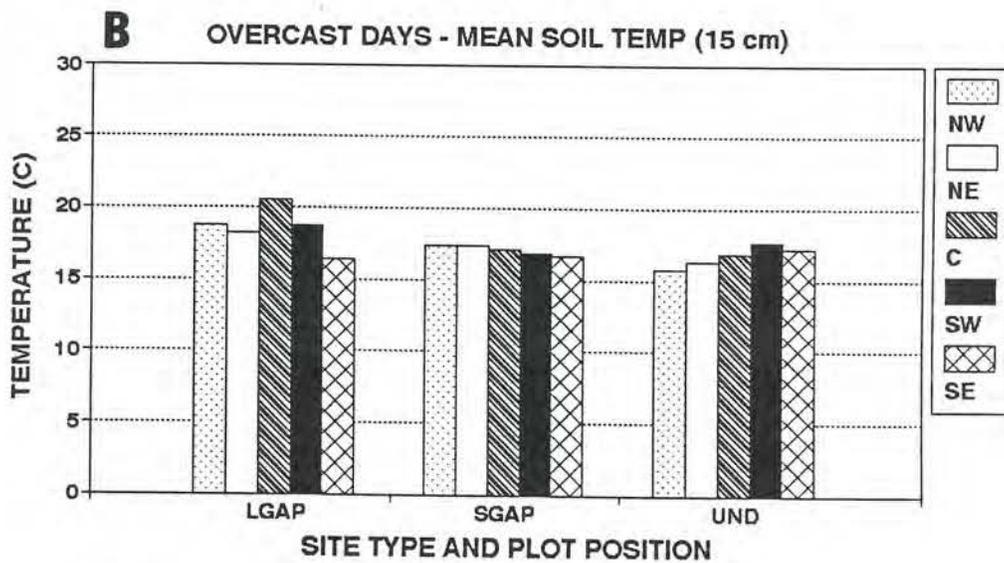
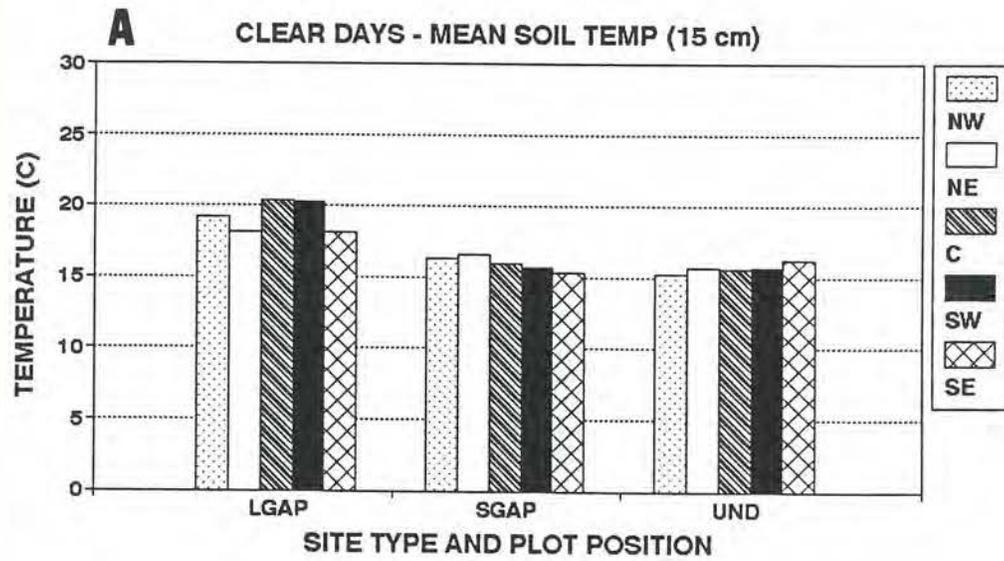


Table 3-7. Discriminant analysis results for clear, overcast, and combined micrometeorological sampling days. Classification percentages are the frequency with which the discriminant functions were able to classify each original sample into its own group. Canonical loading factors are the correlations between each original variable and the scores for each discriminant axis. A high positive value means that the original variable contributes substantially to sample differences along the discriminant axis.

VARIABLE	CLEAR DAYS (N=5)			OVERCAST DAYS (N=5)			COMBINED DAYS (N=10)		
MULTIVARIATE F-TEST									
Wilks' Lambda	4.81			3.19			5.33		
p <	0.000			0.000			0.000		
CLASSIFICATION SUCCESS (%)									
Site Level									
TOTAL	84			92			83		
LGAP	92			84			84		
SGAP	84			84			78		
LUND	76			100			82		
Plot Level									
TOTAL	52			37			34		
LGAP	72			40			32		
SGAP	52			24			40		
LUND	32			52			30		
UNIVARIATE F-TEST PROBABILITY LEVELS									
Mean PPF	0.000			0.000			0.000		
Suboptimal PPF	0.000			0.000			0.000		
Optimal PPF	0.000			0.000			0.000		
Superoptimal PPF	0.000			0.582			0.000		
Air Temp	0.709			1.000			0.978		
Deep Soil Temp	0.102			0.730			0.009		
CANONICAL LOADING FACTORS	AXIS 1	AXIS 2	AXIS 3	AXIS 1	AXIS 2	AXIS 3	AXIS 1	AXIS 2	AXIS 3
Mean PPF	0.56	0.22	-0.30	-0.46	0.58	0.03	-0.35	0.39	-0.70
Suboptimal PPF	-0.26	0.44	0.69	0.76	0.53	0.20	0.65	0.58	0.12
Optimal PPF	0.21	-0.28	0.18	-0.22	0.65	-0.07	-0.32	0.34	0.36
Superoptimal PPF	0.66	0.50	-0.34	-0.08	0.30	-0.26	-0.24	0.40	-0.84
Air Temp	0.11	0.04	-0.08	-0.02	0.04	0.04	-0.07	0.07	-0.13
Deep Soil Temp	0.15	-0.12	0.24	-0.08	0.22	-0.39	-0.18	0.24	0.15
CANONICAL CORRELATION	0.96	0.86	0.63	0.96	0.68	0.49	0.92	0.65	0.42

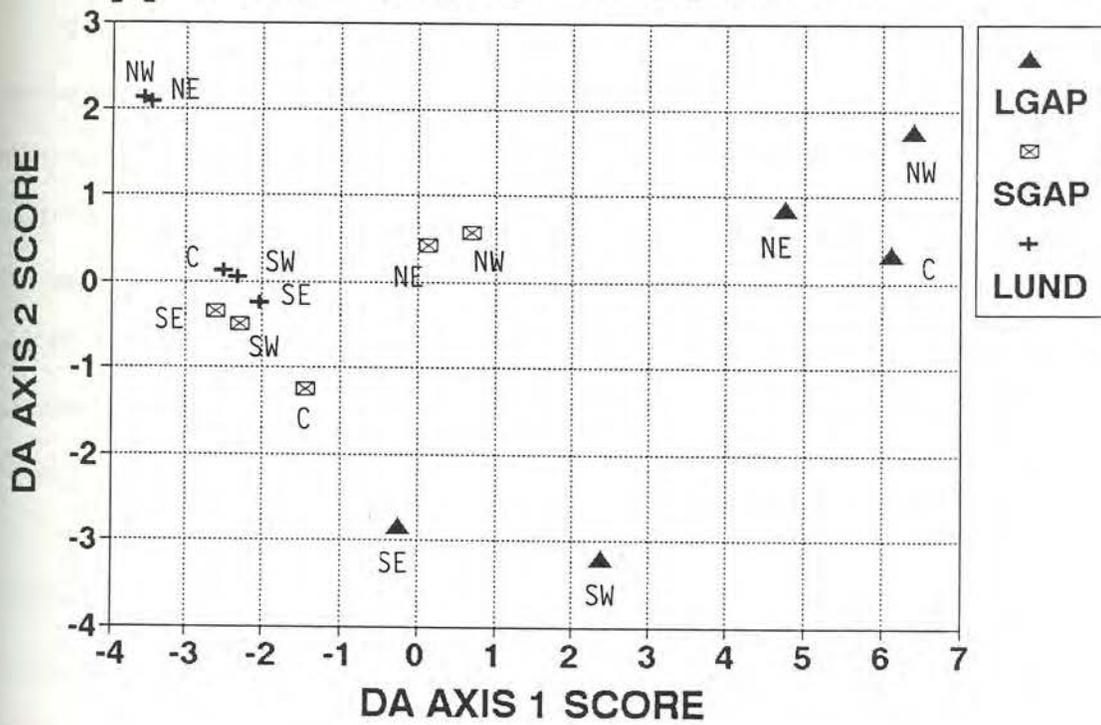
the large gap plots are more variable than the small gap plots, which are in turn more variable than large understory plots.

The scatterplots confirm this interpretation (Figure 3-23). The overall shape of the point cloud is anchor-like in three dimensions, with the large gap plots forming the main axis of the anchor and the small gap and understory plots forming the lower crossbar. The three sites are reasonably distinguished, but the large gap is more separate than the other sites, whose plots overlap. The overlap is particularly noticeable for the small gap SE and SW and the understory C, SW, and SE. This confirms that the south sides of small gaps are similar to understory conditions. The NW, NE, and C plots of large gaps are quite distinct, due to the durations of direct beam irradiance. The average distances among plots are greater for large gaps than the other sites, so much of the overall gap-understory gradient is determined by large gap variability.

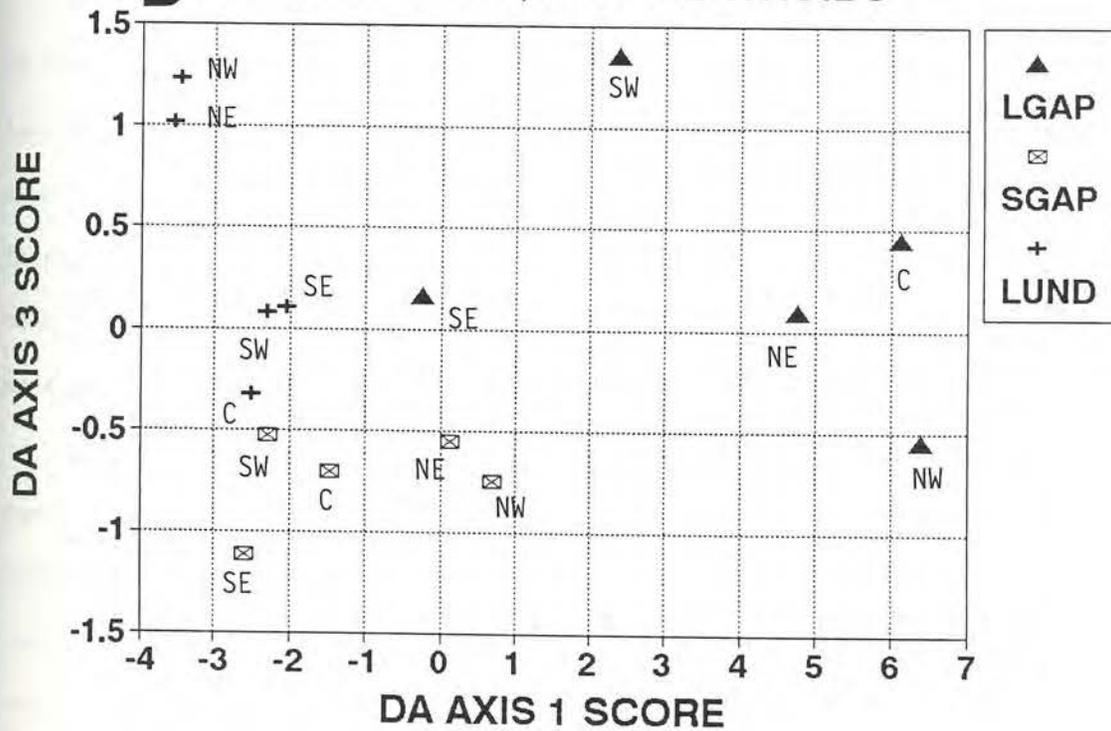
The canonical loadings (Table 3-7) produce the following interpretations of the axes. Axis 1 represents mean PPFD and the frequency of superoptimal PPFD, and is thus a measure of average light levels with an emphasis on high extremes. Axis 2 is loaded by both superoptimal and suboptimal PPFD, and thus represents the tendency for a plot to show either high or low extremes within a given mean irradiance range. This explains the positions of the large gap SE and SW plots, which show intermediate scores on axis 1 and low scores on axis 2, since they receive higher diffuse light levels and some direct beam, but are not prone to either extreme. Axis 3 is less clear, but seems to represent the frequency of suboptimal PPFD within any given light level. Thus the understory plots all score higher on axis 3 than the small gap

Figure 3-23. Scatterplots of site/plot centroids for the clear day discriminant analysis of micrometeorological data. (A) Discriminant axis 2 versus axis 1, (B) Discriminant axis 3 versus axis 1. Based on loading factors, axis 1 represents mean irradiance levels, axis 2 represents the occurrence of irradiance extremes (high or low), and axis 3 represents the frequency of suboptimal PPFD within any given light level.

A CLEAR DAY SITE/PLOT CENTROIDS



B CLEAR DAY SITE/PLOT CENTROIDS



plots, even for those with comparable mean irradiance on axis 1.

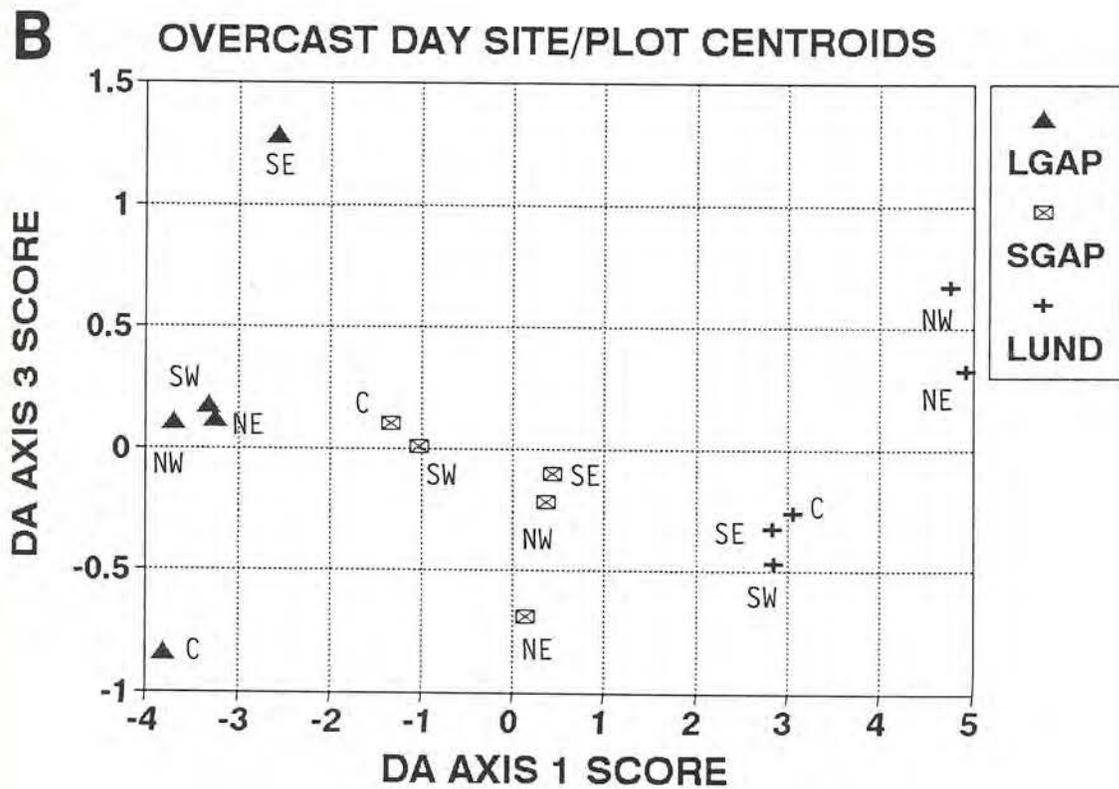
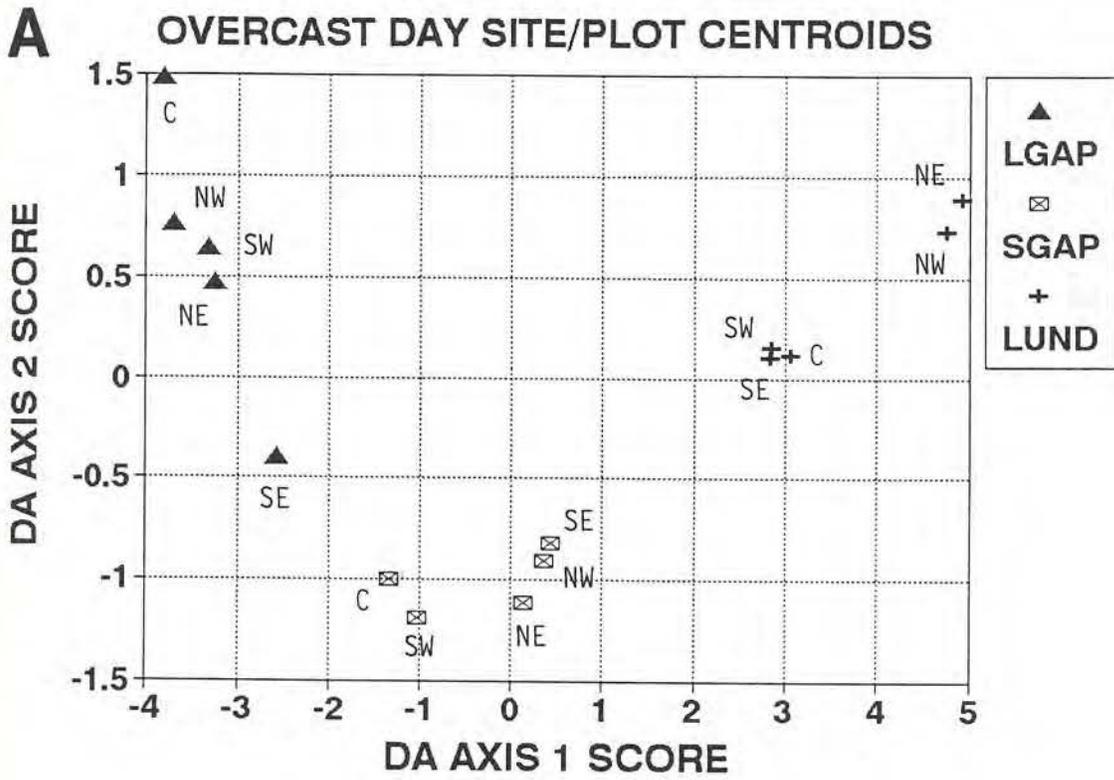
Several concluding points for the clear days are suggested by the scatterplots. The center and north plots of the large gap are quite distinct from the south sides, and in fact the SE plot is closer to the small gap site. The NW and NE understory plots are just as removed in the opposite direction as the exposed large gap plots. The small gap NW and NE plots are close to large gap SW and SE in mean irradiance (axis 1 scores), but because they receive more direct beam and thus high PPFD levels, they score higher on axis 2.

Overcast days produce statistics and scatterplots somewhat different than clear days. Again the multivariate F-test is highly significant ($p < 0.000$), and only PPFD variables are univariately significant (Table 3-7). In this case, because of the dampened PPFD levels throughout the sites, superoptimal PPFD levels do not vary significantly among sites.

The site level classification success is greater overall (92%) than on clear days, with the understory now higher (100%) than either the large gap (84%) or small gap (84%). Plot level success (37%) is worse than on clear days, with the understory again being better (52%) than large (40%) or small (24%) gap. So sites are again discriminated better than plots within sites, but unlike clear days the understory plots are more uniform than for either gap size.

The scatterplots (Figure 3-24) reflect the high discrimination among sites, since all three sites are clearly separated and the plots within sites are more tightly clustered than on clear days. The 3-D point cloud has more of a boomerang shape than an anchor. The axis 1 scores produce a mirror image of the clear day scatterplots, with the

Figure 3-24. Scatterplots of site/plot centroids for the overcast day discriminant analysis of micrometeorological data. (A) Discriminant axis 2 versus axis 1, (B) Discriminant axis 3 versus axis 1. Based on loading factors, axis 1 represents the frequency of suboptimal PPF, axis 2 represents overall irradiance, and axis 3 is largely undefined.



large gap plots on the left and understory plots on the right. This difference is a matter of sign and not significant. So the relative positions of the sites are comparable to the clear day plots even though variability within sites is reduced. The tightness of plot clustering within sites declines from small gap to understory to large gap. The overall breadth of axis 1 is less on overcast days (standardized scores ranging from -3.75 to 5) than on clear days (-3.5 to 6.5). The same is true for axis 2, where the overcast day range (-1.25 to 1.5) is less than clear day range (-3.3 to 2.1). These axis breadths support the argument that the overall gradient is dampened on overcast days (i.e., high PPFD extremes are eliminated).

The canonical loadings suggest that axis 1 is controlled by the frequency of suboptimal PPFD levels, while axis 2 is a mixture of PPFD variables representing overall irradiance variability. The interpretation for axis 3 is unclear. The first axis in discriminant space is the axis that explains most of the variation in the data, and the fact that suboptimal PPFD controls axis 1 indicates the importance of low irradiances on overcast days in separating sites and plots.

Some plot relationships have changed in comparison to the clear days. The C, SE, and SW understory plots are farther removed from the small gap plots than for clear days. The north plots of the small gap are less like large gap south plots and more like the other small gap plots. And the relationships among the large gap plots are not dictated by the N-S dimension. The C and SE plots are the most distant, while the NW, SW, and SE are clustered fairly tightly. This reflects two things. First, as discussed in Section 3.5.1., the centers of large gaps receive consistently higher PPFD on overcast days. Second, the understory of the

intact forest behind the SE plot of this large gap in Block 1 has substantial light attenuation by eastern hemlock (*Tsuga canadensis*) saplings, lowering its overall PPFD levels away from the other plots.

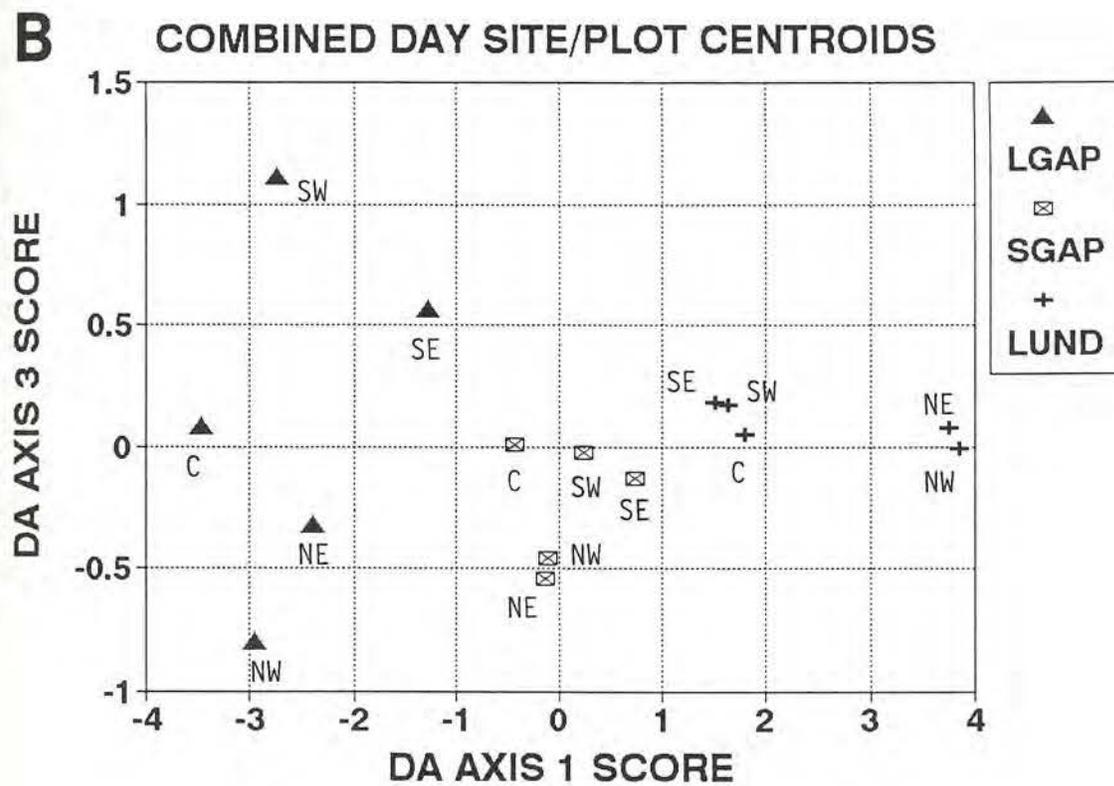
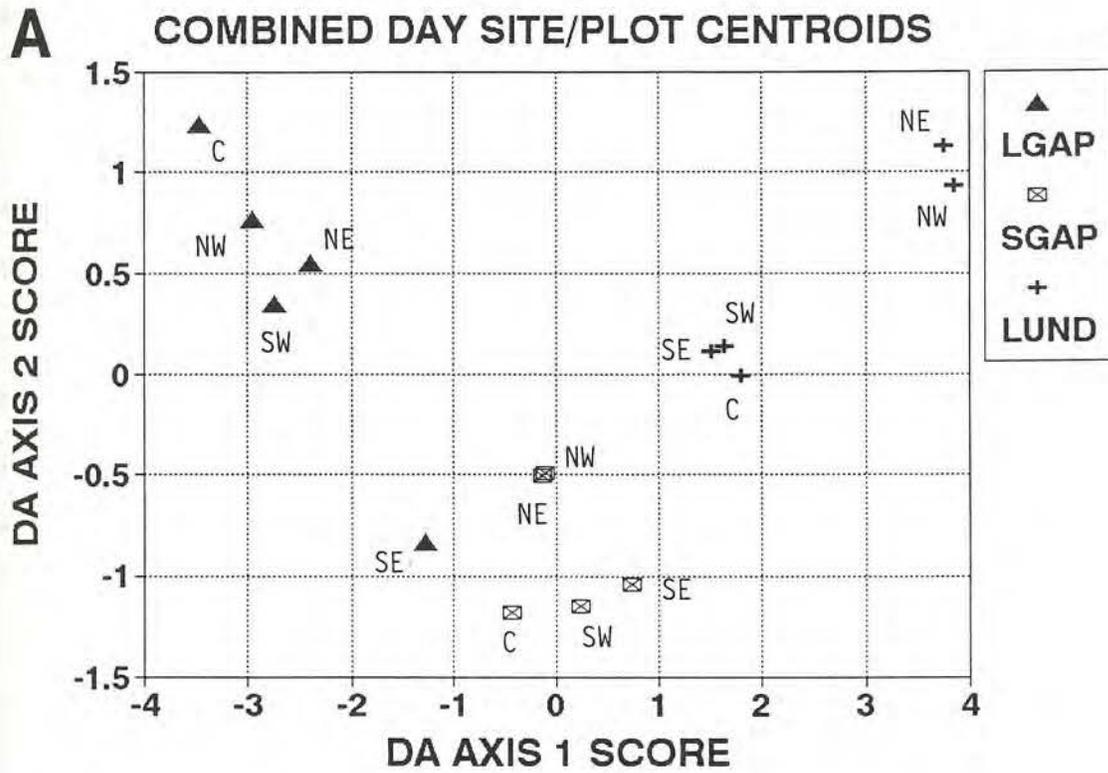
Overcast days thus show a narrower gap-understory gradient. But the similarity of plots within sites increases, such that overall site classification success is high while within-site plot classification success is low.

The combined days analysis produced results generally intermediate between clear and overcast days. The multivariate F-test is highly significant ($p < 0.000$) (Table 3-7). All input variables except air temperature are univariately significant, including deep soil temperature.

Site-level classification success is good (83%), the same as clear days, but lower than overcast days. The three sites do not differ significantly in classification success, with the large gap (84%) slightly higher than understory (82%) and small gap (78%). Plot-level success is lower overall (34%) than either clear or overcast days. The small gap shows better plot classification success (40%) than either large gap (32%) or understory (30%). All plot-level values are less than on both clear and overcast days, except for the small gap, which is greater on combined than overcast days.

The scatterplots (Figure 3-25) reflect this intermediate situation. They are more like the overcast plots than the clear plots, implying that overcast days contribute more to combined data structure. The breadth of axes 1 and 2 are like overcast days, and the point cloud shape is again like a boomerang. The sites are more distinct (plot clusters tighter) than on clear days, but less distinct than overcast

Figure 3-25. Scatterplots of site/plot centroids for the combined day discriminant analysis of micrometeorological data. (A) Discriminant axis 2 versus axis 1, (B) Discriminant axis 3 versus axis 1. Based on loading factors, axis 1 represents the frequency of suboptimal PPF, axis 2 represents overall irradiance levels, and axis 3 represents the frequency of peak PPF within any given light level.



days.

The axes are interpreted as follows. Axis 1 represents the tendency toward suboptimal PPF_D, and axis 2 is overall irradiance level. Both are the same as for overcast days. Axis 3 is again vague, but may represent the frequency of peak PPF_D levels.

The large gap plots are the most variable in comparison to the other sites, especially when axis 3 is considered, although the C versus SE distinction on overcast days is reduced here. The NW and NE plots are still quite distinct from the other three plots in the understory.

Several points can be made in the way of a summary for this section. First, multivariate analysis displays relationships among sites and plots not easily visualized through the diurnal traces and bar graphs of mean values presented in previous Sections. Second, the three-dimensional relationships support the univariate interpretations. Third, essentially all of the multivariate distinctions in this section are based on irradiance variables. Had windspeed and especially relative humidity data been sufficiently comprehensive for inclusion, the patterns may have changed somewhat. However, irradiance patterns regulate most other physical microsite characteristics (Lee 1978; Gates 1980), and thus the patterns presented here based on PPF_D are probably correct. Furthermore, it is interesting that the several facets of the PPF_D environment used here as separate input variables do provide different kinds of information that distinguish sites and plots (Chazdon 1986).

The overall gradient of sites and plots on combined days is:

LGC...LGNW...LGSW...LGNE...LGSE...SGC...SGNE=SGNW...SGSW...SGSE...

LUSE=LUSW=LUC, LUNE=LUNW

Clear days produce the broadest gradient, mostly due to the stretching of the large gap plots away from all other sites and plots. Thus most of the combined-days gradient is due to large gap variability on clear days. The sites/plots are more evenly dispersed in discriminant space on overcast and combined days, even though the discriminant functions are still able to distinguish sites. Finally, the importance of suboptimal PPFd in controlling axis 1 on combined days suggests that any notable differences in photosynthetic performance by the three species in this PPFd range should elicit differential species success across the combined-days gradient of sites and plots.

3.6. DISCUSSION

Many individual points were already made during the presentation of results in Sections 3.2 through 3.5., and therefore this discussion has two purposes: (1) comparison to published data on forest gap and understory microclimates, and (2) a condensed summary of the nature of the gap-understory microclimatic gradient. The emphasis for (1) is on studies in which gap and understory environments were measured, and not on the larger literature involving theoretical and empirical characterizations of vertical microclimatic profiles in intact forests.

As noted in the Introduction (Section 1), remarkably little data exist on microenvironmental variation within and across relatively small forest canopy openings. The forestry literature on this point usually concerns gap sizes greater than the most natural gaps, due to the economics and silvics of forest management and harvest practices. For example, Marquis (1965) presented a detailed visual summary of direct beam exposure near summer solstice in square, rectangular, and circular

clearings from 0.10 acres ($\sim 400\text{m}^2$) to 0.50 acres ($\sim 2000\text{m}^2$) in size. The results were based on solar movement and gap geometry, and did not include field measurements.

However, Marquis (1965) also considered the effects of orienting narrow (23-50 feet) strip cuttings along N-S, E-W, and NW-SE axes, and in a later paper (Marquis 1966) reported the results of growing paper and yellow birch in simulated strip cuttings of comparable sizes. Strips 50 feet wide and oriented E-W approximate the N-S dimensions of the large gaps produced here. Again, no measurements of light in the field were reported.

Minckler (1961) measured visible radiation (not PPFD) with a handheld exposure meter at the center and edges along cardinal axes (N, E, S, W) in circular openings of six sizes, the diameters of which ranged from 0.25 to 2.00 times average tree height. Readings taken five times daily at each position on 3-6 clear days throughout the season were averaged to provide seasonal comparisons. Based on the percentage of full sun measured in larger clearings, the smallest gaps ($\sim 35\text{m}^2$) received 2-3 times as much light as the understory of "well-stocked hardwood stands". The north edge received more light than the center for gap sizes up to 1.0 tree height ($\sim 290\text{m}^2$), after which the two positions were approximately equal. The south edge was comparable to the center and north only in the smallest gap, and on average received less than half the percentage full sun as the other two plots in all other gap sizes.

In a similar study in southern Illinois, Minckler et al. (1973) measured visible radiation at various positions in circular openings of six sizes, the diameters of which ranged from 0.25 to 2.00 times average

tree height. For the 80-90' tall forests in this study, this would correspond roughly to an areal range of 30-1870m². They found that gaps of 0.75 tree height or less (<265m²) produced a N > C > W > E > S gradient of light intensities, and that gaps of 1.0 tree height or more (>465m²) reversed the north and center ranks to produce a C > N > W > E > S gradient.

More recent studies have measured PPFD instead of visible radiation, and the results are directly comparable to this research and relevant to photosynthetic performance. Chazdon and Fetcher (1984) measured PPFD in four sites at Finca La Selva, Costa Rica: 0.5-hectare clearing, 400m² natural gap, 200m² natural gap, and understory. Sensors were placed in the centers of the three openings. Ten-minute PPFD means taken over 12-hour days were contrasted between the wet and dry seasons during all cloud conditions. The 400m² gap showed 20-35%, the 200m² gap 9%, and the understory only 1-2% of the total daily PPFD received in the clearing. Mean daily PPFD during the dry season on days representing median irradiance conditions was 643 micromol/m²/s in the clearing, 145 in the 400m² gap, 60 in the 200m² gap, and 6 in the understory. Clear days produced a maximum of 778, 165, 71, and 12 micromol/m²/s, respectively. There were no consistent differences across the two seasons for the gaps and understory. Total daily PPFD ratios among sites during the dry season showed that the 400m² gap received 2.4 times as much light as the 200m² gap and 20-25 times that of the understory. The 200m² gap received 9 times the understory levels.

The gap sizes used by Chazdon and Fetcher (1984) overlap those used here and comparisons between the studies thus involve interpolations. The understory and gap results are uniformly lower than the data

presented in this study for seasonal summations of combined and clear days (Tables 3-3, 3-6), in spite of the higher solar altitudes at the tropical latitude of La Selva. Reasons probably include the greater leaf area index and higher atmospheric humidities in the rainforest.

Furthermore, peak PPF_D values on the clearest days were only 1559 micromol/m²/s in the 400m² gap and <200 micromol/m²/s in the 200m² gap. These values contrast significantly with the higher gap PPF_D peaks (Figure 3-6) in this study. The 9-fold difference between their 200m² gap and the understory compares favorably with the 11-fold difference between the large gap center and understory mean for combined days reported here (Table 3-6).

The importance of diurnal variability in PPF_D among sites discussed in Section 3.5. was also emphasized by Chazdon and Fetcher (1984), who commented on the importance of PPF_D frequency distributions as opposed to just mean daily PPF_D values. They pointed out that there is smaller day-to-day variability, but greater diurnal variability, as gap size increases. They also commented on the greater relative importance of small absolute changes in PPF_D in the range 0-100 micromol/m²/s, due to the linear nature of the photosynthetic response in this range. Again, this echoes points made in Sections 3.5. and 3.6.

Chazdon (1986) measured PPF_D in the understory and the centers and edges of gaps of three sizes (150m², 200m², and 400m²) during an analysis of understory palm ecophysiology at La Selva. She found that gap centers had consistently higher median, maximum, and minimum values of total daily PPF_D than gap edges. But as with the data presented by Chazdon and Fetcher (1984), all values for clear (maximum) and combined (median) days are lower for the centers of interpolated gap sizes than

the results presented here in Tables 3-4 and 3-6. The median and maximum values for total daily PPF_D in the 150m² and 200m² gaps are in the range for the small gaps (75m²) used here. Even the 400m² gap doesn't approach the values for the large gap (300m²) used here: (1) 5.79 versus 15.76 mol/m²/day on median/combined days, respectively; and (2) 15.00 versus 24.39 mol/m²/day for maximum/clear days, respectively. While lower values may have been expected, the degree to which the La Selva gap results differ from the Harvard Forest data is notable.

Chazdon (1986) commented on the spatial variability in understory diffuse irradiance, measuring a 2-3 fold difference over 10 meters. This is reminiscent of the 3-fold difference in average daily PPF_D between the north and south plots of the large understory (Tables 3-4 through 3-6), which occurred over a distance of approximately 13 meters. Chazdon also measured PPF_D along a N-S transect in the 200m² gap. The north edge received three times as much total daily PPF_D (1.66 mol/m²/day) as the south (0.56 mol/m²/day) in February, but this difference dissolved by May when the sun passed directly overhead. Consequently the N-S gradient so prevalent in gaps at the Harvard Forest latitude (42.5°N) is dampened greatly at La Selva (10.5°N), a pattern analyzed theoretically by Canham (1988b).

Torquebiau (1988) measured PPF_D in two vertical canopy stratification types (layered versus continuous) and a 320m² gap in Sumatra. Data from the gap center, the "transition zone" 13m into the understory, and full understory show respective daily PPF_D means of 181, 30, and 6 micromol/m²/s when averaged over two days of variable cloud cover. This represents a six-fold difference from gap center to transition zone, and a 30-fold difference versus the understory. If the

seasonally summed combined days data in the Harvard Forest research are roughly comparable to the variably cloudy days sampled by Torquebiau, then it is clear that the former are uniformly higher, with the center of the large gap receiving $365 \text{ micromol/m}^2/\text{s}$ and the most shaded understory site receiving $15 \text{ micromol/m}^2/\text{s}$. On the other hand, the ratio between these sites, a 24.3-fold difference, is not too far from the 30-fold ratio found in Sumatra. As Torquebiau noted, his understory values are lower than those reported by Chazdon and Fetcher (1984), while their 400m^2 gap was comparable in total daily PPF to his 320m^2 gap.

Denslow et al. (1990) measured PPF in four natural gaps ($275\text{-}355\text{m}^2$) and the understory in Costa Rica as part of an experimental study of gap partitioning among seven *Miconia* and *Piper* shrub species. Their data were taken at 70cm in the gap center, gap edge, and the full understory over a two-week period for each of the four gap sites. Total daily PPF (dawn to dusk) ranged from $4\text{-}11.5 \text{ mol/m}^2/\text{day}$ at gap centers (9-23% full sun), $1.5\text{-}5.5 \text{ mol/m}^2/\text{day}$ at gap edges (3-11% full sun), and $0.5\text{-}1.5 \text{ mol/m}^2/\text{day}$ (0.4-2.0% full sun) in the understory. These are average values for the 14-day sample periods. Assuming that the authors used a 12-hour dawn-to-dusk interval, these values are all lower than the combined days results for the large gap and understory in the Harvard Forest study.

In addition to PPF measurements, two other studies have reported temperature data for gaps. Fetcher et al. (1985) measured air temperature and vapor pressure at two-hour intervals in the full understory, a new 400m^2 natural gap, a 0.5-hectare clearing, and the upper canopy stratum in Costa Rica. In general, gap temperatures were like the upper canopy, and both were lower than the clearing and higher

than the understory. Nighttime temperatures were similar at all locations. During the first year following gap formation, gap temperatures exceeded understory temperatures by a maximum of 2.5° (at solar noon), and were significantly higher during the 9am-7pm period. Due to rapid regrowth in the gap, temperatures were indistinguishable from the understory from the second year onward.

Mladenoff (1987) measured air, litter, and soil (10cm) temperatures in the understory and single-tree gaps in hemlock-hardwood forests in northern Michigan. Since gap sizes and the details of temperature sampling were not reported, it is difficult to relate his results to this study. Midday temperatures just below the litter layer (roughly comparable to the 1cm data taken in the Harvard Forest study, showed greater differences between gap and understory ($0-8^{\circ}\text{C}$, depending on month) than the 10cm soil temperatures ($0-2^{\circ}\text{C}$). Maximum and minimum air temperatures showed the smallest difference between gaps and understory.

Finally, Phillips and Shure (1990) reported midday air and soil temperature data for three locations (center, edge, and halfway between) in four square clearcut patch sizes (160, 800, 4000, and 20000m^2) in western North Carolina. The data are from one day in each month from June to September 1983, and do not include site replicate measurements. The data presented for 11 September showed midday air and soil temperature differences of less than 1.0°C for all positions in the 160m^2 and 800m^2 gaps.

Several points can be made in summarizing the nature of the gap-understory gradient in this study. The gradient is quite broad, spanning plot positions that are fully exposed to potential direct beam irradiance for the entire growing season (large gap NW, NE) to plots

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that experience direct beam only as sunflecks (small gap south plots and all understory plots) (Section 3.4.). Most of the actual breadth of the gradient in absolute terms is due to large gap variability, especially on clear days (Section 3.5.2.).

The gradient changes seasonally with solar altitude in a complex fashion. Several months before and after solstice, the large gap north plots are the most isolated from all other plots, since they are the only locations to receive extended direct beam. As the season approaches solstice, increasing solar altitude and higher incident PPF values cause the large gap north plots to continue to exhibit increases in PPF levels and diurnal durations of direct beam irradiance. But the large gap centers and small gap north plots eventually experience extended durations of direct beam, and diffuse irradiance levels rise throughout the forest as the sun moves closer to zenith. The gradient is both broadest and most continuous at this point, especially on clear days. Following solstice, the gradient essentially reverses its development as autumnal equinox draws closer.

Hutchinson and Matt (1977) demonstrated that there is seasonal asynchrony between solar movement and canopy leaf phenology at temperate latitudes, such that the early spring is the only time when solar altitudes are great enough to generate higher irradiances through the leafless forest to the forest floor. By the time leaf senescence occurs in autumn, the sun has dropped too low toward the horizon to generate comparable irradiances. The seasonal development and regression of the gap-understory gradient is affected by this asynchrony as well. For days at equal distances from solstice, the spring gradient will be broader than the autumn gradient.

The effects of seasonal and diurnal solar movement on the gradient are multiplicative, in that the relative differences among sites and plots are increased by the interaction. If either periodicity were held constant, the gradient would show narrower extremes and less continuity than when they interact.

The gradient is strongly influenced by weather at all points in the season. Overcast conditions dampen spatial and diurnal variability enormously (Sections 3.5.1. through 3.5.3.), a fact noted by many authors (e.g., Reifsnyder et al. 1971; Hutchinson and Matt 1977). The discriminant analyses in Section 3.5.3. display this dampening visually, but also show that site-level distinctions (i.e. large gap, small gap, understory) increase while plot-level variation within sites declines considerably. It appears that the PPF gradient shrinks proportionately at the site-level during overcast days, such that the same ratios of total daily PPF and mean daily PPF hold among sites on clear and overcast days. The overall effect of variable weather conditions depends on the frequency of their occurrence as well as seasonal differences in relative abundances of cloud conditions.

Of the variables included in this study, irradiance is most important. This is so not only because irradiance drives temperature (and vapor pressure) variations, but because photosynthetically active light is so important to plant success. The results for mean daily air and soil temperatures suggest that they do not contribute much in absolute terms to the gradient. Furthermore, mean daily PPF, though it produces a distinct site/plot gradient on clear days and site gradient on overcast days, does not describe the gradient well alone. The frequencies of suboptimal and superoptimal PPF levels are even more

dramatic than mean PPF_D levels among sites and plots (Figures 3-17, 3-19), and the discriminant analysis for combined days suggested that the factor accounting for most of the variation in sites and plots (axis 1) was the frequency of suboptimal PPF_D (0-25 micromol/m²/s) (Section 3.5.3.). In like manner, the frequency of air temperatures above 25°C produced a modest gradient whereas mean daily temperatures did not (Figure 3-21). The upshot is that diurnal variability provides much of the distinction among sites and plots, distinctions not revealed by mean daily values.

Furthermore, diurnal variations show significant asynchrony among microclimatic variables. There is spatial asynchrony of direct beam and mean PPF_D levels between east and west sides of gaps that is paralleled in part by air and soil surface temperatures. The NE plots of large gaps thus receive superoptimal PPF_D levels later in the day at higher air temperatures than the NW plots. Conversely, the NE plots are not exposed to direct beam during the earlier morning hours when leaf water potentials are highest, relative humidities are typically highest, and photosynthesis is less limited by water stress. Both surface and deep soil temperatures lag behind PPF_D changes, producing temporal asynchrony in the temperature profile. Soil and air temperatures fluctuate out of phase to a degree that depends on time of season and weather conditions, and therefore shoot and root physiologies experience switching temperature relationships as well.

These and other forms of asynchrony are most prominent in the large gap and much reduced in the understory. They add a third vector of distinction among the site and plot positions, on top of the seasonal and diurnal single-factor patterns.

Finally, it is apparent that we need to define more precisely what the criteria are for judging the existence of a microenvironmental gradient and its effectiveness in sorting out any differences in species niches. For example, although the breadth of the gradient and the extreme values of light and temperature are much greater among sites on clear days, implying that such extremes would better separate species behaviors, it may be that low-light photosynthetic behavior is a critical key, and that overcast days contribute heavily to discrimination among species. Thus our judgment on the microenvironmental gradient is relative, based on the species in question and not on any absolute criteria.

This is true for comparisons within individual plants as well. For example, leaves are able to buffer themselves from elevated air temperatures through both physiological (latent heat loss) and behavioral (leaf drooping) mechanisms. In contrast, roots cannot move and do not possess comparable physiological adjustment mechanisms. Thus an absolute difference among plots of, say 5°C , may have a greater relative effect on root performance than on leaf performance. Then, if co-occurring species differ in root placement in the soil profile and/or adjustment to high temperatures, the belowground environment may play a decisive role in differential species success.

It should be obvious that the gap-understory microenvironmental gradient is not fixed in space, and that it fluctuates continuously on several temporal scales. The gradient is truly four-dimensional and quite difficult to summarize succinctly. If enough sensors were available, it would be possible to plot isopleths of irradiance and temperature variables and visualize how the gradient changes diurnally

and seasonally under different macroclimatic conditions. Lacking enough spatial sample points for contours, the best that can be done here is to present the rank order of the fifteen site/plot positions, based on mean PPFD levels and diurnal ranges of both PPFD and temperature:

LGNW ~ LGNE ~ LGC > SGNW ~ SGNE > LGSW ~ LGSE > SGC > SGSW ~

SGSE > LUC ~ LUSE ~ LUSW > LUNE ~ LUNW.

CHAPTER 4

SURVIVAL, GROWTH AND ARCHITECTURE OF ADVANCE-REGENERATED SEEDLINGS IN GAPS AND UNDERSTORY

4.1. METHODS

The survival and growth of the 2160 transplanted seedlings were measured through complete surveys at the end of each growing season from 1987 through 1989. The seedlings had been planted in October 1986, so all survival curves include four points. Since all hierarchical levels in the design contained the same initial number of seedlings (e.g. 36 seedlings in every plot), statistical analyses and graphs were based on actual 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; Section 4.2.1.). The same methods were used to test whether or not survival varied with initial age, height, or basal diameter (Section 4.2.2.). *Seedlings were partitioned into 10 classes within each variable: (1) 2-20 years for age, in 2-year intervals, (2) 4-40cm for height, in 4-cm intervals, and (3) 1.40-5.00mm for basal diameter, in 0.40mm intervals.*

Due to the July 1988 occurrence of relatively sudden wilting and subsequent death of numerous seedlings, an additional full survey of seedling status was made in early August 1988 to determine the site- and species-specific nature of the mortality. A pathogen was suspected as having played a role, and consequently is discussed as such in Section 4.2.3.

The pre-gap age, height and basal diameter (1cm above root collar)

of all surviving seedlings were recorded in September 1987, one year after transplanting and 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.

The growth data were also analyzed for treatment effects over time through analysis of variance (ANOVA). A split-split-plot model with selected interactions (Table 4-1) was fitted to several variables, including pre-gap age, height, and basal diameter, 1988 leader extension, 1989 leader extension, 1989 branch extension, 1989 total extension (leader plus branches), 1987-89 total leader extension, 1987-89 total branch extension, 1987-89 total shoot extension, 1987-89 cumulative height change, and 1987-89 cumulative basal diameter change.

Each 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. None of the pre-gap 1987 variables required transformation, but all of the growth variables were ln-transformed to produce more normally-distributed data, and the ANOVA model was fitted to transformed values. Homoscedasticity was confirmed by applying the F-max test (Sokal and Rohlf 1981) to residuals following model-fitting.

The explanatory power of the model was determined by calculating

Table 4-1. The split-split-plot ANOVA model applied to growth and architectural data. Several interactions were excluded from the model.

LEVEL	SOURCE OF VARIATION	DEGREES OF FREEDOM	EXPLANATION
MAIN	BLOCK [1,2,3]	2	Difference Among Block Replicates, Tested Over ERROR(1)
	SITE [LG,SG,LU,SU]	3	Difference Among Site Types, Tested Over ERROR(1)
	ERROR(1) = BLOCK x SITE	6	
SPLIT	PLOT [NW,NE,C,SW,SE]	4	Difference Among Plot Positions Overall, Regardless of Site, Tested Over ERROR(2)
	SITE x PLOT	12	Variable Plot Relationships Across Site Types, Tested Over ERROR(2)
	ERROR(2) = (BLOCK x PLOT) + (BLOCK x SITE x PLOT)	32	
SPLIT-SPLIT	SPECIES [PEN,RUB,SAC]	2	Difference Among Species Overall, Regardless of Site Type and Plot Position, Tested Over ERROR(3)
	PLOT x SPECIES	8	Variable Relationships Among Species Across Plot Positions, Regardless of Site Type, Tested Over ERROR(3)
	SITE x SPECIES	6	Variable Relationships Among Species Across Site Types, Regardless of Plot Position, Tested Over ERROR(3)
	SITE x PLOT x SPECIES	24	Variable Relationships Among Species Across Plot Positions Within Sites, Tested Over ERROR(3)
	ERROR(3) = RESIDUAL	2060	
TOTAL		2159	2160 Experimental Units (Seedlings) - 1

the correlation coefficient (R^2) for the scatterplot of residuals versus normalized scores. With one exception, these coefficients exceeded 90% without removing outliers. The exception (1987-89 net basal diameter change) required the removal of 15 outliers from a total of 1705 data points.

Post-hoc multiple comparisons of groups within treatments were done in two ways. First, Tukey box plots (Sokal and Rohlf 1981) were graphed for both the input data (ln-transformed) and the predicted scores (following model-fitting). These plots indicate, through 95% confidence intervals around medians, which groups within a treatment differ from each other. The plots also identify the presence of modest and extreme outliers. The second post-hoc comparison method was the use of the Tukey HSD test. In a recent comprehensive review of multiple comparisons following ANOVA, Day and Quinn (1989) recommended the Tukey HSD as one of the few tests that both preserves experiment-wise error rate and is robust enough to handle unequal cell sizes. This test provides probability levels for significant differences among all possible pairwise combinations of groups within treatments. A probability level of $p=0.05$ was used as the significance cutoff for all pairwise tests.

Shoot architectural variables were measured in 1987 and 1989 on survivors only. The 1987 pre-gap 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) individual branch origins on the stem, divided into upper, middle, and lower thirds; and (3) mean leaf (laminar) length. Additional notes were taken on what were often complexly branched individuals.

Total leaf areas per shoot were estimated through species-specific regressions of leaf area on laminar length (Section 4.4.1.). Leaves were collected from naturally-established young seedlings of all three species. Their laminar lengths were measured to the nearest 1.0mm, and their areas were determined individually to the nearest 0.01cm^2 with a Lambda Instruments 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. Since the coefficients did not differ greatly across pairs within species, the leaf pairs were pooled and curves were fitted to the pooled data. This provided a single function for each species for estimating shoot leaf area from the mean laminar length. Total leaf areas were calculated in this fashion for the 1989 architectural data.

The means and standard errors for the architectural data were compared across 1987 and 1989. In addition, the same analysis of variance model used for growth variables was applied to 1989 mean leaf length, mean leaf area, and total leaf area.

As with survival, it was important to know if post-gap growth was related in any consistent way to pre-gap age, height, and basal diameter. Scatterplots of pre- and post- variable pairs were graphed. The original intention was to fit linear or curvilinear functions to these plots. However, as will be seen, no predictable relationships emerged. The scatterplots themselves are presented (Section 4.3.2.) to emphasize the surprising lack of dependence of post-gap response on pre-gap status.

It became obvious during the above analyses that the effects of shoot damage - specifically leader loss, dieback, and branching - would

have to be analyzed more closely. By 1989, extensive leader loss and branching had occurred, producing enormous variability in shoot architectures as compared to the relative simplicity of the undamaged seedlings transplanted in 1986. It was apparent that an adequate judgment on whether or not growth differences supported gap partitioning would require separate analyses of undamaged and damaged seedlings, in addition to their combined analysis. So summary statistics were calculated for these two sub-groups and the Tukey HSD test applied to groups within treatments (Section 4.5.).

4.2. SURVIVAL

4.2.1. SURVIVAL ACROSS TIME AND TREATMENTS

Table 4-2 summarizes survival in absolute numbers and percentages for various hierarchical breakdowns within the study. Total survival in the year following transplanting (1986-87) was 95%, with no notable differences among species or sites. Thus the bare-root transplanting technique following leaf senescence and the provision of over 18 months in the ameliorated understory before exposure in the new gaps (10/86-4/88) produced satisfying survival rates, insuring the initial success of the experiment.

The overall survival rate after three years (35 months) was 79%. Mortality rates within years increased steadily, from 5% in 1986-87 to 7% in 1987-88 and 9% in 1988-89.

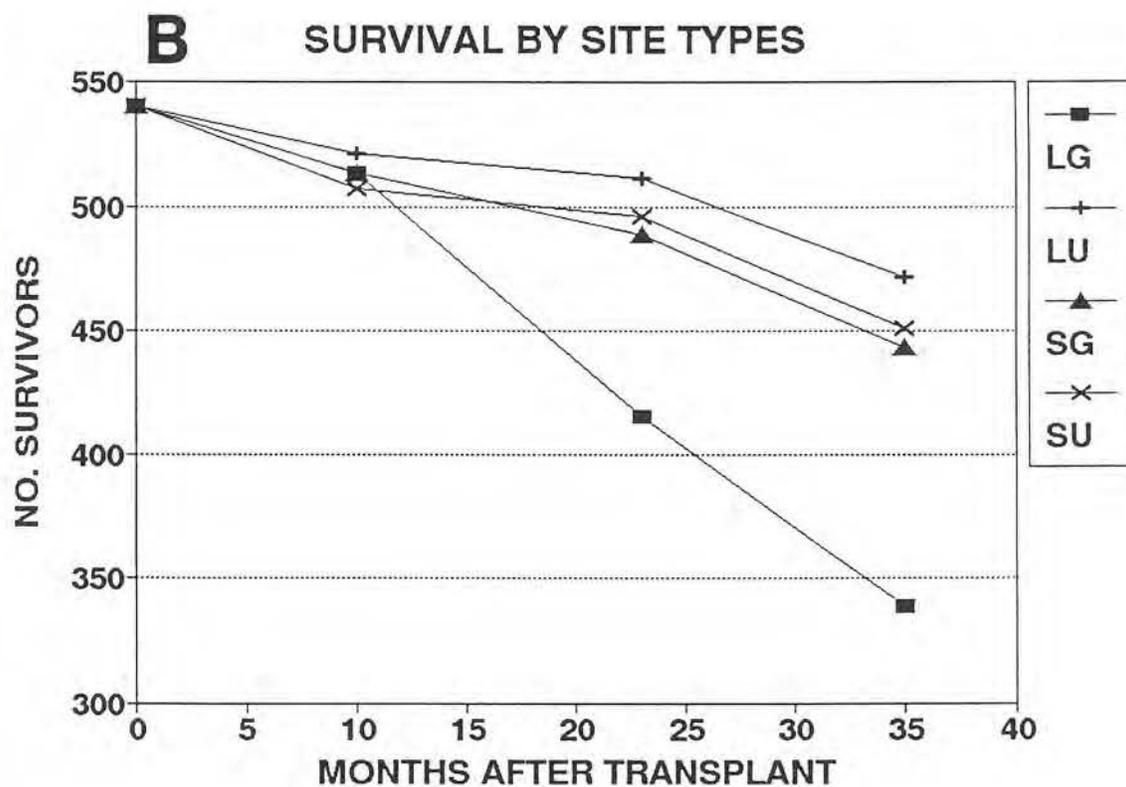
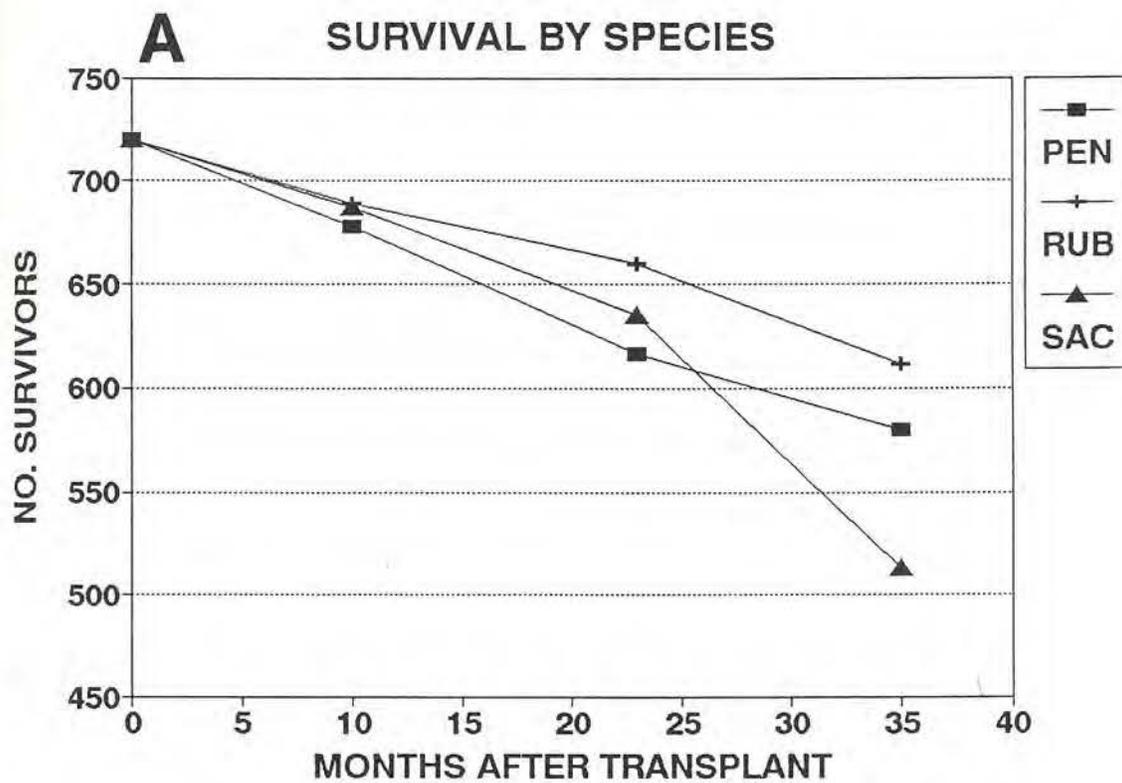
The three species showed divergent survival patterns over the three years (Figure 4-1, Table 4-2). Mortality rates did not change markedly for any of the three species during the first growing season following gap creation (at 10 months). The red and striped maple curves are quite

Table 4-2. (Next two pages) Survival by various categories over the course of the study.

CATEGORY	YEAR MONTHS	NUMBER ALIVE				PERCENT ALIVE				
		1986 0	1987 10	1988 23	1989 35	1987 10	1988 23	1989 35		
STUDY TOTAL	ALL	2160	2054	1911	1705	95	88	79		
SPECIES	P	720	678	616	580	94	86	81		
	R	720	689	660	612	96	92	85		
	S	720	687	635	513	95	88	71		
BLOCK	B1	720	696	618	440	97	86	61		
	B2	720	686	660	596	95	92	83		
	B3	720	672	633	569	93	88	79		
SITE TYPE	LG	540	513	415	339	95	77	63		
	LU	540	521	511	472	96	95	87		
	SG	540	513	489	443	95	91	82		
	SU	540	507	496	451	94	92	84		
SITE/SPP	LG	P	180	165	117	96	92	65	53	
	LG	R	180	176	158	144	98	88	80	
	LG	S	180	172	140	99	96	78	55	
	LU	P	180	174	172	164	97	96	91	
	LU	R	180	176	173	161	98	96	89	
	LU	S	180	171	166	141	95	92	78	
	SG	P	180	172	163	156	96	91	87	
	SG	R	180	168	165	155	93	92	86	
	SG	S	180	173	161	132	96	89	73	
	SU	P	180	167	164	161	93	91	89	
	SU	R	180	169	164	152	94	91	84	
	SU	S	180	171	168	138	95	93	77	
	SITE/PLOT	LG	C	108	102	77	61	94	71	56
		LG	NE	108	102	74	51	94	69	47
		LG	NW	108	99	57	32	92	53	30
LG		SE	108	105	102	98	97	94	91	
LG		SW	108	105	105	97	97	97	90	
LU		C	108	105	103	97	97	95	90	
LU		NE	108	102	96	89	94	89	82	
LU		NW	108	106	106	98	98	98	91	
LU		SE	108	102	102	90	94	94	83	
LU		SW	108	106	104	98	98	96	91	
SG		C	108	97	92	81	90	85	75	
SG		NE	108	101	94	81	94	87	75	
SG		NW	108	106	103	94	98	95	87	
SG		SE	108	104	96	92	96	89	85	
SG		SW	108	105	104	95	97	96	88	
SU		C	108	103	100	87	95	93	81	
SU		NE	108	95	91	82	88	84	76	
SU		NW	108	104	102	96	96	94	89	
SU		SE	108	103	101	97	95	94	90	
SU		SW	108	102	102	89	94	94	82	

CATEGORY	YEAR MONTHS	NUMBER ALIVE				PERCENT ALIVE		
		1986 0	1987 10	1988 23	1989 35	1987 10	1988 23	1989 35
LG C P		36	31	17	13	86	47	36
LG C R		36	36	32	30	100	89	83
LG C S		36	35	28	18	97	78	50
LG NE P		36	33	19	11	92	53	31
LG NE R		36	35	31	27	97	86	75
LG NE S		36	34	24	13	94	67	36
LG NW P		36	31	13	6	86	36	17
LG NW R		36	34	25	20	94	69	56
LG NW S		36	34	19	6	94	53	17
LG SE P		36	35	33	33	97	92	92
LG SE R		36	35	34	32	97	94	89
LG SE S		36	35	35	33	97	97	92
LG SW P		36	35	35	33	97	97	92
LG SW R		36	36	36	35	100	100	97
LG SW S		36	34	34	29	94	94	81
LU C P		36	35	34	33	97	94	92
LU C R		36	36	36	33	100	100	92
LU C S		36	34	33	31	94	92	86
LU NE P		36	34	34	32	94	94	89
LU NE R		36	34	31	29	94	86	81
LU NE S		36	34	31	28	94	86	78
LU NW P		36	34	34	33	94	94	92
LU NW R		36	36	36	34	100	100	94
LU NW S		36	36	36	31	100	100	86
LU SE P		36	35	35	34	97	97	94
LU SE R		36	35	35	30	97	97	83
LU SE S		36	32	32	26	89	89	72
LU SW P		36	36	35	35	100	97	97
LU SW R		36	35	35	35	97	97	97
LU SW S		36	35	34	28	97	94	78
SG C P		36	32	30	28	89	83	78
SG C R		36	31	30	29	86	83	81
SG C S		36	34	32	23	94	89	64
SG NE P		36	35	32	29	97	89	81
SG NE R		36	34	34	28	94	94	78
SG NE S		36	32	28	23	89	78	64
SG NW P		36	35	34	32	97	94	89
SG NW R		36	35	34	33	97	94	92
SG NW S		36	36	35	29	100	97	81
SG SE P		36	35	32	32	97	89	89
SG SE R		36	34	33	32	94	92	89
SG SE S		36	35	31	28	97	86	78
SG SW P		36	35	35	33	97	97	92
SG SW R		36	34	34	33	94	94	92
SG SW S		36	36	35	29	100	97	81
SU C P		36	34	33	33	94	92	92
SU C R		36	34	33	29	94	92	81
SU C S		36	35	34	25	97	94	69
SU NE P		36	31	31	31	86	86	86
SU NE R		36	31	28	25	86	78	69
SU NE S		36	33	32	26	92	89	72
SU NW P		36	35	33	33	97	92	92
SU NW R		36	36	36	35	100	100	97
SU NW S		36	33	33	28	92	92	78
SU SE P		36	34	34	33	94	94	92
SU SE R		36	33	32	32	92	89	89
SU SE S		36	36	35	32	100	97	89
SU SW P		36	33	33	31	92	92	86
SU SW R		36	35	35	31	97	97	86
SU SW S		36	34	34	27	94	94	75

Figure 4-1. Survival of seedlings by species (A) and site type (B) over the course of the study. The points represent full censuses taken in the fall (September or October) of each of the years 1986-89.



similar, although the mortality rate for red was slightly lower than striped in 1987-88 and slightly higher in 1988-89. Sugar maple showed a sharp drop from 1988 to 1989 for unclear reasons. As of October 1989, the species differed significantly in the time course of survival ($X^2=8.98$, $p<0.025$; Table 4-3), with RUB > PEN > SAC at the end of three years.

Survival also differed among site types (Figure 4-1). The understory and small gap sites showed parallel trends over time, with the highest mortalities in 1988-89 and the lowest in the first year following gap creation. The large gaps diverged dramatically from the other sites immediately following gap creation, and exhibited a fairly constant mortality in the subsequent two years. As a consequence of the 20% greater losses in large gaps, the sites differed significantly in survival trends by the end of 1989 ($X^2=24.85$, $p<0.001$; Table 4-3), with LUND > SUND > SGAP > LGAP.

Figure 4-2 displays species survival within site types. All species showed greater losses in the large gaps and essentially parallel responses in the other three sites. There were differences, however. Red maple showed the least mortality in large gaps (20%), while striped maple showed the greatest (47%). In all other sites, the order of survival was PEN > RUB > SAC. Again, sugar maple showed accelerated mortality in 1988-89 across all sites, suggesting that the causal factor was not the site treatment. In support of this, red maple also exhibited a slight acceleration in all but the large gap plots.

Figure 4-3 plots the same data as Figure 4-2, but directly compares species within sites. In spite of the noticeable drops in sugar maple during 1988-89 in the small gap and understory sites, only the large gap

Table 4-3. Chi-square and G-tests for differential survival patterns across the three study years by groups in various breakdowns.

COMPARISON	X2 or G	prob	RANK ORDER
SPECIES	8.98	< 0.025	R > P > S
SITES	24.85	< 0.001	LU > SU > SG >> LG
SPECIES WITHIN SITES			
LGAP	12.79	< 0.005	R >> S = P
SGAP	5.80	> 0.100	n.s.d.
LUND	1.81	> 0.100	n.s.d.
SUND	1.79	> 0.100	n.s.d.
PLOTS WITHIN SITES			
LGAP	49.77	< 0.005	SE = SW > C > NE > NW
SGAP	2.22	> 0.500	n.s.d.
LUND	0.87	> 0.900	n.s.d.
SUND	1.90	> 0.100	n.s.d.
SPECIES WITHIN PLOTS WITHIN SITES			
LGAP	15.36	= 0.052	R > P = S in NW,NE,C
SGAP	0.33	> 0.99	n.s.d.
LUND	0.78	> 0.99	n.s.d.
SUND	1.26	> 0.99	n.s.d.

Figure 4-2. Survival of seedlings by species over the course of the study. The points represent censuses taken in the fall (September or October) of each of the years 1986-89. (A) *Acer pensylvanicum*, (B) *Acer rubrum*, (C) *Acer saccharum*.

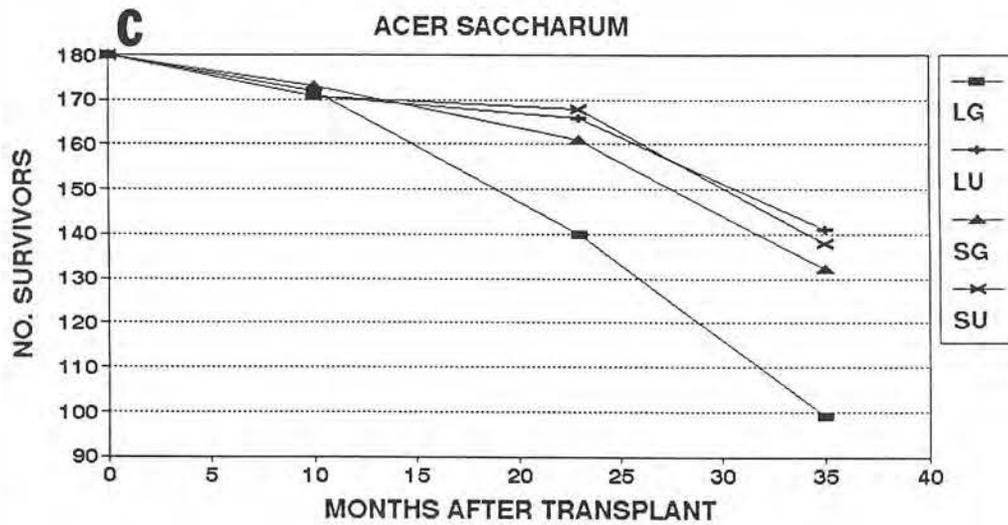
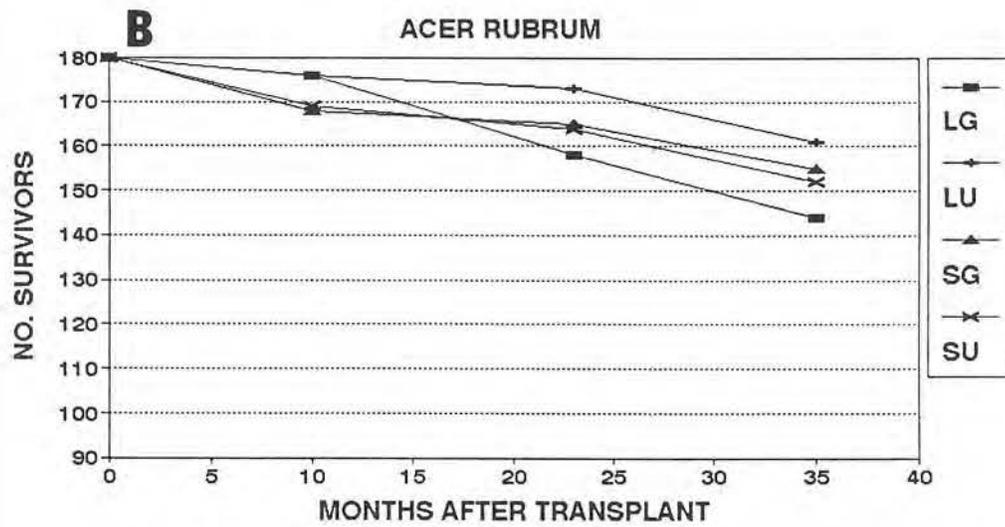
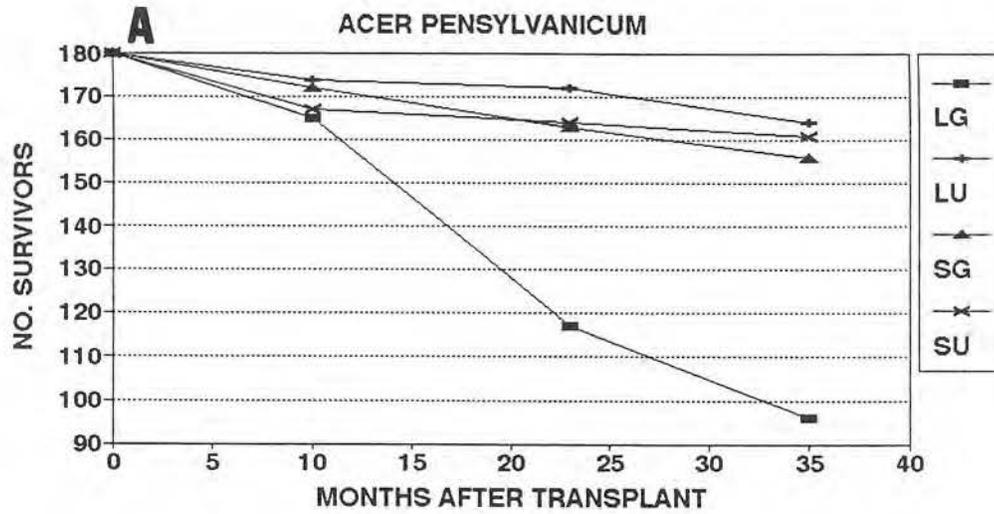
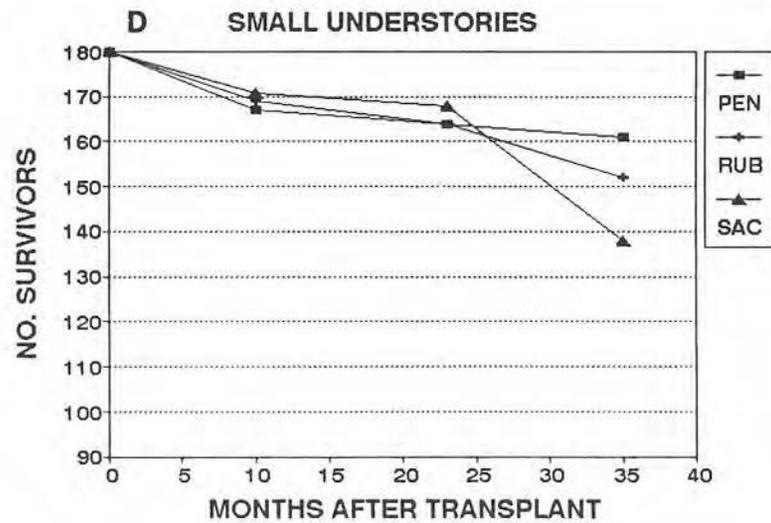
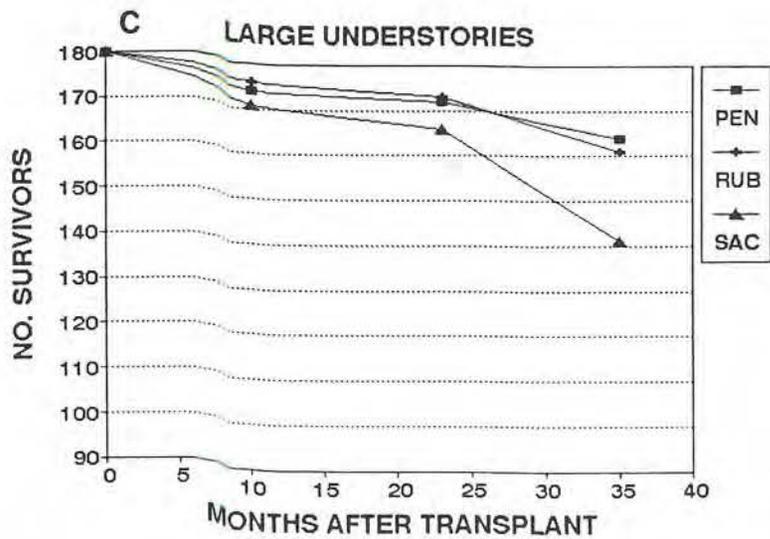
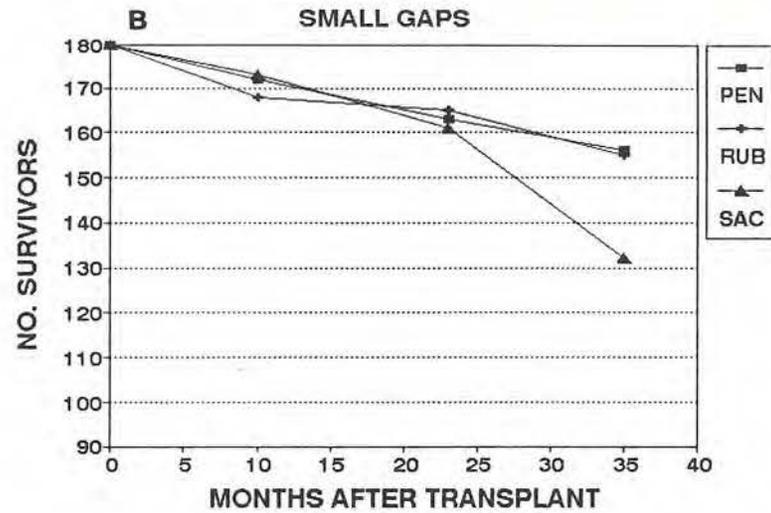
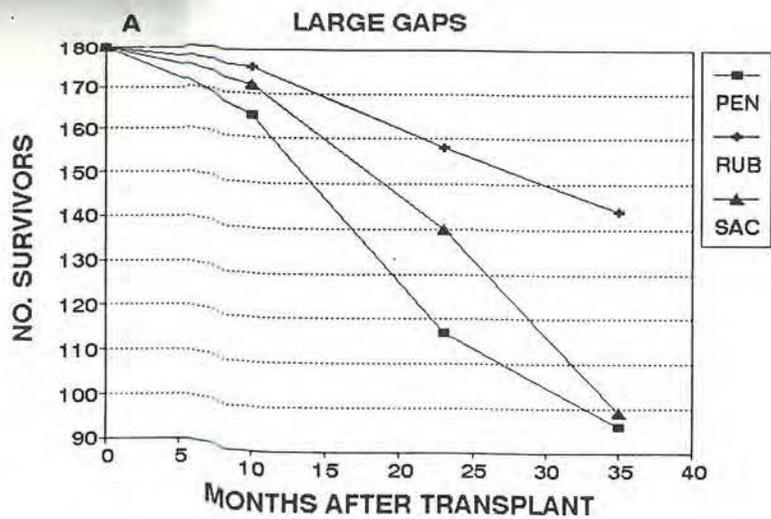


Figure 4-3. Survival of seedlings by species within site types over the course of the study. The points represent full censuses taken in the fall (September or October) of each of the years 1986-89. (A) Large gaps, (B) Small gaps, (C) Large understories, (D) small understories.

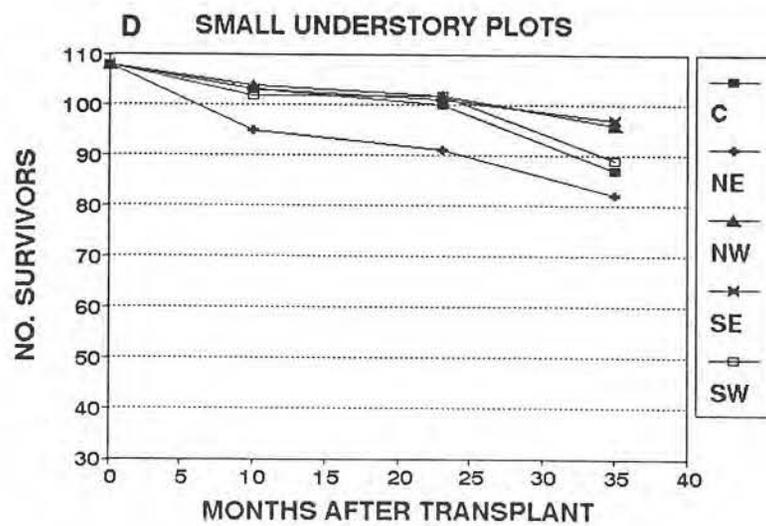
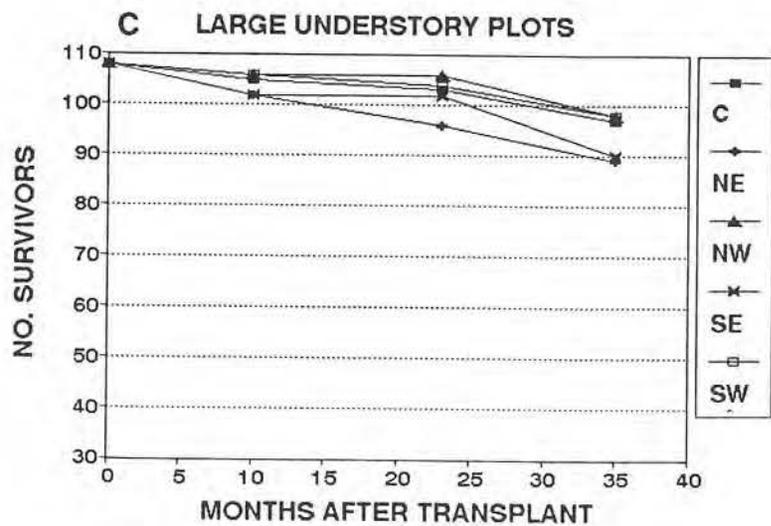
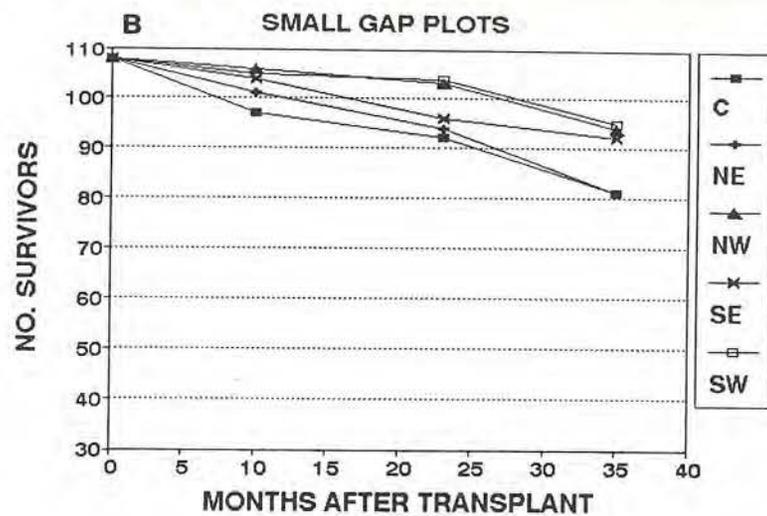
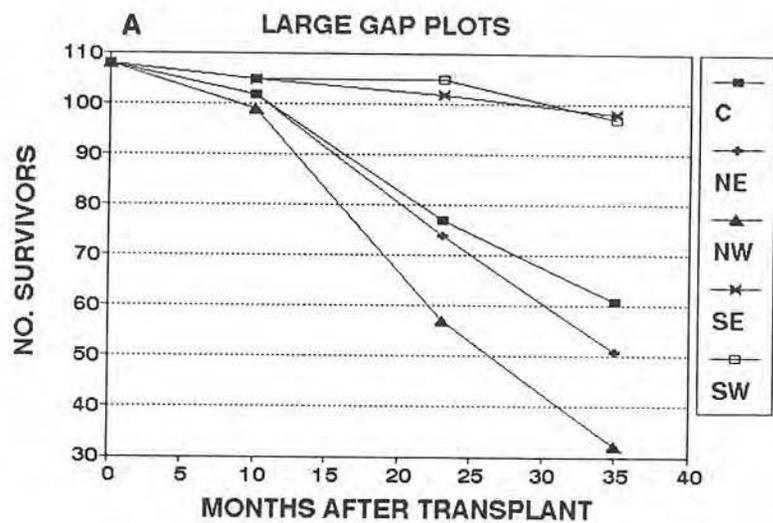


elicited significant differences among species as of 1989 (RUB > SAC = PEN, $X^2=12.79$, $p<0.005$; Table 4-3). The other sites produced uniform relative rankings among species (PEN => RUB > SAC), even though the differences were non-significant. The two understory sites had slightly higher survival by all species than the small gaps.

Plot positions within sites yielded some significant differences for all species combined (Figure 4-4), but only in the large gaps, where SE = SW > C > NE > NW ($X^2=49.77$, $p<0.005$). The plot differences in the large gap diverged since just after gap creation. In contrast, none of the other three sites yielded significant differences among plots (Table 4-3). The maximum difference between plots was 60% in large gaps, and only 9-14% in the other sites. All plots in the understory and small gap sites showed greater than 75% survival through 1989, and the south plots of the large gap even showed better than 90% survival. But the large gap C, NE, and NW plots showed only 30-56%. Whereas there was a clear north-south gradient of survival in the large gaps, no such pattern occurred, even a non-significant pattern, in the small gaps.

Table 4-3 summarizes G-statistics for two-way contingency analysis of differential survival by species within plots for each site. Again, the only significant differences occurred in the large gap, where R > P ~ S in the NW, NE, and C plots ($G=15.36$, $p=0.052$). In fact, the results in all other sites were very non-significant. So the conclusion is that the patterns exhibited among plot positions within sites (Figure 4-4) are supported by the analysis of individual species behaviors in these plots. Apparently all three species survived in parallel fashion across all positions except the center and north plots of large gaps.

Figure 4-4. Survival of seedlings by plot positions within site types over the course of the study. The points represent full censuses taken in the fall (September or October) of each of the years 1986-89. (A) Large gaps, (B) Small gaps, (C) Large understories, (D) Small understories.



4.2.2. SURVIVAL VERSUS PREVIOUS AGE AND SIZE

Even though the transplanted seedlings were selected within a fairly narrow size range (especially height), there were initial variations that could play a role in post-gap survival. For example, larger seedlings would be expected to have, on average, greater quantities of stored carbohydrates with which to adjust physiologically and morphologically to transplant shock and gap release. However, the results of testing for survival across initial age, height, and basal diameter classes were uniformly non-significant for all hierarchical breakdowns (Table 4-4). The probability values were not only insignificant, but overwhelmingly so. So there is a complete lack of any effect of previous status. This raises interesting questions about the importance of sustained growth during the suppressed stage before gap release, as well as the interpretation of age class data. These and other issues will be taken up in the Discussion (Section 4.6.).

4.2.3. PATHOGEN-RELATED MORTALITY IN AUGUST 1988

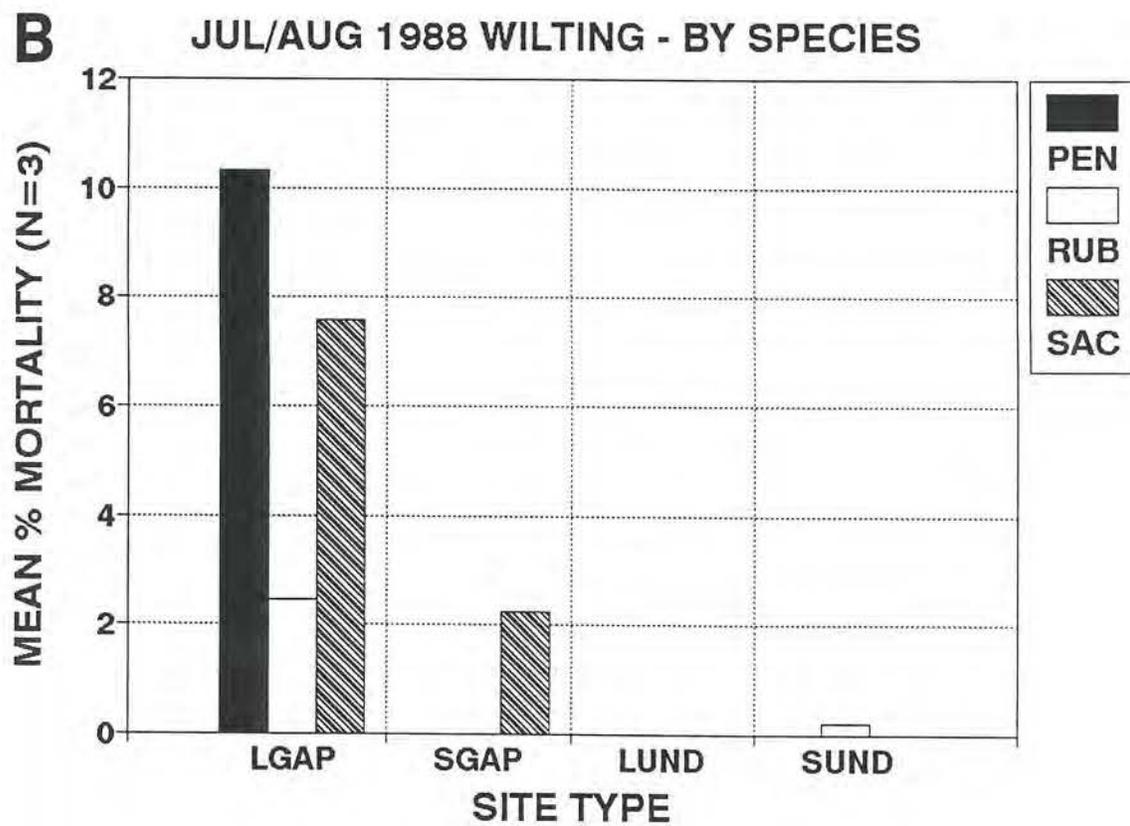
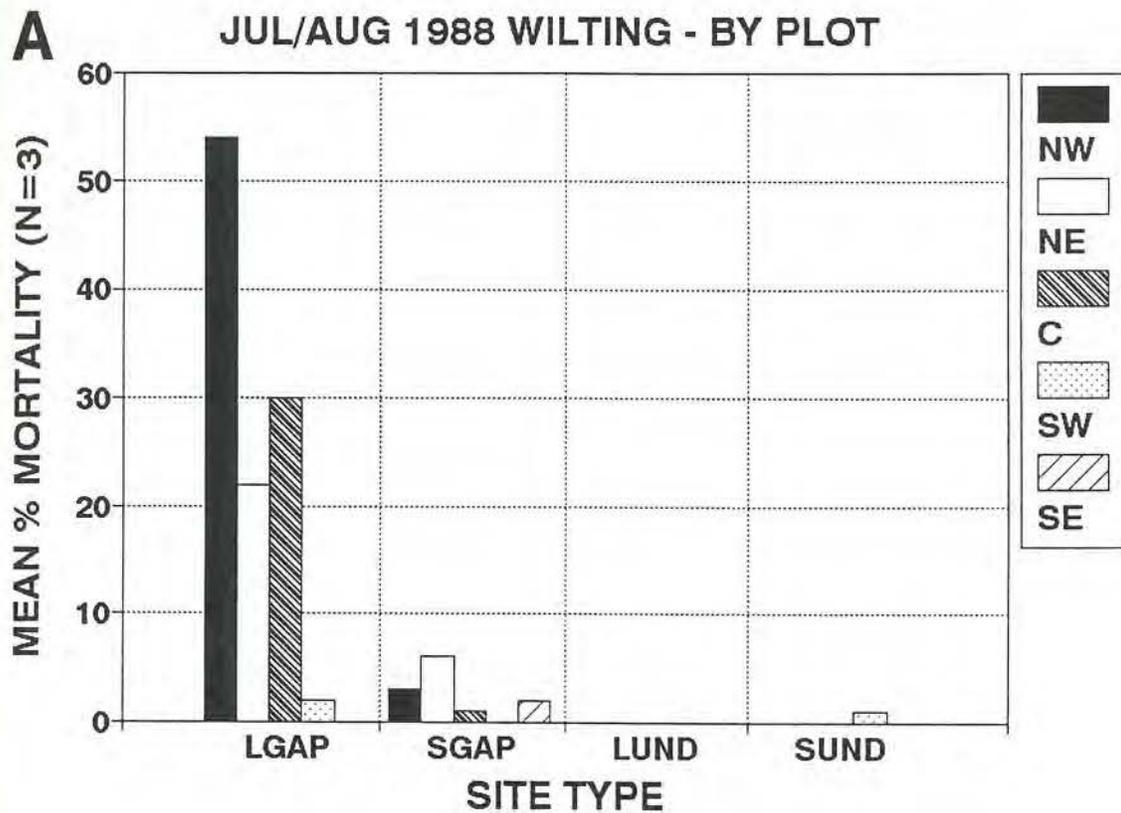
In 1988, a relatively warm and dry (2-4cm below average) May and June were followed by an unusually wet July (8cm above average). Numerous seedlings began to wilt suddenly in late July during the wettest part of the growing season. Over a three week period, the leaves of 109 seedlings wilted, browned but did not abscise, and the stems gradually dried and died from the top down. The wilting appeared to be site- and species-specific.

The results of a full seedling survey in mid-August 1988 are shown in Figure 4-5. The largest losses, in both absolute terms and the percentage of seedlings alive just prior to the wilting, occurred in the

Table 4-4. G-tests for the effects of pre-gap age, basal diameter, and height classes on differential survival.

CATEGORY	AGE		BAS DIAMETER		HEIGHT	
	G	prob <	G	prob <	G	prob <
TOTAL	1.13	0.99	4.68	0.90	1.98	0.99
PEN	0.86	0.99	1.67	0.99	0.89	0.99
RUB	0.97	0.99	2.47	0.99	0.15	0.99
SAC	0.24	0.99	5.36	0.90	4.37	0.90
LGAP	2.18	0.99	5.00	0.90	4.33	0.90
SGAP	0.36	0.99	3.07	0.97	0.15	0.99
LUND	0.11	0.99	1.51	0.99	1.61	0.99
SUND	0.18	0.99	1.43	0.99	0.85	0.99
LGAP PEN	3.65	0.97	3.12	0.97	4.52	0.90
LGAP RUB	2.04	0.99	3.57	0.97	0.72	0.99
LGAP SAC	0.29	0.99	1.13	0.99	1.22	0.99
SGAP PEN	1.37	0.99	1.58	0.99	0.16	0.99
SGAP RUB	0.31	0.99	0.44	0.99	0.09	0.99
SGAP SAC	0.33	0.99	2.06	0.99	0.93	0.99
LUND PEN	0.03	0.99	0.07	0.99	0.02	0.99
LUND RUB	0.06	0.99	2.34	0.99	1.49	0.99
LUND SAC	0.05	0.99	1.16	0.99	2.24	0.99
SUND PEN	0.04	0.99	0.37	0.99	0.32	0.99
SUND RUB	0.10	0.99	0.30	0.99	0.16	0.99
SUND SAC	0.13	0.99	3.00	0.97	3.23	0.97

Figure 4-5. Occurrence of rapid wilting and mortality in July-August 1988, by plot position (A) and species (B) within site types. Data are the percentage of those seedlings that had survived until 7.15.88.



more exposed plots of the large gaps (NW, NE, and C). These plots suffered 20-53% mortality. Some losses occurred on the south side of large gaps (3%) and in the small gaps (3-6%), and just one seedling died in the understory.

Among the three species, striped maple lost the largest percentage in the large gap, followed by sugar maple and then red maple. Only sugar maple succumbed in the small gaps, and only red maple lost any seedlings (1) in the understories. Some of the wilted individuals have recovered since August 1988, typically resprouting from basal meristems. But most (>80%) have died.

The cause of the wilting is most likely an interaction between physical stress and a pathogen. It is clear that the mortality was site- and plot-specific, that it was most severe in plots experiencing the greatest radiation loads and potential for thermal stress (Section 3.5.). The seedlings in the north and center plots had been observed closely prior to the wilting during regular phenological and gas-exchange sampling, and there was no doubt that they were not as vigorous as those in the south plots and other sites. However, the wilting occurred so rapidly during a relatively wet period that it is difficult to believe it could have been due to physical stress alone.

Tree pathologists at the University of Massachusetts, Amherst suggested that the shoestring fungus, *Armillaria mellea*, may be responsible. *Armillaria* is a generalist root-rot genus with species and strains widespread throughout temperate regions (Sinclair et al. 1987). It is known to be a prominent pathogen in our region (Spaulding 1940), and is regarded as being most successful in attacking both conifers and hardwoods of any age or size class that are already stressed by other

physical or biological agents. The true identity of the pathogen has not been confirmed as of the present, but the working hypothesis is that *Armillaria mellea* is the most likely candidate.

Although the wilting was dramatic and site-specific, the total number of individuals affected (109) was not large enough to cause mortality rates among species or sites to be noticeably greater in 1988 than in 1989 (Figure 4-1). On a site/plot basis, mortality rates were slightly greater in 1988 than in 1989 in the exposed plots of large gaps (Figure 4-4). So the pathogen effectively eliminated significant numbers of seedlings from the high-exposure end of the gap-understory gradient, but not in such a way as to alter overall mortality rates across the study when compared to the following year (1989).

4.3. GROWTH

4.3.1. GROWTH ACROSS TIME AND TREATMENTS

This discussion of growth results is divided into four components, presented in the following order: (1) 1987 pre-gap initial status, (2) 1988 growth, (3) 1989 growth, and (4) 1987-89 cumulative growth. Summary statistics are presented for all variables in all years. ANOVA results are tabulated for selected variables, and the 1987-89 cumulative growth results are graphed.

4.3.1.1. 1987 PRE-GAP INITIAL STATUS

The pre-gap status of the transplanted seedlings is summarized by various breakdowns in Table 4-5, with ANOVA results in Table 4-6. The species differed significantly in age ($F=353.36$, $p<0.001$), with striped maple (9.7 yrs) older than sugar (8.1 yrs) and red maple (6.6 yrs). This

Table 4-5. Summary of 1987 pre-gap initial status and 1988 growth.

CATEGORY	87 AGE (yrs)			87 HEIGHT (mm)			87 BDIAM (0.01mm)			88 LEADER EXT (mm)			88 BDIAM CHANGE			88 BDIAM (0.01mm)		
	N	MEAN	S.E.	N	MEAN	S.E.	N	MEAN	S.E.	N	MEAN	S.E.	N	MEAN	S.E.	N	MEAN	S.E.
TOTAL	1864	8.1	0.06	2092	166	1.2	2094	256	1.3	1903	14.5	0.45	1909	22	1.0	1904	280	1.5
PEN	647	9.7	0.09	695	153	2.4	694	258	2.3	612	11.9	0.55	614	27	1.6	612	287	2.5
RUB	601	6.6	0.09	699	161	1.7	700	245	2.2	656	20.7	1.13	660	26	1.9	658	273	2.7
SAC	616	8.1	0.09	698	183	2.1	700	266	2.2	635	10.6	0.28	635	12	1.4	634	281	2.3
LGAP	475	8.3	0.11	523	162	2.1	522	257	2.7	413	18.9	1.73	416	29	2.8	414	290	3.5
SGAP	453	7.9	0.11	524	169	2.2	524	255	2.5	489	14.9	0.62	488	27	1.8	487	286	2.8
LUND	459	8.3	0.12	528	164	2.1	528	255	2.5	508	12.9	0.57	510	18	1.5	508	275	2.6
SUND	477	8.1	0.12	517	167	3.3	520	257	2.7	493	12.1	0.36	495	14	1.5	495	273	2.8
BLOCK 1	634	8.0	0.10	706	169	1.9	705	262	2.4	614	11.9	0.39	617	14	1.4	616	278	2.6
BLOCK 2	624	8.6	0.10	702	167	2.5	703	254	2.1	659	14.1	0.50	660	26	1.5	658	283	2.3
BLOCK 3	606	7.8	0.10	684	160	1.9	686	252	2.2	630	17.4	1.19	632	24	2.0	630	280	2.7
LGAP PEN	159	10.0	0.16	172	146	3.2	171	252	4.6	116	12.5	1.33	117	29	4.6	116	285	6.3
RUB	158	6.8	0.17	176	161	3.4	176	252	4.4	157	31.0	4.23	159	43	5.6	158	297	6.5
SAC	158	8.0	0.17	175	180	3.8	175	267	4.8	140	10.8	0.83	140	12	3.1	140	285	5.4
SGAP PEN	164	9.2	0.19	176	152	3.3	175	253	4.3	163	13.9	1.16	162	37	3.2	162	293	5.0
RUB	140	6.3	0.16	172	169	3.4	173	249	4.7	165	19.9	2.25	165	33	3.1	165	284	5.3
SAC	149	8.0	0.17	176	185	4.2	176	264	3.8	161	10.8	0.52	161	12	2.9	160	280	4.3
LUND PEN	163	9.8	0.17	176	154	3.3	176	259	4.4	171	11.3	1.28	171	24	2.8	170	286	4.5
RUB	146	6.5	0.17	178	156	3.2	178	241	4.1	171	16.6	0.96	173	16	2.6	172	260	4.2
SAC	150	8.4	3.96	174	184	4.1	174	265	0.2	166	10.7	0.49	166	14	2.1	166	280	4.6
SUND PEN	161	9.8	0.20	171	162	8.1	172	266	4.8	162	10.2	0.41	164	19	2.4	164	285	4.9
RUB	157	6.5	0.18	173	157	3.4	173	237	4.4	163	16.0	0.84	163	13	2.5	163	252	4.8
SAC	159	8.0	0.17	173	183	4.6	175	268	4.5	168	10.1	0.43	168	11	2.9	168	281	4.5
LGAP C	91	8.1	0.24	102	159	4.2	103	259	5.7	77	40.0	8.26	77	53	11.4	76	316	12.1
NE	95	8.3	0.27	104	155	4.4	104	246	5.9	74	15.7	1.63	75	23	6.3	74	278	7.6
NW	94	8.4	0.24	104	164	5.5	101	263	6.2	57	16.7	2.49	57	20	4.2	57	286	8.7
SE	95	8.0	0.27	106	163	4.9	107	253	6.0	101	12.4	1.10	102	28	3.6	102	282	5.3
SW	100	8.5	0.25	107	171	4.2	107	266	6.1	104	13.2	1.45	105	20	3.1	105	288	6.1
SGAP C	83	7.7	0.27	102	175	5.0	103	253	5.7	92	12.6	1.19	92	27	4.3	92	283	6.8
NE	96	8.0	0.24	103	170	5.2	103	251	5.6	94	13.7	1.08	94	21	3.1	94	277	6.1
NW	91	8.3	0.28	107	171	4.8	107	263	5.1	103	16.5	1.39	103	36	4.0	103	299	6.1
SE	86	7.6	0.22	105	166	4.5	105	253	5.5	96	13.9	1.17	96	31	3.7	96	285	6.3
SW	97	7.9	0.25	107	162	4.8	106	256	5.7	104	17.4	1.78	103	22	5.0	102	283	6.2
LUND C	96	7.9	0.26	107	163	4.8	107	260	5.3	103	14.4	0.98	103	21	3.7	103	282	5.6
NE	89	8.2	0.28	105	163	4.0	105	244	5.5	95	11.2	0.64	96	15	3.2	96	262	5.1
NW	96	8.4	0.22	107	157	5.0	107	249	5.4	104	11.1	0.60	106	15	3.6	104	269	5.6
SE	90	8.5	0.27	102	163	4.0	102	261	5.9	102	13.4	2.17	101	18	3.0	101	280	6.6
SW	88	8.6	0.29	107	176	5.3	107	260	5.3	104	14.1	1.27	104	20	2.9	104	283	5.8
SUND C	97	8.1	0.26	106	178	12.3	106	263	6.3	100	12.6	0.99	100	11	3.2	100	277	7.0
NE	92	8.3	0.25	97	162	5.6	99	251	6.0	90	11.2	0.63	91	16	4.2	91	272	6.4
NW	100	9.0	0.29	106	165	4.6	106	260	6.1	102	11.1	0.78	102	7	2.7	102	265	5.4
SE	95	7.4	0.25	105	167	5.4	105	253	5.4	99	14.0	0.80	100	28	3.2	100	284	5.5
SW	93	7.8	0.29	103	163	5.8	104	258	6.6	102	11.5	0.76	102	9	3.2	102	267	7.0

Table 4-6. ANOVA results for 1987 pre-gap status, 1988 leader extension, and 1989 growth variables.

SOURCE	df	PRE-GAP 87 AGE	PRE-GAP 87 HEIGHT	PRE-GAP 87 BAS DIAMETER	88 LEADER EXTENSION	89 LEADER EXTENSION	89 BRANCH EXTENSION	89 TOTAL EXTENSION
BLOCK	2	3.32	1.74	2.54	2.28	1.02	0.07	0.04
SITE	3	0.87	0.51	0.12	0.58	2.55	3.65	6.85 *
PLOT	4	2.26	0.33	1.22	0.89	0.43	4.80 **	2.74 *
SPECIES	2	353.36 ***	81.34 ***	24.92 ***	119.01 ***	11.25 ***	351.29 ***	563.92 ***
BLOCK x SITE	6	5.51 ***	3.36 **	2.19 *	9.42 ***	5.59 ***	13.50 ***	24.48 ***
BLOCK x PLOT	8	1.65	1.59	2.46 *	1.41	3.55 ***	1.94	3.24 **
SITE x PLOT	12	0.81	0.73	0.29	1.44	0.51	6.09 ***	4.76 ***
SITE x SPP	6	1.83	1.30	2.31 *	2.77 *	10.98 ***	8.53 ***	22.46 ***
PLOT x SPP	8	2.67 **	2.79 **	1.58	2.09 *	1.80	2.59 **	3.46 ***
BLOCK x SITE x PLOT	24	3.25 ***	2.38 ***	2.69 ***	2.58 ***	2.91 ***	1.38	3.65 ***
SITE x PLOT x SPP	24	2.18 ***	2.23 ***	1.45	1.19	0.88	1.60 *	0.97
TOTAL df		1863	2091	2093	1905	728	1005	1707
VARIANCE EXPLAINED BY THE MODEL (%)		98.7	98.2	97.5	98.9	98.8	99.0	99.7
		*** p < 0.001	** p < 0.01	* p < 0.05				

rank order among species held in all sites. There were no site, plot, site x plot, or site x species differences. There was a significant block x site interaction, indicating that mean age relationships among sites varied across blocks.

Pre-gap heights also showed significant species differences ($F=81.34$, $p<0.001$), with sugar (183mm) taller than red (161mm) and striped (153mm). This pattern held in all sites, and in fact the overall ANOVA pattern was the same as with pre-gap age - significant block x site and lower level interactions. Note that these height differences were not outstanding, on average no more than 30mm.

The species differed in basal diameter ($F=24.92$, $p<0.001$), with sugar maple (2.66mm) larger than striped (2.58mm) and red maple (2.45mm). Even more so than for height, these differences (0.21mm, 8% overall) are probably not biologically relevant, even though they are statistically significant. The species rank order held in all sites, with striped maple occasionally not different from sugar maple. The ANOVA pattern was somewhat different than for age and height. The species term was not as large, and there was no significant site x plot x species term. Two more interactions, block x plot and site x spp, were significant.

Several points should be noted in summarizing the pre-gap status of the seedlings. First, the species did not show the same rank order for age, height, and basal diameter. So there was no composite age/size distinction among them. Second, the growth rates were generally very low, and the youngest, smallest species (red) showed the greatest growth rates for both height (RUB = 24.4mm/yr, SAC = 22.6mm/yr, PEN = 15.8mm/yr) and basal diameter (RUB = 0.37mm/yr, SAC = 0.33mm/yr, PEN =

0.27mm/yr). Third, no single-factor term other than species was significant, and it was overwhelmingly so.

The occurrence of significant spatial variation in initial status would be cause for concern were it not for the fact that subsequent survival and growth were completely unrelated to initial status. The survival tests for this were presented in Section 4.2.2. and the growth results are discussed below in Section 4.3.2. Because of the uniform lack of any post-gap versus pre-gap relationships, the pre-gap variables were not entered as covariates into the ANOVA model.

The conclusion for this section is that differences existed in the initial pre-gap age and size of the seedlings, particularly among species. But the species differences and the site-related variation did not play a role in post-gap performance.

4.3.1.2. 1988 GROWTH

Growth in 1988 is summarized in Tables 4-5 and 4-6. Species differed significantly in leader extension ($F=119.01$, $p<0.001$), with red (20.7mm) almost twice that of striped (11.9mm) and sugar (10.6mm). The last two species were not significantly different. The same rank order and Tukey HSD pairwise differences of species occurred across all four sites: RUB > PEN = SAC. The greatest absolute differences existed in large gaps, while the small gap and understories were very similar. This variation in relative differences produced a significant site x species interaction ($F=2.77$, $p<0.05$).

The sites did not show a significant overall difference ($F=0.58$, n.s.). Within the rank order of LGAP > SGAP > LUND > SUND, the Tukey HSD tests indicated pairwise differences, with LGAP greater than both LUND

and SUND, and SGAP greater than SUND. By far the most striking difference across plots within sites (Table 4-5) was that the large gap center seedlings showed 2.0-3.5 times the leader growth of the other four plots, and in fact the remaining plots showed nearly uniform growth. The Tukey HSD results support this impression; the only site/plot differences occurred in the large gap, where the center was greater than all other statistically equivalent plots. Consequently, the site x plot interaction was nonsignificant ($F=1.44$, n.s.).

The ANOVA pattern is very similar to the pre-gap variables, especially basal diameter. Again, the overwhelming term was species ($F=119.01$, $p<0.001$), and both site x spp and plot x spp interactions were significant. The block interactions (block x site and block x site x plot) were also significant at the $p<0.001$ level. Surprisingly, the site x plot x species term was not ($F=1.19$, n.s.), suggesting that species differences were maintained across plot positions within site types.

As compared to pre-gap height growth rates, all species showed declines: 15.8 to 11.9mm/yr for PEN, 24.4 to 20.7mm/yr for RUB, and 22.6 to 10.6mm/yr for SAC. Clearly sugar maple declined the most and red maple the least. Across sites, the only increase above pre-gap levels was by red maple in large gaps (31.0mm/yr). The overall decline indicates that all species were negatively affected by the gap treatments and/or non-experimental factors (e.g., weather) in the first year.

The patterns of basal diameter growth in 1988 were comparable to leader growth in some ways and divergent in others (Table 4-5). First, the rank order among species was different, with $PEN = RUB > SAC$ (based

on Tukey HSD). The order was slightly different in small gaps (PEN > RUB = SAC) than in understories (PEN > RUB > SAC), and was shifted to RUB > PEN = SAC in large gaps. Among sites, LGAP = SGAP = LUND > SUND. There were no significant differences among plots within any of the four sites, in spite of the fact that the large gap centers appeared to be much greater than the surrounding plots.

The species differed in post-gap versus pre-gap basal diameter growth rates: 0.27 (pre-gap) to 0.27mm/yr (post-gap) for PEN, 0.37 to 0.26mm/yr for RUB, and 0.33 to 0.12mm/yr for SAC. Striped maple held even while red maple dropped by nearly a third and sugar maple by nearly two-thirds. All species declined in the understory sites, while striped maple showed greater growth in both large and small gaps and red maple showed greater growth in large gaps as well.

For 1988 then, red maple tended to add more height and striped maple added more basal diameter, while sugar maple was last for both variables. The species were unable to maintain or increase previous growth rates except in the large gaps (red maple for leader growth, red and striped maple for basal diameter) and small gaps (striped maple only, for basal diameter). The impression for the first year of treatment effects is that all species were undergoing a double adjustment: (1) to the new microenvironments in gaps, as evidence by increased growth by red and striped, and (2) to a lingering effect of the transplanting, as indicated by the depressed growth by all species in the understories. It is conceivable that the slightly warmer and significantly drier conditions in May and June of 1988 (Figure 3-2) contributed to this depression overall, but this is untestable.

4.3.1.3. 1989 GROWTH

Growth in six variables in 1989 is summarized in Tables 4-6 and 4-7. For leader extension, the species again showed significant differences ($F=11.25$, $p<0.001$), but the rank order was different from 1988, with $PEN = RUB > SAC$. The absolute mean growth increments were 49.8mm, 21.5mm, and 5.3mm, respectively, indicating a great divergence among species as opposed to both pre-gap and 1988 growth rates. The site \times species interaction was very significant ($F=10.98$, $p<0.001$), and Tukey HSD comparisons within sites showed variations on the basic order: $PEN > RUB > SAC$ in large gaps; $PEN = RUB > SAC$ in small gaps and small understories; and $PEN = RUB$, $PEN = SAC$, and $RUB > SAC$ in large understories.

The sites showed insignificant differences overall ($F=2.55$, n.s.), but the Tukey HSD comparisons indicated $LGAP = SGAP > SUND = LUND$. There were no significant differences among plots in either small or large understories. In small gaps, the center plot was lower than all other equivalent plots. The large gap plots showed a more complicated pattern. The rank order was C, NE, SE, NW, SW and the first four plots were all significantly greater than the SW. But the first three sequential pairs were each insignificantly different (i.e., $C = NE$, $NE = SE$, and $SE = NW$). The overall site \times plot interaction was nonsignificant ($F=0.51$, n.s.).

The overall leader growth rates in 1989 were much greater than 1988 and 1987 pre-gap rates for striped maple (49.8 vs. 11.9 vs. 15.8mm/yr, respectively). Red maple rates were higher than 1988 but lower than pre-gap (21.5 vs. 20.7 vs. 24.4mm/yr for 1989, 1988, and 1987, respectively), while sugar maple continued the decline in rates (22.6

Table 4-7. Summary of 1989 growth.

CATEGORY	LEADER EXTENSION (mm)			BRANCH EXTENSION (mm)			TOTAL EXTENSION (mm)			BDIAM CHANGE (0.01mm)			BDIAM (0.01mm)			HEIGHT (mm)		
	N	MEAN	S.E.	N	MEAN	S.E.	N	MEAN	S.E.	N	MEAN	S.E.	N	MEAN	S.E.	N	MEAN	S.E.
TOTAL	723	34.3	2.58	1104	60.0	4.24	1701	53.5	2.99	1702	39	2.1	1702	322	2.8	1705	170.9	2.51
PEN	444	49.8	4.00	198	45.4	7.99	578	53.8	4.21	579	62	3.5	579	352	4.7	580	202.5	4.94
RUB	76	21.5	2.79	564	93.3	7.39	610	88.9	6.88	611	40	4.1	611	315	5.7	612	151.8	3.83
SAC	203	5.3	0.25	342	13.5	2.37	513	11.1	1.60	512	11	1.9	512	298	3.3	513	158.0	3.77
LGAP	114	76.0	10.20	251	142.2	16.56	338	131.2	12.80	339	81	7.9	339	376	9.8	339	194.3	7.67
SGAP	191	58.4	6.41	308	58.1	4.53	440	66.0	4.26	442	56	3.4	442	344	5.1	443	183.0	4.95
LUND	208	11.0	1.30	283	23.9	1.53	472	19.2	1.12	471	11	1.8	471	289	3.2	472	154.1	3.30
SUND	210	12.9	1.12	262	22.4	1.35	451	19.0	0.97	450	20	2.1	450	296	3.6	451	159.1	4.38
BLOCK 1	220	35.6	4.62	355	45.7	5.92	540	44.5	4.36	540	37	3.5	540	319	4.8	540	166.8	4.23
BLOCK 2	254	37.0	5.01	394	47.5	4.76	595	47.2	3.87	595	40	2.9	595	326	4.0	596	171.5	4.38
BLOCK 3	249	30.5	3.67	355	88.1	10.39	566	68.7	6.81	567	40	4.2	567	322	5.8	569	174.2	4.41
LGAP PEN	71	113.5	14.55	37	113.9	32.91	96	127.9	16.58	96	120	11.9	96	412	13.6	96	248.3	15.44
RUB	15	32.3	8.05	139	214.5	26.36	143	211.9	25.65	144	99	15.5	144	401	19.4	144	200.3	12.09
SAC	28	4.1	0.36	28	4.1	0.36	99	17.8	7.90	99	15	5.7	99	306	9.7	99	133.1	9.65
SGAP PEN	118	86.5	9.39	72	44.0	12.16	154	86.9	9.41	156	99	6.7	156	394	10.0	156	231.1	10.50
RUB	17	34.8	8.38	146	93.0	6.10	154	92.0	5.95	155	46	4.2	155	330	7.5	155	157.2	5.56
SAC	56	6.3	0.67	90	12.7	1.32	132	11.3	1.03	131	17	3.7	131	302	6.4	132	156.5	6.96
LUND PEN	120	14.2	2.19	52	18.8	3.91	167	16.0	1.98	166	22	4.1	166	308	6.3	167	169.8	4.96
RUB	23	11.5	1.43	145	33.8	2.23	161	32.1	2.10	161	6	2.3	161	269	4.9	161	127.8	4.88
SAC	65	5.1	0.32	86	10.2	1.16	144	8.4	0.76	144	5	1.9	144	291	4.8	144	165.2	6.81
SUND PEN	135	15.9	1.61	37	17.2	2.57	161	17.3	1.54	161	35	4.0	161	320	6.4	161	181.4	9.02
RUB	21	14.0	2.46	134	32.0	1.91	152	30.2	1.76	151	14	2.5	151	268	5.2	152	125.8	5.03
SAC	54	5.1	2.24	91	10.4	1.71	138	8.9	1.17	138	9	3.7	138	297	6.0	138	169.8	7.09
LGAP C	14	138.0	52.78	51	386.4	64.47	61	354.7	55.62	61	182	34.8	61	506	41.4	61	290.9	27.70
NE	12	87.5	25.10	42	122.8	21.16	51	121.7	18.21	51	63	12.0	51	357	17.7	51	173.6	14.38
NW	3	110.3	48.31	30	146.6	33.23	32	147.8	31.24	32	61	22.9	32	360	27.3	32	176.8	24.59
SE	38	92.3	16.72	66	61.3	11.51	98	77.1	10.78	98	65	8.7	98	347	10.9	98	174.1	11.63
SW	47	39.1	9.83	62	38.3	6.44	96	43.9	6.22	97	49	5.9	97	339	9.4	97	170.5	9.41
SGAP C	39	32.9	7.77	51	52.3	8.03	81	48.8	6.94	81	45	6.3	81	329	10.8	81	177.5	9.42
NE	29	36.2	9.59	56	57.4	8.04	81	52.6	6.75	81	36	6.0	81	314	9.7	81	152.1	9.41
NW	42	79.8	14.34	69	62.6	9.42	93	82.5	9.27	94	72	7.9	94	375	11.0	94	197.6	11.09
SE	43	68.8	16.10	64	54.3	9.05	92	69.9	9.59	92	57	1.0	92	342	11.2	92	186.5	12.72
SW	38	66.0	17.70	68	62.0	13.42	93	72.3	3.95	94	67	0.2	94	354	0.2	95	196.2	11.12
LUND C	46	10.6	3.09	54	24.9	3.53	97	18.8	2.53	97	12	3.1	97	295	6.7	97	163.5	6.81
NE	34	12.4	2.90	57	22.8	2.93	89	19.3	2.24	89	15	4.2	89	280	6.7	89	142.0	6.46
NW	51	6.5	0.68	52	19.1	1.94	98	13.5	1.25	97	9	4.1	97	281	7.2	98	146.5	6.89
SE	35	15.6	5.22	59	27.4	4.89	90	24.0	3.87	90	8	4.4	90	293	8.7	90	155.3	8.41
SW	42	12.1	2.21	61	24.7	2.84	98	20.6	2.07	98	12	3.9	98	295	0.5	98	162.3	8.01
SUND C	39	14.4	2.56	52	23.9	3.13	87	20.7	2.24	87	20	4.5	87	299	8.0	87	161.0	16.32
NE	41	9.3	8.15	45	20.5	3.41	82	15.9	2.05	82	15	5.4	82	291	8.2	82	147.6	8.15
NW	39	13.2	3.11	59	22.7	2.80	96	19.3	2.17	96	22	3.5	96	288	6.8	96	144.0	6.45
SE	48	17.0	3.06	52	28.8	3.54	97	23.8	2.47	97	24	5.0	97	308	7.4	97	175.2	7.07
SW	43	10.2	1.77	54	16.2	1.95	89	14.8	1.65	88	18	4.9	88	291	9.5	89	166.7	8.35

vs. 10.6 vs. 5.3mm/yr). On this basis, the conclusion at the level of the entire study area is that striped maple responded better to the new conditions than red maple, and sugar maple declined substantially. This pattern held within all sites as well.

One fact qualifies this conclusion. As the sample sizes in Table 4-7 indicate, the three species differed widely in the number of seedlings with intact leaders (and thus leader extension) as of October 1989; PEN = 444, RUB = 76, and SAC = 203. Just three years following transplanting, only 10.5% of the original 720 red maple transplants (12.4% of those surviving through 1989) had maintained their leaders. The analogous percentages are 28.2% and 39.6% for sugar maple, and 61.7% and 76.6% for striped maple. Striped maple was clearly able to maintain intact leaders better than sugar maple, and red maple exhibited massive losses.

Since 1989 leader growth was based only on intact leaders, it is difficult to say if the order of success among these species would have been the same if all species had maintained leaders in comparable percentages. In this context, it is worth recalling that the rank order of leader growth in 1988 was RUB > PEN > SAC (Section 4.3.1.2.) The possible causes and the more important effects of leader loss will be discussed in Section 4.5.

By 1989, over half of the surviving seedlings across the entire study exhibited branch growth, with or without intact leaders. Consequently, the amount of branch extension was analyzed in the same manner as leader growth (Tables 4-6, 4-7). The number of seedlings with branch growth differed among species in both absolute terms and the percentage of survivors through 1989: PEN = 198 (34%), RUB = 564 (92%),

and SAC = 342 (67%). This order held in all sites, except for large gaps, where striped maple had slightly higher numbers with branching than sugar maple.

The rank order mirrored the tendency toward leader loss, as would be expected. The analysis discussed here was based on total living 1989 branch extension, regardless of the number of branches or their point of origin on the stem. The analysis also did not separate branch growth on intact versus leaderless seedlings, although the mechanisms responsible for branch initiation, and the contribution of branches to total shoot extension, were probably different in these two cases.

The three species differed significantly in total branch extension in 1989 ($F=351.29$, $p<0.001$), with RUB > PEN > SAC. This pattern held with some variations in all sites (RUB > PEN > SAC in both gap sizes, RUB > PEN = SAC in both understories). The site x species term was significant ($F=8.53$, $p<0.001$), reflecting this variation. Although sugar maple branched with greater frequency than striped maple, the latter put on more branch growth. Red maple branched profusely and put on twice as much branch growth as striped maple and nearly seven times as much as sugar maple (93.3mm vs. 45.4mm vs. 13.5mm, respectively). The relative differences were reduced in the two understories, about the same in small gaps, and sugar maple diverged to become very low in large gaps.

The sites did not show significant differences overall ($F=3.65$, n.s.), but Tukey HSD comparisons indicated that LGAP > SGAP > LUND = SUND. Given the markedly higher mean branch extension in large gaps (142.2mm), it is surprising that sites were not significantly different overall.

The site x plot term was significant ($F=4.76$, $p<0.01$). The Tukey

HSD results showed there were no significant differences among plots within the small gaps, large understories, and small understories. But within large gaps, the pairwise comparisons were such that all adjacent pairs in the rank order C, NW, NE, SE, SW were not significant (i.e., C = NW, NW = NE, NE = SE, SE = SW) while all other plot pairs were. The fact that there were so many plot equivalencies in the large gaps, given the extremely wide divergence in mean extension (24-fold from C to SW), suggests that relatively few seedlings were responsible for the divergence. This agrees with field observations, in that selected individuals in the large gap center plots put on enormous branch growth (up to 2003mm!), usually as basal resprouting from leader dieback. Since red maple was observed to be most responsible for these high branch extensions in the large gap centers, it is not surprising that the site x plot x species term was significant ($F=1.60$, $p<0.05$).

The results for total shoot extension (leader plus branches) are summarized in Tables 4-6 and 4-7. The species were significantly different ($F=563.92$, $p<0.001$), with RUB > PEN > SAC (88.9mm, 53.8mm, and 11.1mm, respectively). This order held in identical fashion across all four sites, but the relative differences among species varied, producing a significant site x species interaction ($F=22.46$, $p<0.001$).

The sites did show an overall significant difference ($F=6.85$, $p<0.05$), with LGAP > SGAP > LUND = SUND (131.2mm, 66.0mm, 19.2mm, 19.0mm, respectively). The site x plot term was also significant ($F=4.76$, $p<0.001$), and the Tukey HSD results confirmed this. There were no significant differences among plots in either understory sites. The NW plot was greater than the C plot in small gaps, while both were equivalent to the remaining three plots. In large gaps, the center plot

was greater than all other plots, which showed several pairwise differences (NW = NE, NE = SE, SE = SW, all others significant).

The site x plot x species interaction was not significant as it had been with branch growth. This was somewhat surprising since it is clear from perusal of the site/species and site/plot sections of Table 4-6 that total extension values were controlled more by branch extension than leader extension. Like leader extension, but unlike branch extension, there was a significant block x site x plot interaction ($F=3.65$, $p<0.001$). So plots did differ across block/site combinations.

It is important to emphasize that the branch extension by many individual seedlings was recovery from leader loss and substantial dieback. Since total extension includes this recovering branch growth, it was frequently the case that seedlings with the greatest dieback loss in stem height showed the largest total extension, even though they actually lost net stem height over the 1987-89 period. Thus the rank orders for species in any of the above extension variables have to be interpreted with caution, since they may not reflect absolute gains in height. This point will be amplified later in this section, where actual stem heights are analyzed.

Statistics for changes in basal diameter in 1989 are summarized in Table 4-7. Since the ANOVA model was not fitted to this variable, the significance of differences among various groups are based on Tukey HSD tests on ln-transformed data. The three species differed significantly, with $PEN > RUB > SAC$ (all pairwise probabilities are $p<0.002$). Striped expanded 50% more than red maple and over 5 times as much as sugar maple (0.62mm vs. 0.40mm vs. 0.11mm). There were no significant species differences in either understory site. In small gaps, $PEN > RUB = SAC$

(0.99mm vs. 0.46mm vs. 0.17mm) while large gaps showed PEN = RUB > SAC (1.20mm vs. 0.99mm vs. 0.15mm).

The sites differed overall, with LGAP = SGAP > LUND = SUND. The Tukey probability values for the significant differences were $p < 0.001$, while the insignificant differences were all $P > 0.60$. In spite of the large basal diameter growth in large gap center plots, no sites showed any significant pair-wise differences among plots.

This measurement of net change in basal diameter was taken on survivors through 1989, but it includes seedlings with extensive dieback and basal resprouting. Thus the net basal diameter change from 1988 to 1989 was negative for many seedlings.

In overall terms, the basal diameter change pattern matched that for leader extension, and differed from branch and total extension. This reinforces the point that branch (and total) extension is (are) strongly related to leader loss and dieback. Net losses in basal diameter were often accompanied by the greatest gains in branch and total extension, and thus plants maintaining intact leaders increased their diameters more on average.

In comparison to 1988, striped maple increased its diameter growth rate by 129%, red increased by 54%, and sugar declined by 9%. So both striped and red maple appeared to be adjusting better to the treatment conditions by the end of the second year than sugar maple.

Cumulative basal diameters resulting from both 1988 and 1989 growth are summarized in Table 4-7. Since the 1987 pre-gap initial diameters did not differ substantially among species (Section 4.3.1.1.), it is not surprising that actual basal diameters in 1989 parallel the results for basal diameter growth in 1989 just presented.

The three species differed significantly in 1989 basal diameter, with $PEN > RUB = SAC$ (3.52mm vs. 3.15mm vs. 2.98mm, respectively). The rank order differed in all four sites, however, with $PEN = RUB > SAC$ in large gaps, $PEN > RUB = SAC$ in small gaps, $PEN > SAC = RUB$ in large understories, and $PEN = SAC > RUB$ in small understories. Striped maple therefore possessed larger basal diameters overall and in most sites. Red maple did better than sugar maple in the gaps, while the reverse was true in the understory. The sites also differed significantly, with $LGAP = SGAP > LUND = SUND$. And the only plot difference within sites occurred in large gaps, where $C > NW = NE = SE = SW$.

All species increased their mean basal diameter compared to 1987 initial values. But they did so disproportionately, so that the 1987 order of $SAC > PEN > RUB$ became $PEN > RUB = SAC$ in 1989. This supports the conclusion that the first two species have adjusted better than sugar maple to the experimental treatments.

Seedling height as of 1989 is summarized in Table 4-7. There was a remarkable correspondence between the 1989 basal diameter and height significant differences among groups. The only exceptions were (1) species differences in large understories, where $PEN = SAC$, $SAC = RUB$, and $PEN > RUB$, and (2) overall site differences, where $SGAP = LGAP$, $LGAP = SUND$, and $SUND = LUND$. This correspondence between height and basal diameter results suggests that the species were responding consistently in terms of both axial (height) and radial (basal diameter) growth.

As compared to the 1987 pre-gap initial heights, only striped maple showed a positive increase (32%), while red (-6%) and sugar maple (-14%) both declined. Thus in terms of actual net change in dimensions, striped maple was far more successful than the other two species. As noted

above, this was in large part due to the greater tendency of red and sugar maples to lose their leaders and die back. Even though red maple in particular showed capable recovery (see branch and total extension results), it was apparently not enough to overcome the losses.

In summary, the six growth variables for 1989 suggest that the three species diverged even more in 1989 than they had in 1988, particularly for cumulative height and basal diameter. Due to more extensive leader loss and dieback by red and sugar maple, these species showed significant branch extension, but it was apparently not enough to recover initial height.

The ANOVA results for extension variables showed that more model terms were significant than for either the 1987 pre-gap variables or 1988 leader extension (Table 4-6). This includes the significance of the site x plot term for 1989 branch and total extension, and the site x species term for all three extension variables. Thus the effects of the treatments generally increased over time. The nearly complete lack of a significant site x plot x species interaction for the 1988 and 1989 growth variables is a very interesting result which will be discussed in Section 4.6.

4.3.1.4. 1987-1989 CUMULATIVE GROWTH

The analysis of net change in growth variables over the 1987-89 period included all survivors as of October 1989 (n=1705). Summary statistics for the five variables are presented in Table 4-8 and ANOVA results are in Table 4-9. In addition, Figures 4-6 through 4-15 graphically illustrate the results in pairs. For each of the five variables, the first figure displays the differences among species,

Table 4-8. Summary of 1987-89 cumulative growth.

CATEGORY	LEADER N	EXTENSION MEAN	(mm) S.E.	BRANCH N	EXTENSION MEAN	(mm) S.E.	TOTAL N	EXTENSION MEAN	(mm) S.E.	BDIAM N	CHANGE MEAN	(0.01mm) S.E.	HEIGHT N	CHANGE MEAN	(mm) S.E.
TOT	1705	29.6	1.29	1105	66.7	4.26	1705	72.8	3.33	1705	63	2.5	1704	3.6	2.30
P	580	50.0	3.35	199	53.8	7.96	580	68.5	4.48	580	91	4.1	580	46.2	3.93
R	612	23.8	1.31	564	99.2	7.43	612	115.2	7.73	612	69	5.2	612	-8.8	3.79
S	513	13.3	0.39	342	20.7	2.49	513	27.1	1.91	513	25	2.4	512	-29.7	3.40
LG	339	45.7	4.35	251	146.3	16.52	339	154.0	14.20	339	115	9.5	339	28.1	7.77
SG	443	40.7	3.31	308	66.0	4.80	443	86.6	4.79	443	86	4.4	443	13.4	4.85
LU	472	18.0	0.90	283	30.8	1.91	472	36.5	1.73	472	31	2.2	472	-11.4	2.82
SU	451	18.5	0.73	263	30.4	1.65	451	36.2	1.39	451	36	2.5	450	-8.5	2.80
BLOCK 1	540	26.7	2.10	355	50.5	5.93	540	59.9	4.57	540	55	4.2	540	-5.2	3.91
BLOCK 2	596	30.2	2.41	394	55.8	4.96	596	67.1	4.30	596	68	3.5	596	2.6	3.86
BLOCK 3	569	31.6	2.16	356	94.9	10.31	569	91.0	7.72	569	66	5.3	568	13.2	4.12
LGAP PEN	96	95.9	12.08	37	121.3	32.76	96	142.6	17.22	96	152	12.6	96	94.5	14.51
RUB	144	35.1	4.70	139	218.1	26.29	144	245.6	28.68	144	148	18.9	144	37.0	12.24
SAC	99	12.5	1.12	75	25.3	10.41	99	31.7	8.87	99	30	7.4	99	-49.3	9.58
SGAP PEN	156	79.6	8.28	72	50.7	12.31	156	103.0	10.14	156	138	9.3	156	76.9	12.25
RUB	155	24.1	2.05	146	100.7	6.82	155	119.0	7.33	155	80	5.6	155	-11.9	6.25
SAC	132	14.4	0.78	90	21.8	2.39	132	29.2	2.15	132	33	4.9	132	-32.0	3.38
LUND PEN	167	21.6	2.19	52	30.6	4.56	167	31.1	3.15	167	47	4.7	167	16.9	4.37
RUB	161	18.5	1.14	145	39.5	2.98	161	54.1	3.23	161	24	2.9	161	-29.5	6.05
SAC	144	13.4	0.66	86	16.2	1.69	144	23.1	1.39	144	20	2.5	144	-24.0	3.02
SUND PEN	161	23.5	1.59	38	25.9	2.97	161	29.6	1.83	161	54	4.5	161	18.2	4.75
RUB	152	18.4	1.09	134	38.7	2.43	152	52.5	2.74	152	30	3.5	152	-27.1	5.90
SAC	138	12.7	0.62	91	19.9	2.45	138	25.8	1.96	138	20	4.6	137	-19.4	27.69
LGAP C	61	76.8	16.17	51	392.7	63.96	61	405.1	62.54	61	245	41.5	61	124.5	15.99
NE	51	37.9	7.93	42	129.9	21.17	51	144.9	19.47	51	102	16.5	51	11.8	15.46
NW	32	31.6	7.71	30	150.2	32.88	32	172.5	33.52	32	87	25.0	32	4.2	12.11
SE	98	48.1	8.12	66	63.0	11.67	98	90.5	11.31	98	93	9.9	98	11.4	8.85
SW	97	32.4	5.44	62	41.3	6.32	97	58.8	6.28	97	71	7.2	97	0.7	8.39
SGAP C	81	29.1	5.08	51	60.1	8.16	81	66.9	8.00	81	74	9.1	81	1.2	9.80
NE	81	26.9	4.40	56	62.0	8.13	81	69.7	7.43	81	58	7.3	81	-16.9	11.03
NW	94	53.1	7.70	69	67.7	9.37	94	102.8	9.80	94	111	9.7	94	25.9	11.32
SE	92	46.5	8.60	64	59.7	8.98	92	88.0	10.15	92	89	8.1	92	19.2	11.82
SW	95	44.7	8.63	68	77.9	15.18	95	100.4	14.64	95	94	12.7	95	31.5	5.79
LUND C	97	19.7	1.93	54	31.6	3.77	97	37.2	3.77	97	34	0.3	97	-1.6	6.35
NE	89	15.8	1.44	57	26.5	3.08	89	32.8	2.74	89	31	6.3	89	-19.9	5.71
NW	98	14.8	0.85	52	25.8	2.26	98	28.4	1.81	98	27	4.7	98	-12.0	7.39
SE	90	20.4	3.36	59	39.0	6.80	90	45.9	6.69	90	30	5.3	90	-9.0	6.30
SW	98	19.6	1.77	61	30.4	3.36	98	38.5	3.14	98	33	4.7	98	-15.2	7.04
SUND C	87	19.9	1.78	52	34.98	3.405	87	40.78	3.191	87	31	5.0	87	-18.4	6.90
NE	82	16.2	1.10	45	24.2	3.53	82	29.5	2.41	82	32	6.6	81	-13.9	7.05
NW	96	16.8	1.65	59	28.6	4.00	96	34.3	3.34	96	30	3.8	96	-20.9	5.05
SE	97	22.3	1.92	53	36.5	3.69	97	42.2	3.17	97	54	6.3	97	5.6	4.46
SW	89	16.9	1.40	54	27.0	3.42	89	33.5	3.06	89	29	6.0	89	3.9	5.6

Table 4-9. ANOVA results for 1987-89 cumulative growth variables, plus 1989 leaf length, mean leaf area, and total leaf area.

SOURCE	df	1987-89 LEADER EXTENSION	1987-89 BRANCH EXTENSION	1987-89 TOTAL EXTENSION	1987-89 NET HEIGHT CHANGE	1987-89 NET BASAL DIAM CHANGE	89 MEAN LEAF LENGTH	89 MEAN LEAF AREA	89 TOTAL LEAF AREA
BLOCK	2	0.97	0.26	0.33	0.93	0.04	0.23	0.46	0.38
SITE	3	3.18	2.45	6.54 *	0.67	5.61 *	0.15	0.14	1.28
PLOT	4	1.77	2.11	2.25	1.24	0.67	1.07	1.08	1.15
SPECIES	2	114.09 ***	219.40 ***	343.70 ***	130.09 ***	119.47 ***	585.68 ***	583.98 ***	353.34 ***
BLOCK x SITE	6	6.90 ***	10.42 ***	19.30 ***	7.10 ***	18.31 ***	16.72 ***	16.66 ***	21.51 ***
BLOCK x PLOT	8	1.34	1.35	2.74 **	2.12 *	6.75 ***	1.25	1.25	1.43
SITE x PLOT	12	2.56 **	3.46 **	2.94 **	1.03	0.61	1.27	1.25	2.11 *
SITE x SPP	6	10.35 ***	9.92 ***	20.90 ***	8.45 ***	12.91 ***	5.61 ***	5.64 ***	11.66 ***
PLOT x SPP	8	3.12 **	2.36 *	3.23 **	3.16 **	7.12 ***	0.49	0.49	0.90
BLOCK x SITE x PLOT	24	1.94 **	0.89	2.53 ***	1.47	4.79 ***	1.98 **	1.97 **	2.51 ***
SITE x PLOT x SPP	24	0.98	1.89 **	1.24	1.43	4.80 ***	0.81	0.82	0.93
TOTAL df		1696	242	1698	1703	1689	1547	1546	1546
VARIANCE EXPLAINED BY THE MODEL (%)		98.7	99.5	99.0	91.0	91.8	95.8	95.7	96.5
		*** p < 0.001	** p < 0.01	* p < 0.05					

sites, species within sites, and plots within sites. The second figure adds species differences by plot position within sites for the large gaps, small gaps, and large understories. The results for the small understories were similar to the large understories, and hence are not graphed.

Total leader extension differed significantly among species ($F=114.09$, $p<0.001$), with $PEN > RUB > SAC$ (Figure 4-6a). The absolute values were 50.0mm, 23.8mm, and 13.3mm, respectively. The site x species term was significant ($F=2.56$, $p<0.001$). Tukey HSD results for species within sites showed the same pattern in both gaps ($PEN > RUB > SAC$), but the species were less divergent in the understories: $PEN = RUB = SAC$ in large understories; $PEN = RUB$, $RUB = SAC$, and $PEN > SAC$ in small understories (Figure 4-6b). Thus both gap sizes separated species better than the understory sites.

The sites were not significantly different overall ($F=3.18$, n.s.), but Tukey HSD tests showed $LGAP = SGAP > LUND = SUND$ (Figure 4-6a). The site x plot term was also significant ($F=2.56$, $p<0.01$). Plots did not differ in either understory site (Figure 4-6c). But the center plot diverged from all other plots in large gaps ($C > SE = NE = SW = NW$). Plot differences in small gaps followed $NW = SE = SW > C = NE$, which is an inscrutably odd spatial pattern. Both gap sizes showed clearer plot differences than the understory sites, though the distinctions were not spectacular.

Figure 4-7 displays the finer resolution of species within plots within sites. Comparative statements about species means are based on visual inspection of the graphs and not on statistical tests. In large gaps, $PEN > RUB > SAC$ in all plots. All species showed the greatest

Figure 4-6. Cumulative leader extension by seedlings surviving with intact leader to October 1989. (A) By species and site type totals, (B) By species within site types, (C) By plot positions within site types.

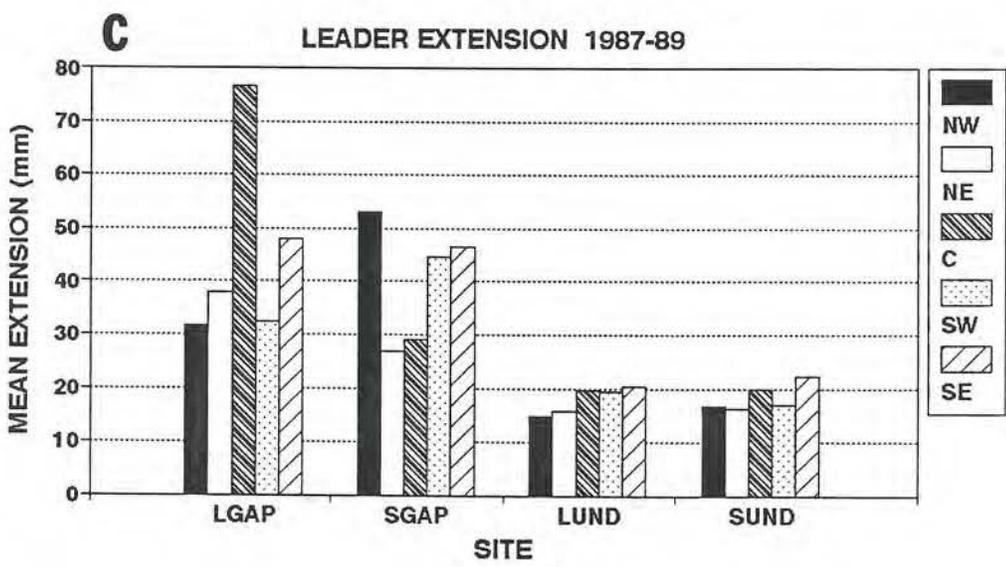
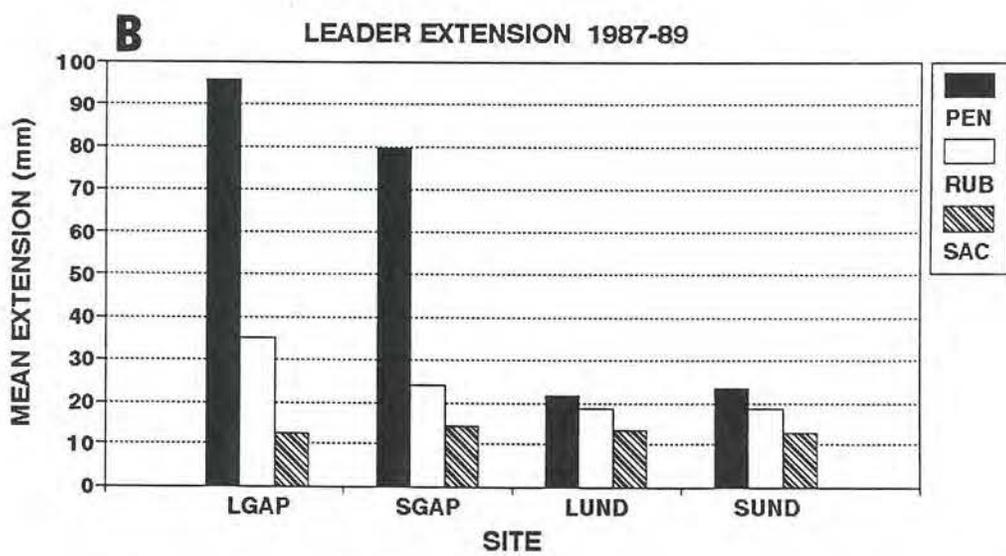
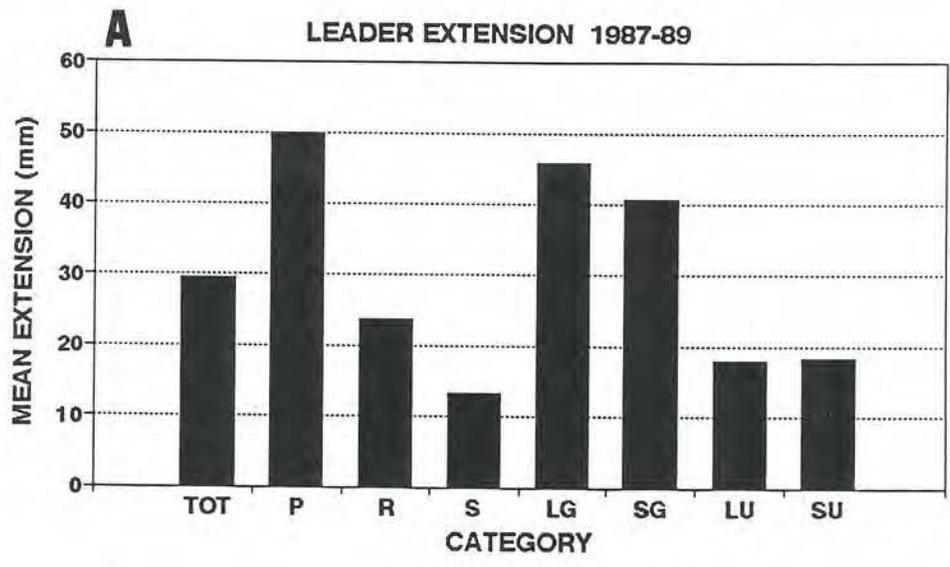
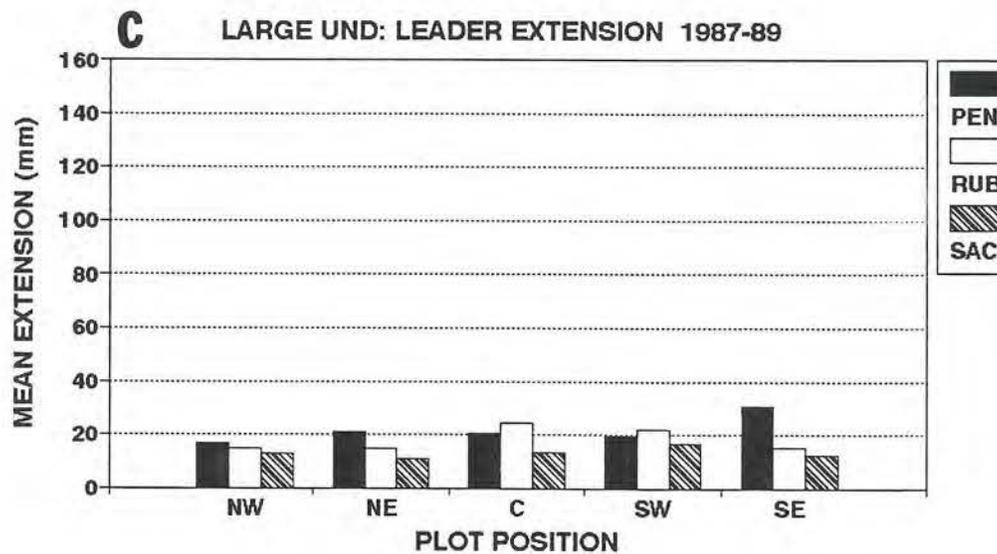
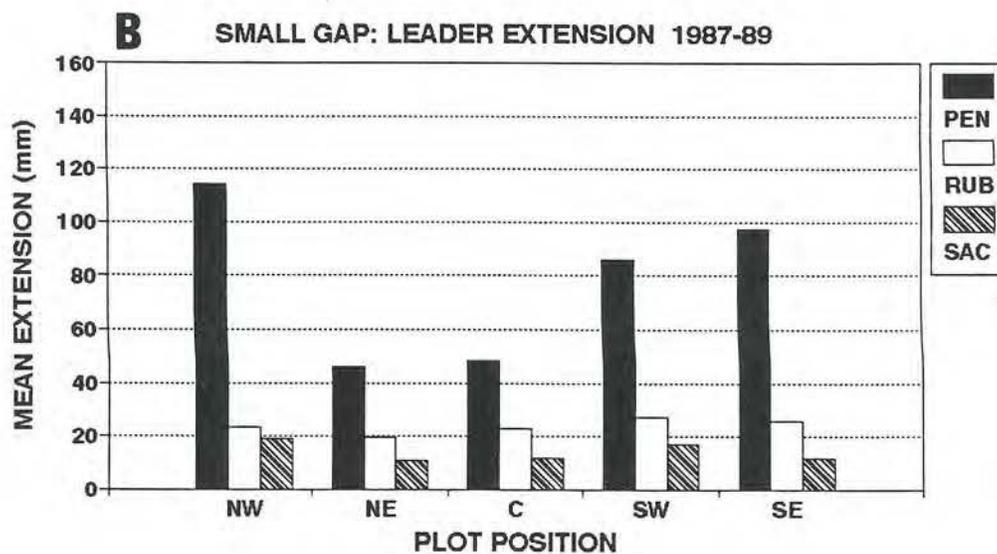
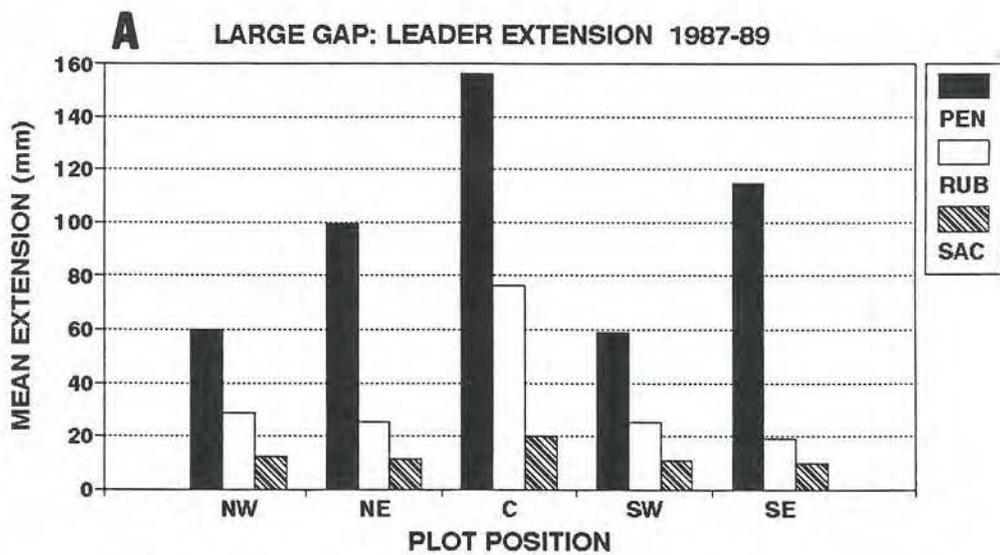


Figure 4-7. Cumulative leader extension by seedlings surviving with intact leaders to October 1989. (A) By species and plots in large gaps, (B) By species and plots in small gaps, (C) By species and plots in large understories.



leader growth in the center plot. However, the relative performance across plots differed among the species. Striped maple showed greater variation. Red maple performance was uniformly about one-third that of the center in all other plots. And, although sugar maple did show a slightly greater extension in the center, the mean values and variation overall were much lower than the other species.

For small gaps, $PEN > RUB \Rightarrow SAC$ in all plots. Red and sugar maple varied little among plots, while striped maple showed greater extension in the NW, SW, and SE plots than in the NE and C. In the large understory, there was minimal variation among plots for all species, and there was no consistent pattern of species rank order except that sugar was last by at least a small difference in all plots.

The overall site preferences for the three species, in terms of mean leader extension, were as follows: (1) striped maple: $LGAP > SGAP > LUND$, (2) red maple: $LGAP > SGAP \Rightarrow LUND$, and (3) sugar maple: $LGAP = SGAP = LUND$. Within large gaps, it appears that striped and red maple may be inhibited by too much radiation in the north plots and too little in the south plots, while the center seems to provide the best environment for leader extension. The small gap pattern is not explicable based on known micrometeorological patterns. There is neither a N-S trend nor a concentric pattern. Since the south plots show leader growth similar to the NW for striped maple, it does not seem that PPF or temperatures are involved. Both red and sugar maple show no variation among plots, suggesting that a microsite- and species-specific factor other than microclimate (soil resources?) is producing the small gap pattern for striped maple.

This analysis of cumulative leader growth includes large numbers of

red and sugar maples that had lost their leaders by May 1989 and thus showed no leader growth in 1989. It is impossible to say how the comparative differences among species would have played out if all species had maintained intact leaders in equal proportions. The important point is that extensive leader loss did occur, and for the populations as wholes, the above patterns characterized net performance over the two years.

The species showed significant differences in total branch growth over 1987-89 ($F=219.40$, $p<0.001$), with $RUB > PEN > SAC$ (Figure 4-8a). Absolute means were 99.2mm, 53.8mm and 20.7mm, respectively. The site x species term was also significant ($F=9.92$, $p<0.001$). This same rank order for species occurred in both gap sizes, while $RUB = PEN \Rightarrow SAC$ in the understory sites (Figure 4-8b). Once again, the gaps separated species better than the understory.

The sites were not significantly different ($F=2.45$, n.s.), but the Tukey HSD tests showed $LGAP > SGAP > LUND = SUND$ (Figure 4-8a). Plot positions were significantly different only in the large gap, where $C > NW = NE > SE = SW$. Thus the most exposed positions within the large gap showed the greatest branch growth (Figure 4-8c). Since red maple showed substantial branching in these plots, both the plot x species term ($F=2.36$, $p<0.05$) and the site x plot x species term ($F=1.89$, $p<0.01$) were significant.

Within the large gaps, the species showed variable rank orders among plots (Figure 4-9): $PEN > RUB > SAC$ in the NW; $RUB > PEN > SAC$ in the NE, C, and SW; and $RUB = PEN > SAC$ in the SE. By far the largest value occurred for red maple in the center plot, nearly twice that of any other species in any plot in any site.

Figure 4-8. Total branch extension (i.e. sum of all living branch segments initiated during 1987-89) by seedlings surviving to October 1989. Data are only for seedlings with branches. (A) By species and site type totals, (B) By species within site types, (C) By plot positions within site types.

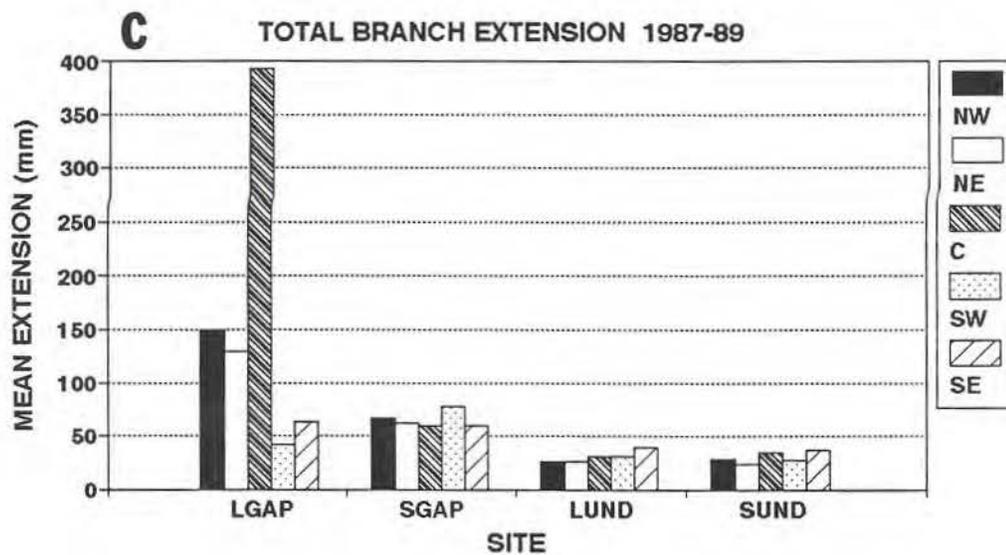
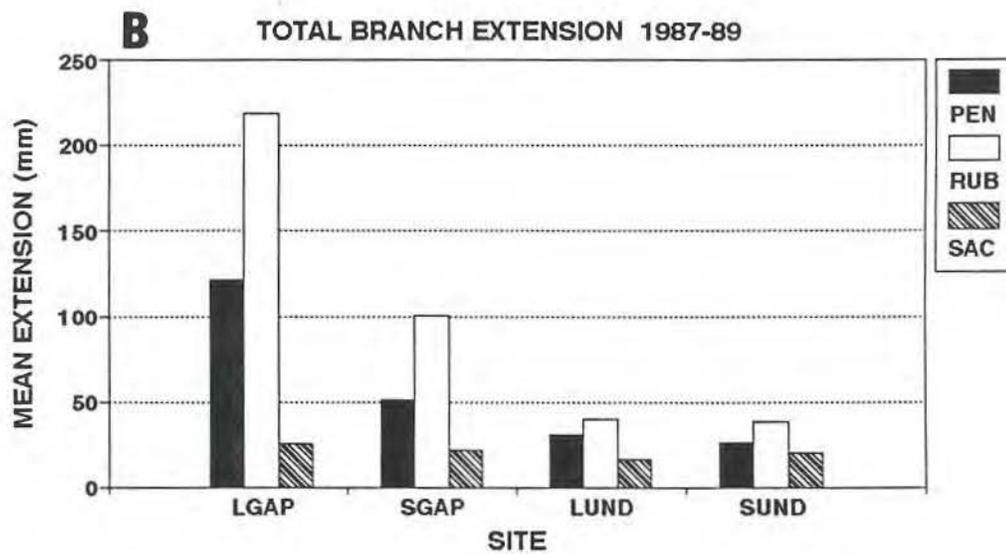
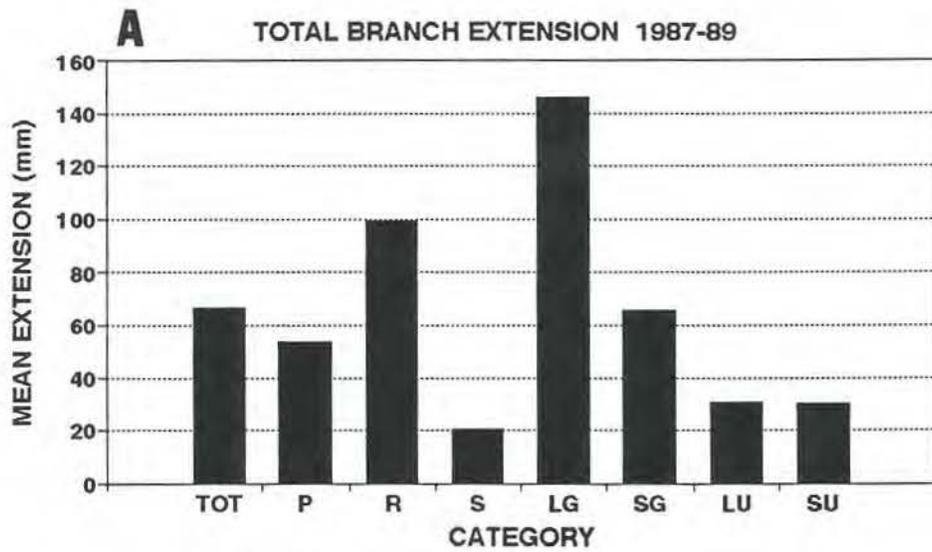
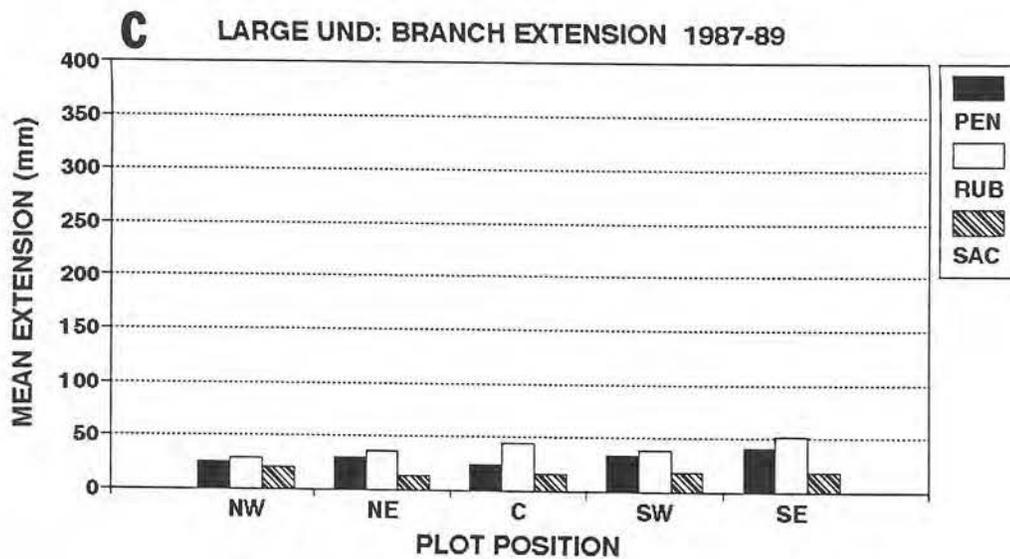
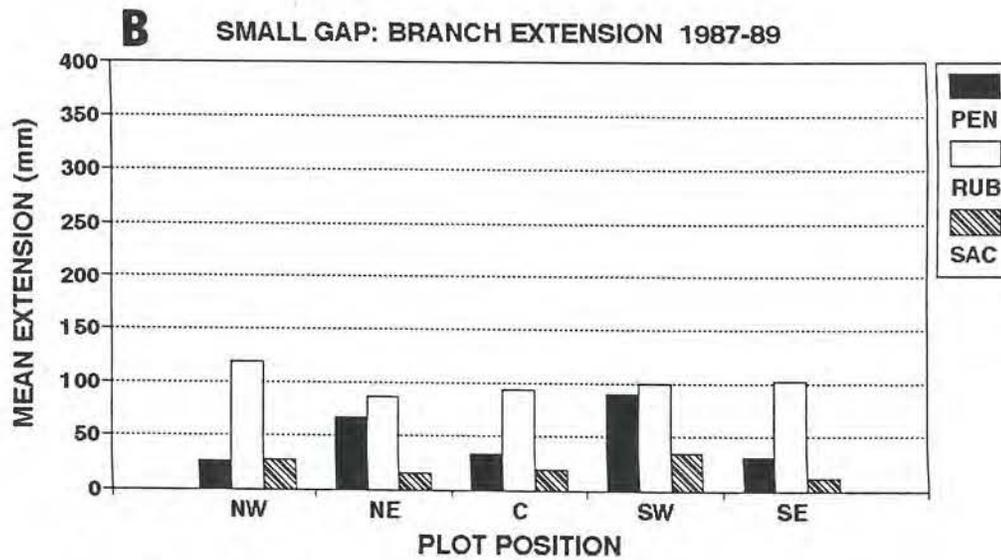
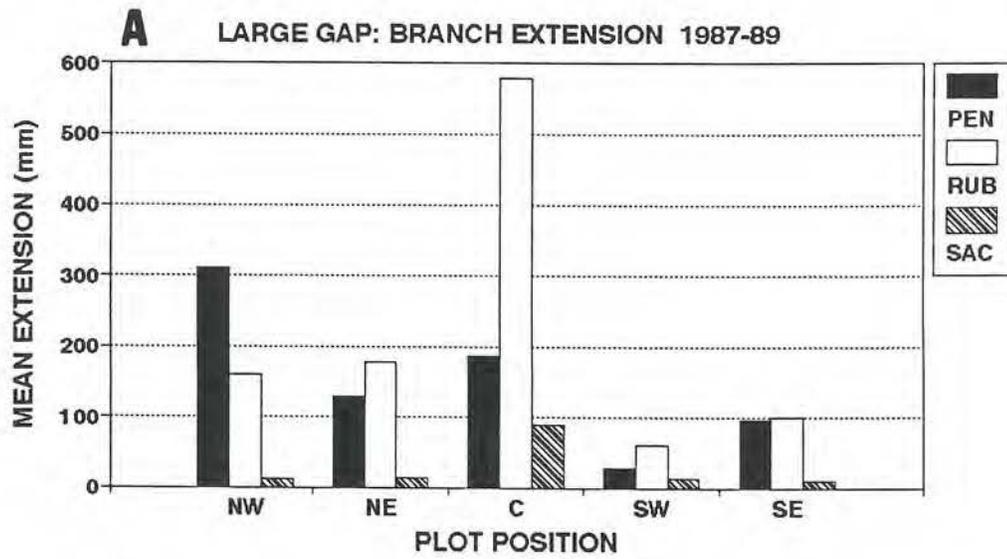


Figure 4-9. Total branch extension (i.e. sum of all living branch segments initiated during 1987-89) by seedlings surviving to October 1989. Data are only for seedlings with branches. (A) By species and plots in large gaps, (B) By species and plots in small gaps, (C) By species and plots in large understories.

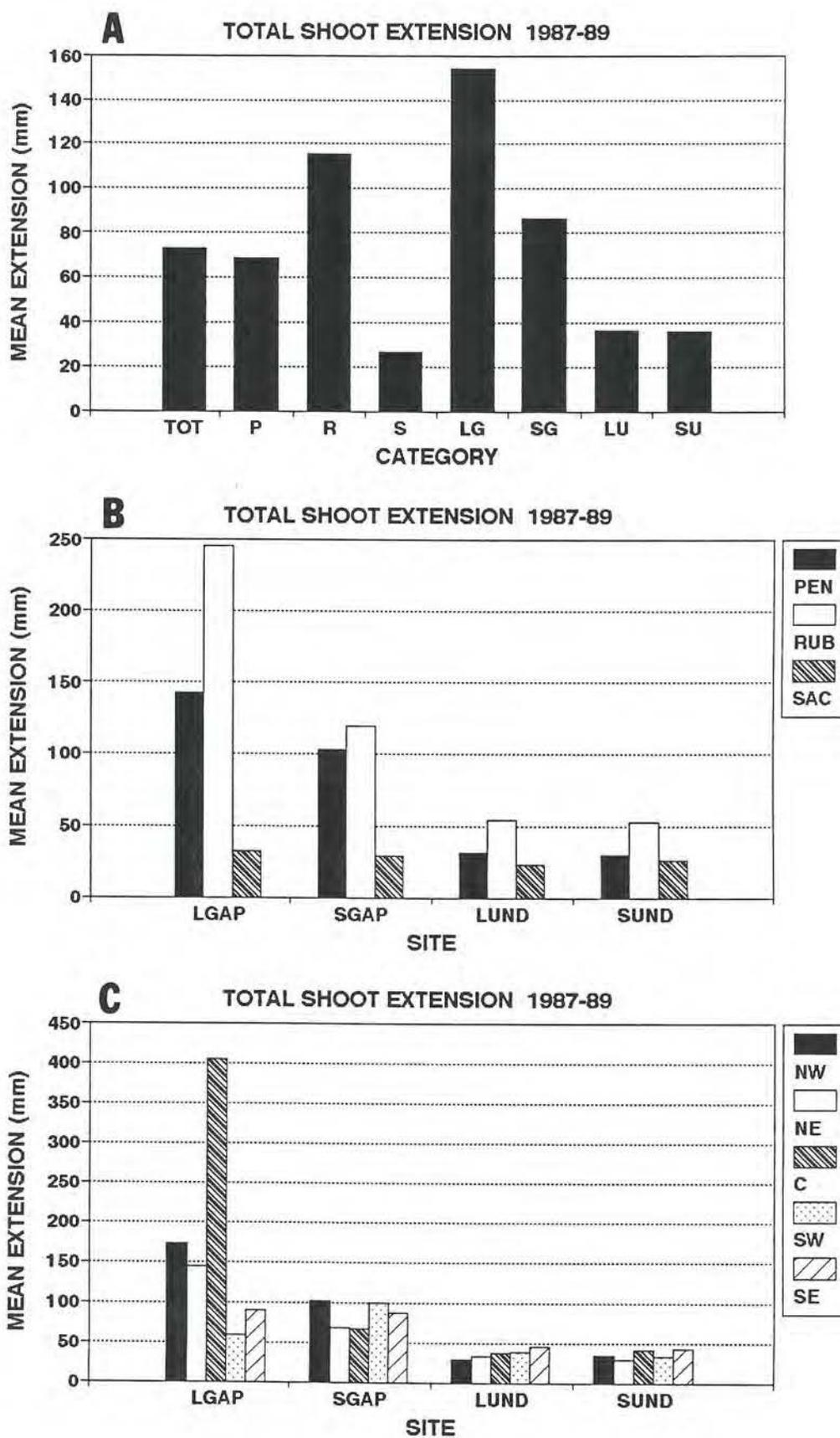


Species patterns within small gap plots were less variable, with RUB => PEN => SAC in all positions. Branch extension in all small gap plots was comparable to the south plots of the large gaps. The same rank order applied in all large understory plots (RUB > PEN > SAC), but the differences were very small.

Cumulative branch extension across species and treatments can be summarized as follows. First the same rank order (RUB => PEN => SAC) applied in all sites and plots except for the large gap NW, where PEN > RUB > SAC. Thus branching patterns among the species were consistent. Second, the large gap center was by far the most striking plot, with a combined species total that was 2.5 times that of any other site/plot. So the significant difference between large and small gaps was largely due to this one plot position. In fact, since striped maple did not respond to the large gap center like red maple, most of the difference between these two species overall can also be ascribed to this plot position. Finally, all species tended to show greater branch growth in the small gap plots than the large and small understory plots, but the absolute differences were not great.

As with the 1989 results, total shoot extension paralleled branch extension (Table 4-8). There were significant differences among species ($F=343.70$, $p<0.001$), with RUB > PEN > SAC (Figure 4-10a). The site x species term was significant ($F=20.90$, $p<0.001$), with species showing the same pattern in both gap sizes (RUB > PEN > SAC) but slightly different relationships in both understory sizes (RUB > PEN = SAC). Red and striped maple showed the same site preferences overall, while sugar maple showed little difference among sites (Figure 4-10b). Both gap sizes separated the species better than understory sizes.

Figure 4-10. Total shoot extension (leader plus branches) by seedlings surviving to October 1989. Data are for stem segments alive in October 1989, and do not include any leader or branch segments initiated during 1987-89 that died back before October 1989. (A) By species and site type totals, (B) By species within site types, (C) By plot positions within site types.



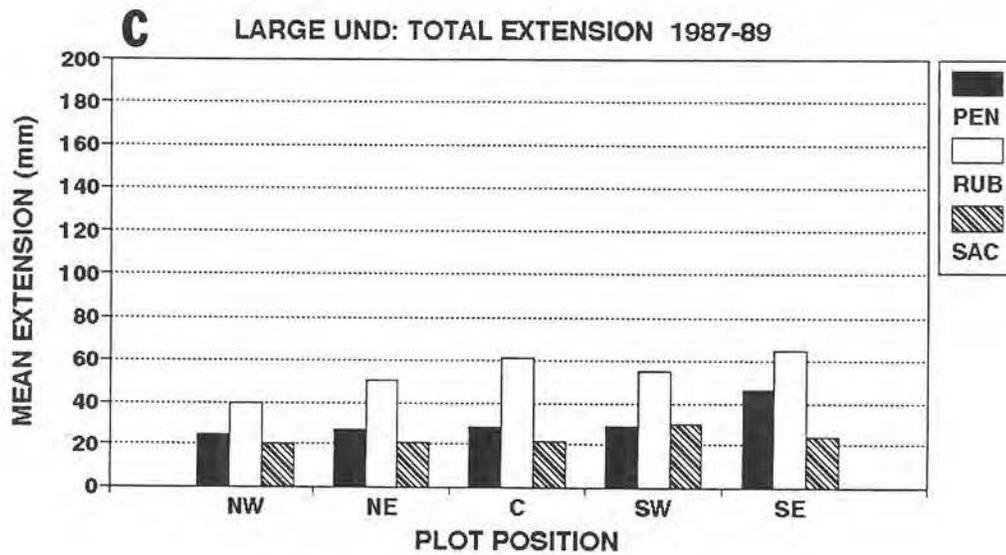
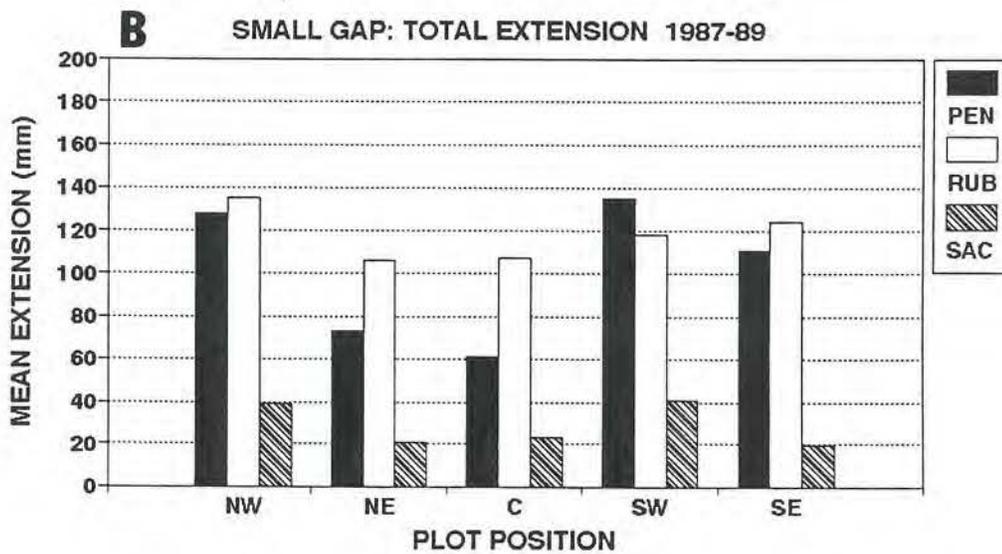
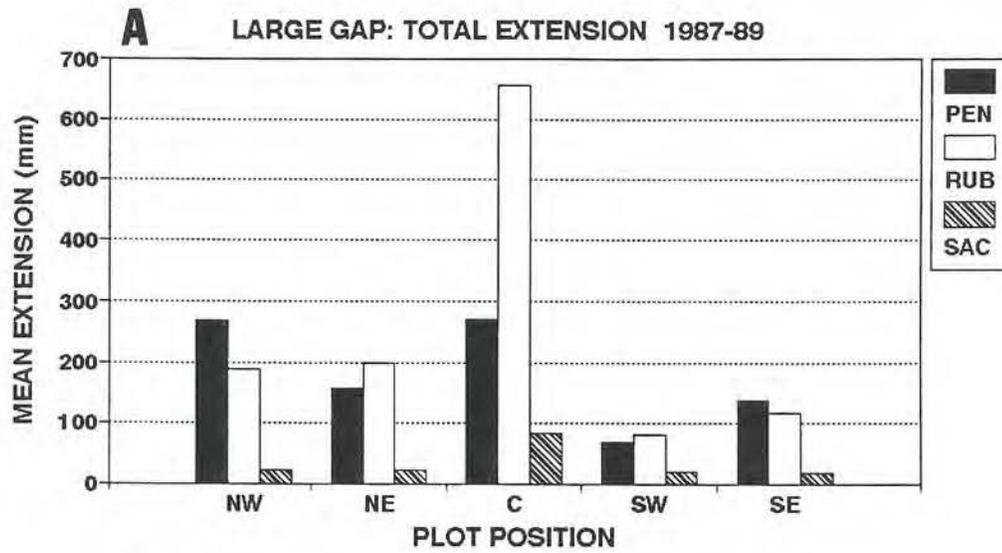
The four sites differed significantly ($F=6.54$, $p<0.05$), with $LGAP > SGAP > LUND = SUND$ (Figure 4-10a). The site \times plot interaction was significant ($F=2.94$, $p<0.01$), due primarily to large gaps, since there were no plot differences in either understory site and the only difference in small gaps was between the NW and C plots (Figure 4-10c).

Species patterns within plots and sites were mostly similar to that for branch extension (Figure 4-11). The most important difference was that striped maple was much closer to red maple in total extension than in branch extension across most sites and plots, especially in small gaps. Again, the most divergent behavior was by red maple in the large gap centers, where $RUB > PEN > SAC$. Without this site/plot position, the general pattern across the large and small gap plot positions was $RUB < PEN > SAC$, while the pattern in the large understory was $RUB > PEN \Rightarrow SAC$.

The contributions of leader and branch growth to total extension differed among the species and sites. In large gaps, branch growth was a greater contributor to total growth for red and striped maple in all plots. This was especially true for red maple. Sugar maple seemed to get equal leader and branch contributions. In small gaps, striped maple definitely benefitted most by leader growth, red maple had greater branch growth, and again sugar maple had equal components. Finally all species showed consistently greater (but very small) branch growth than leader growth in the large understory plots.

As with 1989 growth, it was important to determine whether or not leader and branch extension actually led to height gains by the seedlings surviving through October 1989. There were significant differences among species in net height change ($F=130.09$, $p<0.001$), with

Figure 4-11. Total shoot extension (leader plus branches) by seedlings surviving to October 1989. Data are for stem segments alive in October 1989, and do not include any leader or branch segments initiated during 1987-89 that died back before October 1989. (A) By species and plots in large gaps, (B) By species and plots in small gaps, (C) By species and plots in large understories.



PEN > RUB > SAC (Figure 4-12a). As Table 4-8 indicates, only striped maple showed a net gain in height (46.2mm) while both red (-8.8mm) and sugar (-29.7mm) actually declined. The site x species interaction was also significant ($F=8.45$, $p<0.001$), with PEN > RUB > SAC in large gaps, PEN > RUB = SAC in small gaps and small understories, and PEN > SAC = RUB in large understory (Figure 4-12b).

There was a nonsignificant difference overall among sites ($F=0.67$, n.s.; Figure 4-12a) but Tukey HSD tests indicated pairwise differences: LGAP = SGAP, SGAP = SUND, and SUND = LUND, such that LGAP > SUND, LUND and SGAP > LUND. The site x plot term was insignificant ($F=1.03$, n.s.), due to the fact that there were no significant differences among plots in either understory and the only difference in small gaps was between the SW and NE plots (Figure 4-12c). The pattern in large gaps was C > NE = SE = NW = SW. The distinction between the large gap center and all other sites and plots (Table 4-8) was the most striking feature of net height change in the experiment, and paralleled the conclusion for branch extension, total extension, and to a lesser extent, leader extension. There was something unusual indeed about the large gap centers that favored growth by all species.

The species showed comparable patterns in nearly all sites and plots, the only exception being the large gap centers (Figure 4-13). Across the 15 site/plot positions, striped maple always showed positive gains in height, sugar maple always showed losses, and red maple varied (3 plots with gains, 12 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.

Thus in terms of net height change, striped maple was the clear

Figure 4-12. Cumulative stem height change 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 plot positions within site types.

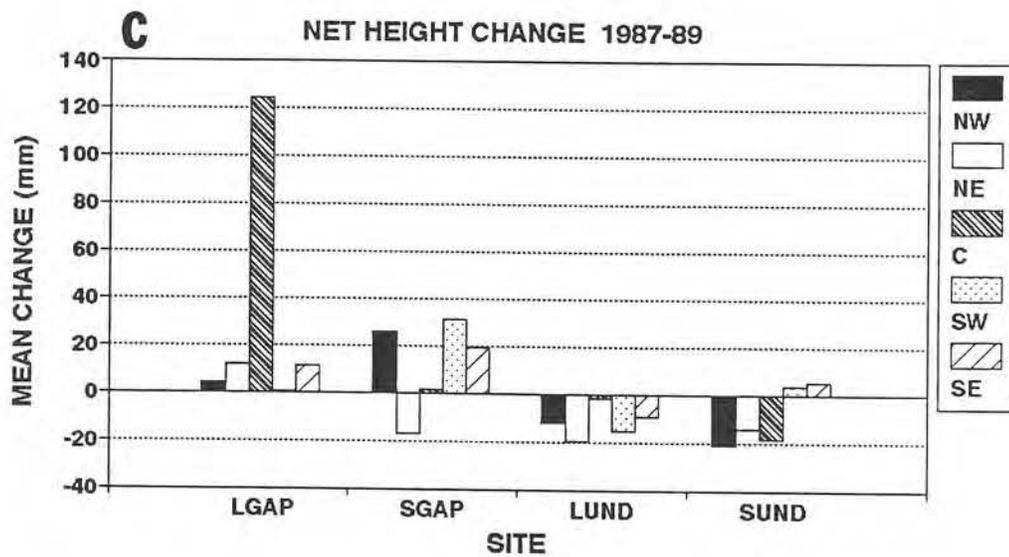
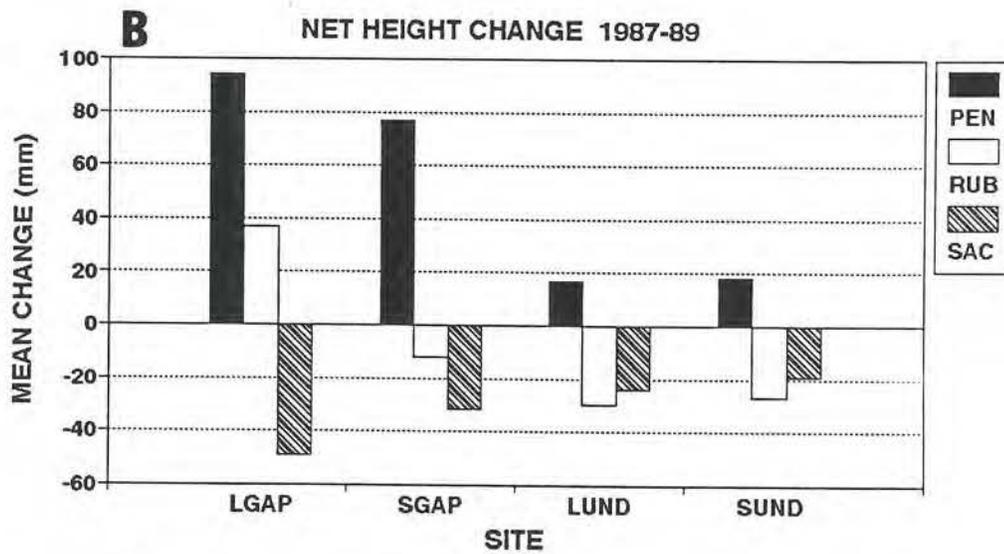
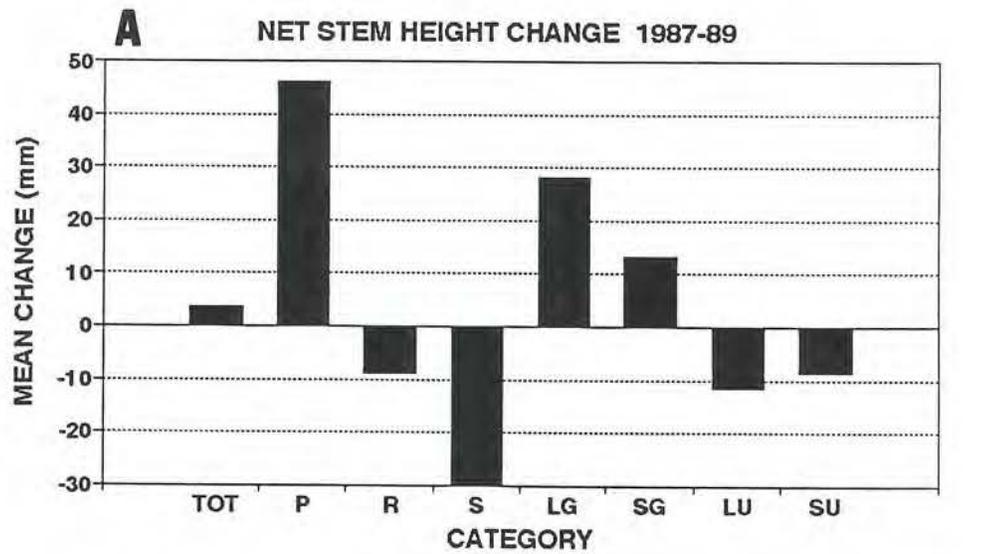
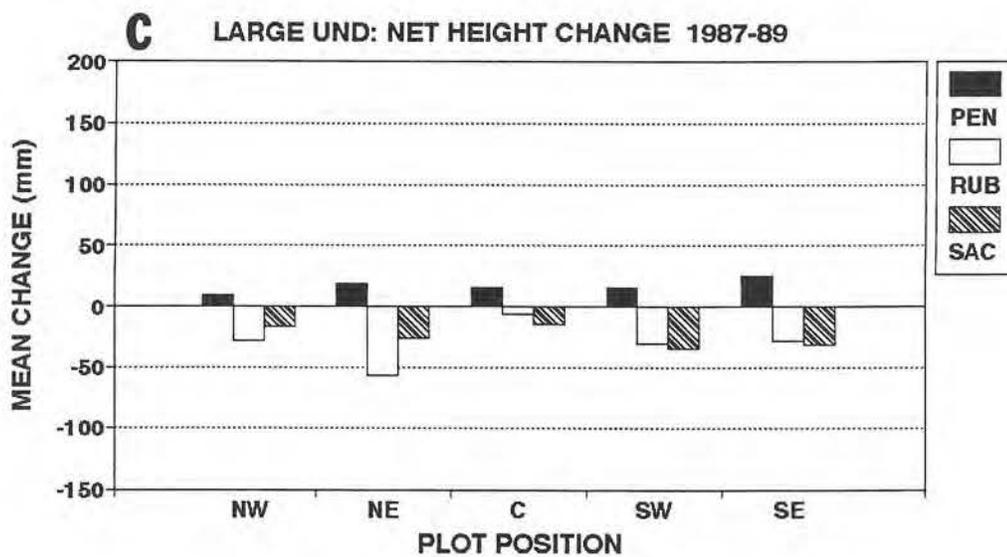
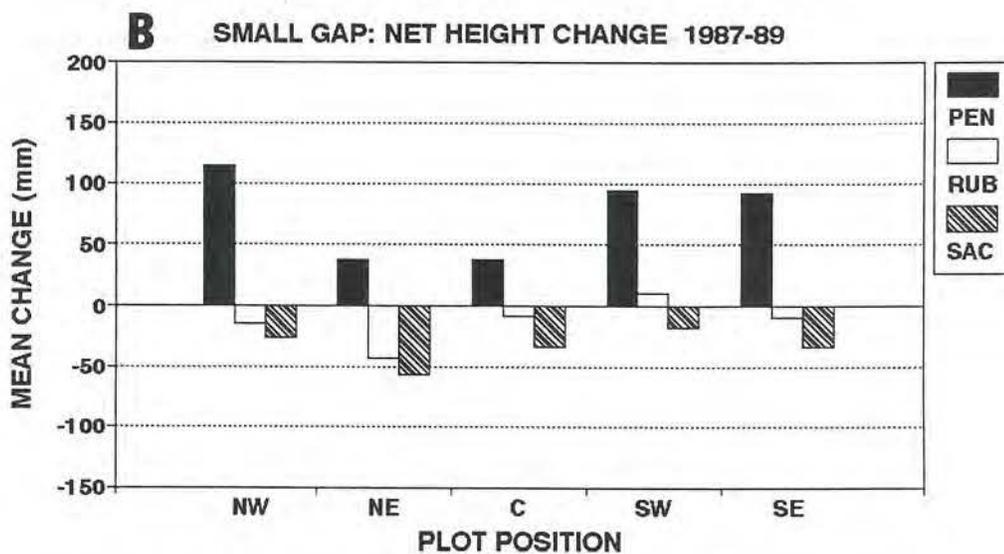
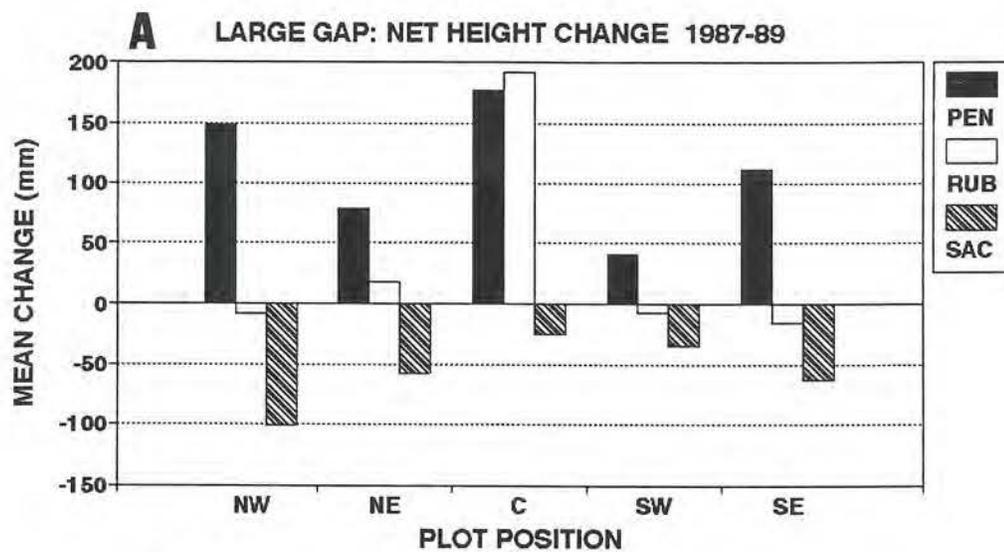


Figure 4-13. Cumulative stem height change for seedlings surviving to October 1989. Data represent the difference between 1987 (pre-gap) and 1989 highest living meristem, measured perpendicular to the ground. (A) By species and plots in large gaps, (B) By species and plots in small gaps, (C) By species and plots in large understories.



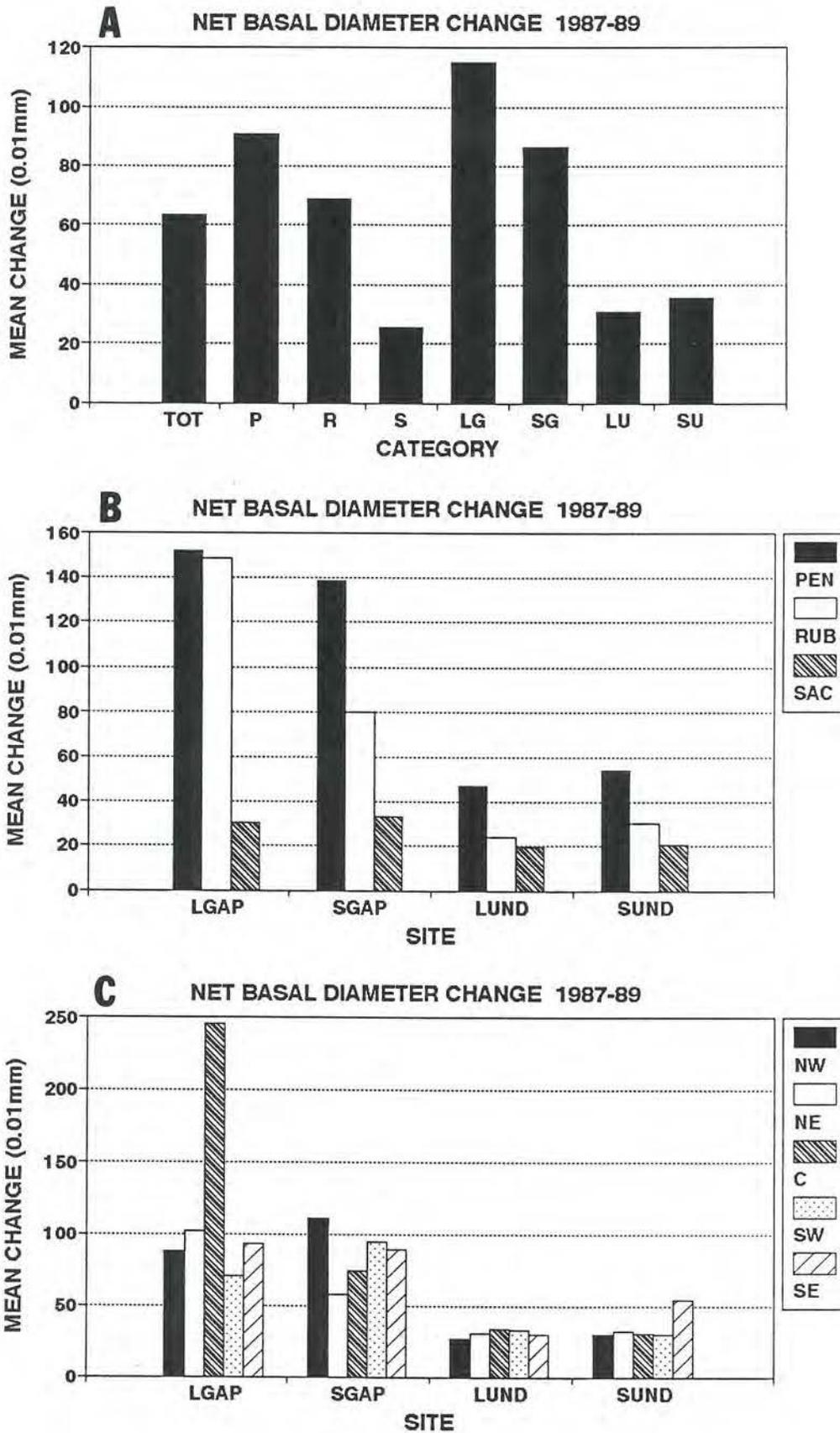
winner everywhere except large gap center, sugar maple was the clear loser, and red maple showed notable growth in only one plot position (large gap center). It should be remembered that these results include much dieback and regrowth, especially by red maple. Neither striped nor sugar maple matched the ability of red maple to die back to the base in large gap centers and then sprout up in one growing season with two to three times as much new height as had existed previously. For all species combined, the gaps produced net height gains, with LGAP > SGAP, while the understory sites yield net height losses, with LUND = SUND.

Finally, the maximum mean height change in any site was only -9cm, in any plot only -12cm, and by any species in any plot only -19cm. These are not stupendous growth rates, especially since red and sugar maple showed height losses in nearly all sites and plots. Overall, the entire community of seedlings showed a net height gain over two years of less than 0.5cm.

The final growth variable analyzed over the 1987-89 period was net basal diameter change. There were significant differences among species ($F=119.47$, $p<0.001$), with PEN > RUB > SAC (Figure 4-14a). The site x species interaction was significant ($F=12.91$, $p<0.001$), with PEN = RUB > SAC in large gaps, PEN > RUB > SAC in small gaps, and PEN = RUB = SAC in both understory sites (Figure 4-14b). Thus the species were distinguishable in both gap sizes, but not in the understory.

Unlike the other four 1987-89 cumulative growth variables, net basal diameter change differed significantly among sites ($F=5.61$, $p<0.05$), with LGAP = SGAP > LUND = SUND (Figure 4-14a). The site x plot interaction was not significant ($F=0.61$, n.s.), since no plot differences occurred in the small gaps, large understories, or small

Figure 4-14. Cumulative basal diameter change for seedlings surviving to October 1989. Data represent the difference between 1987 (pre-gap) and 1989 stem diameters measured 1cm above the ground surface. Differences of 0.1mm or less are within the experimental error in resampling unmarked points, and are not significant. (A) By species and site type totals, (B) By species within site types, (C) By plot positions within site types.



understories. Again, however, the center plot led to a significant difference in large gaps, with $C > NE = SE = NW = SW$ (Figure (4-14c)).

For species within sites and plots, the predominant pattern was $PEN > RUB > SAC$ in nearly all site/plot combinations (Figure 4-15). The exceptions were that $RUB > PEN > SAC$ in large gap centers, and $RUB < SAC$ in the large understory.

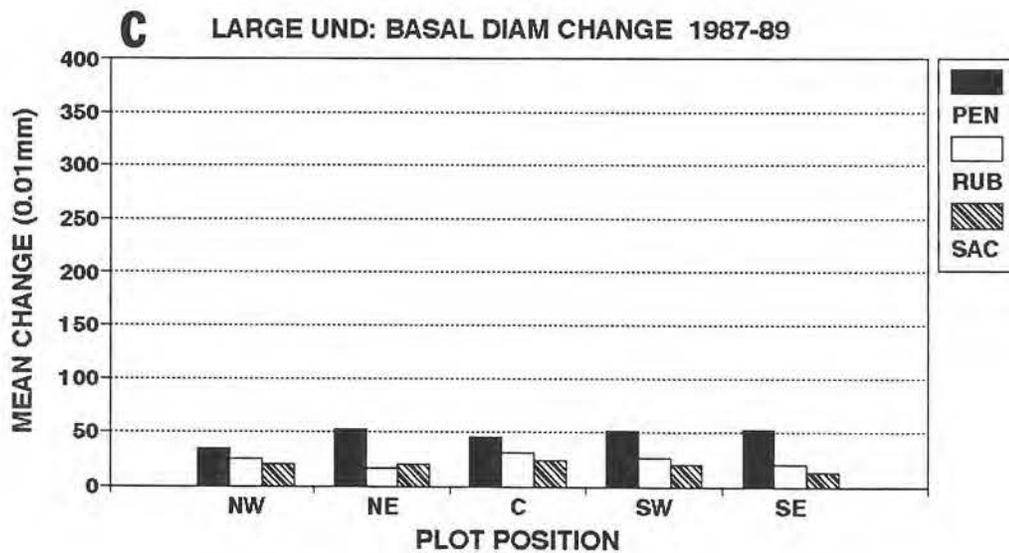
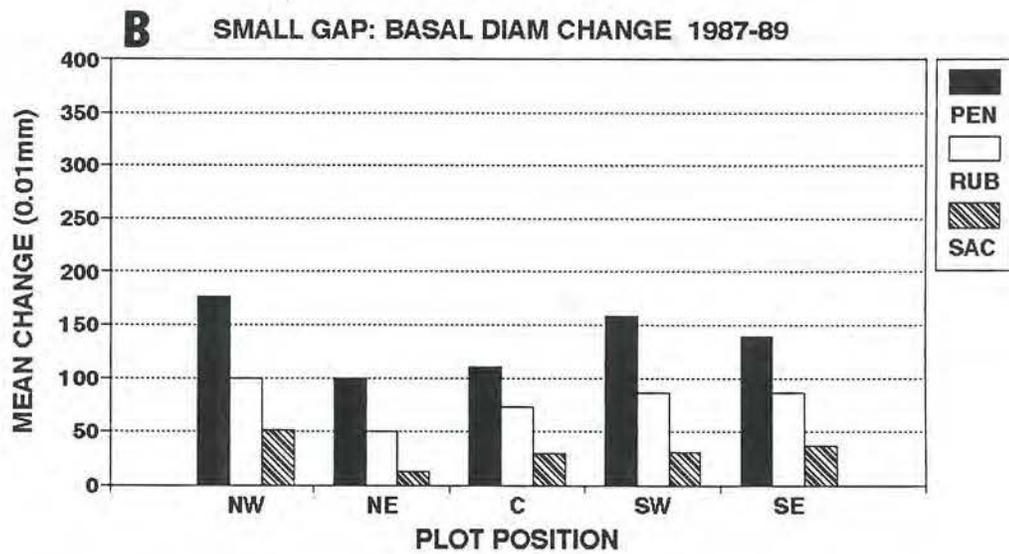
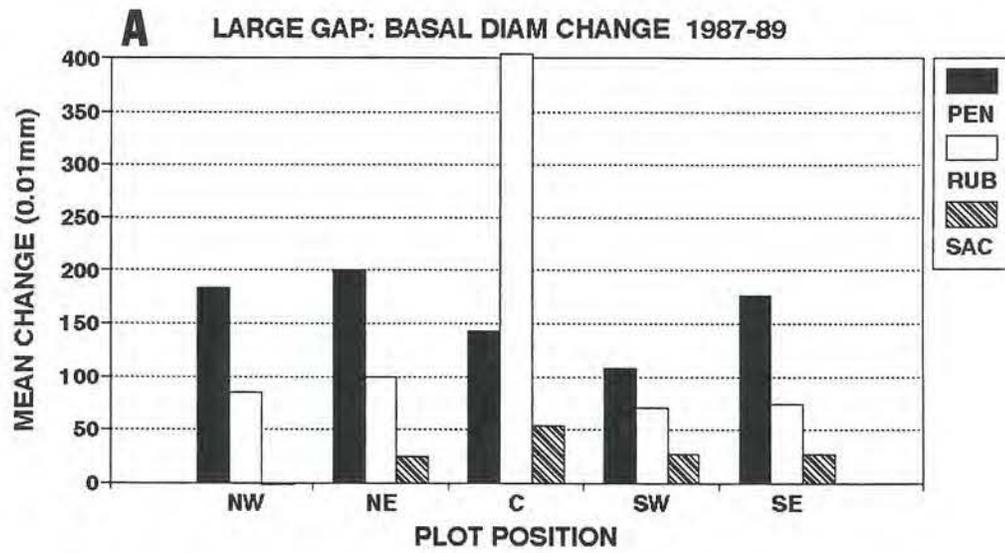
Unlike net height change, all species showed positive basal diameter gains in all sites and plots. And while the overall mean gains by species did not exceed 1.00mm ($PEN = 0.91mm$, $RUB = 0.69mm$, and $SAC = 0.25mm$), these increases still represented 9%-35% gains, which were greater than the proportional gains (and losses) in height. Thus the species seemed to be more successful at growing radially than axially.

There were divergent behaviors by the three species, however. Striped maple showed relatively uniform gains across all large and small gap plots, with reduced gains in the understory. Red maple gains were also essentially the same in large and small gap plots, except for large gap centers, where it excelled. It was also reduced in the understory. Finally, sugar maple showed almost no preference for any site/plot combination.

4.3.2. GROWTH VERSUS PREVIOUS AGE AND SIZE

As mentioned in Section 4.1., the original expectation was that post-gap growth would be related to pre-gap status for at least some species in some sites. However, as with survival, this turned out not to be the case. Figures 4-16 through 4-21 display the relationships between four of the five 1987-89 net growth variables and pre-gap age, stem height, and basal diameter. Scatterplots were also examined for

Figure 4-15. Cumulative basal diameter change for seedlings surviving to October 1989. Data represent the difference between 1987 (pre-gap) and 1989 stem diameters measured 1cm above the ground surface. Differences of 0.1mm or less are within the experimental error in resampling unmarked points, and are not significant. (A) By species and plots in large gaps, (B) By species and plots in small gaps, (C) By species and plots in large understories.



individual sites and species, but since the patterns differed little from the pooled plots, only the latter are presented here. The purpose of presenting the twelve graphs is to emphasize the remarkable lack of correspondence between pre-gap status and post-gap performance.

Post-gap growth versus pre-gap age plots are shown in Figures 4-16 and 4-17. Note that total leader growth and stem extension were always positive, but net height and basal diameter change were frequently negative. None of the scatterplots showed a notable trend, except that the extremes (very young or old) were less likely to exhibit larger growth rates. In contrast, the likelihood and amount of net loss in height or basal diameter showed no non-random pattern whatsoever.

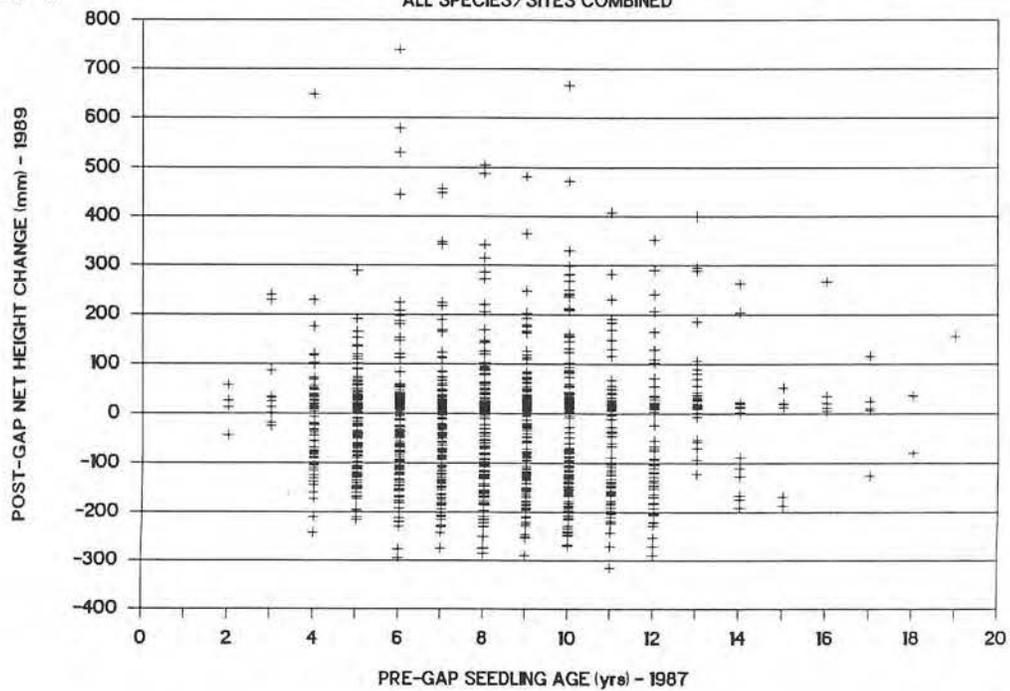
Post-gap growth versus pre-gap height showed comparable patterns (Figures 4-18 and 4-19). The straight line of points in Figure 4-18a represents the lower boundary of possible height loss. These are seedlings that died and therefore "lost" all height. As with pre-gap age, the extremes tended to be disfavored - very short or very tall seedlings were less likely to exhibit the higher growth rates. Likewise, there was no tendency for smaller or larger seedlings to show consistently greater net losses. The slightly negative slope for seedlings showing net basal diameter loss versus pre-gap height (Figure 4-18b) is an artifact of the positive relationship between initial height and diameter.

The scatterplots for growth versus pre-gap basal diameter support the previous conclusions, although the disfavoring of extremes is less noticeable (Figures 4-20 and 4-21). The slight tendency toward a negative slope for seedlings showing net height loss versus pre-gap diameter (Figure 4-20a) was also an artifact of the positive

Figure 4-16. Post-gap cumulative height change (A) and basal diameter change (B) over 1987-89 versus pre-gap seedling age. Data are for all seedlings (n=2160), including those dead by October 1989.

A**POST-GAP HT CHANGE vs. PRE-GAP AGE**

ALL SPECIES/SITES COMBINED

**B****POST-GAP BDIAM CHANGE vs. PRE-GAP AGE**

ALL SPECIES/SITES COMBINED

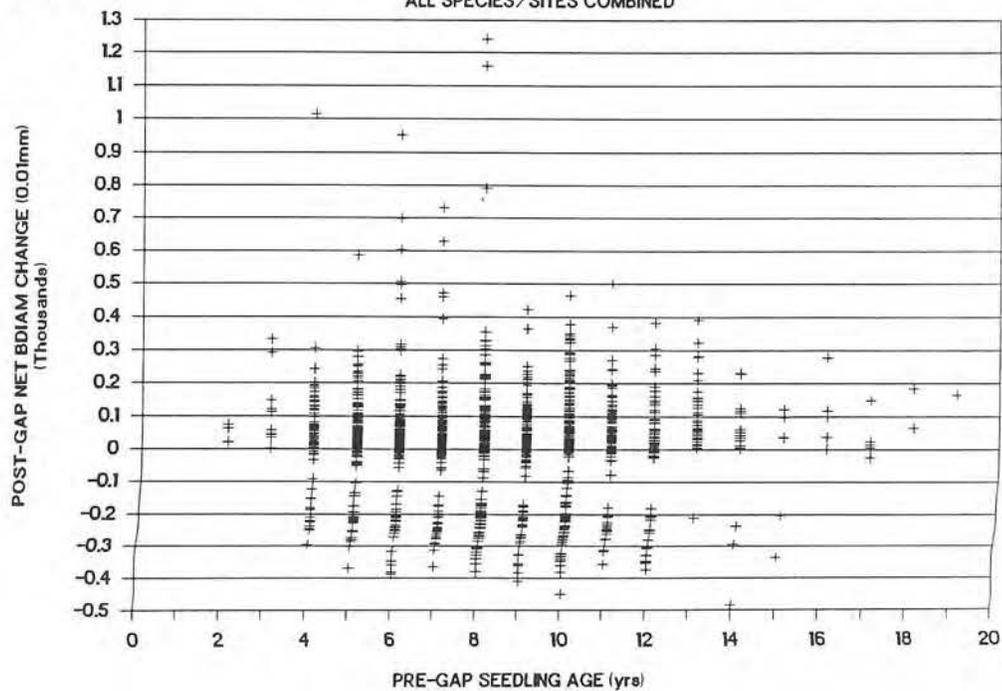
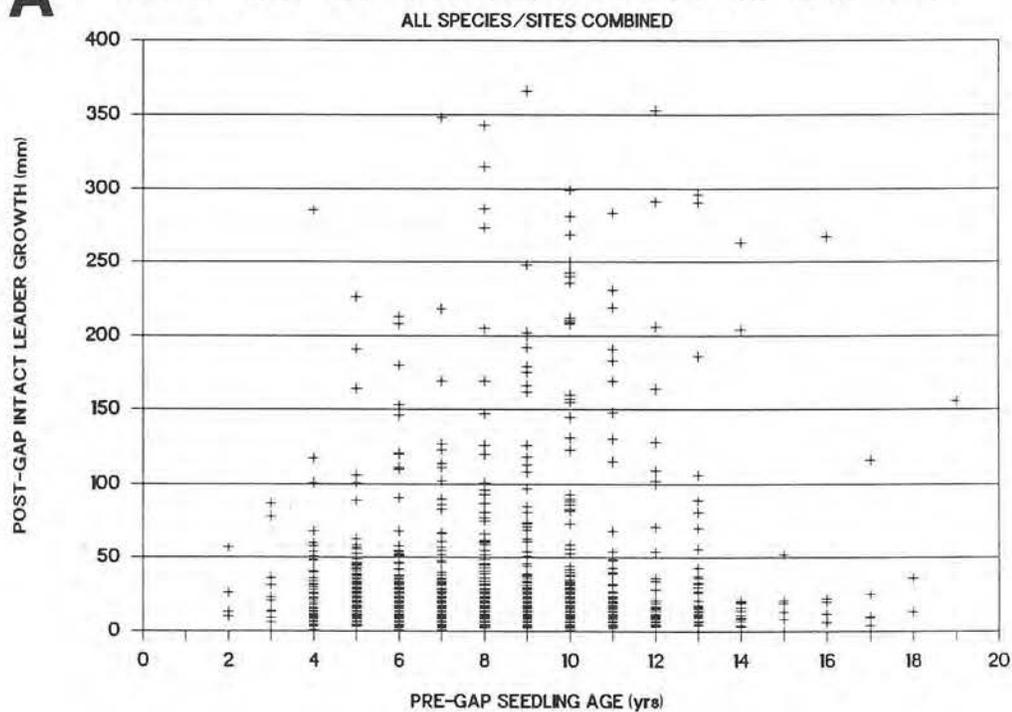


Figure 4-17. Post-gap leader extension (A) and total stem extension (leader plus branches) (B) over 1987-89 versus pre-gap seedling age. Data are for all seedlings (n=2160), including those dead by October 1989.

A POST-GAP LEADER GROWTH vs. PRE-GAP AGE



B POST-GAP TOTAL STEM EXTENSION vs. PRE-GAP AGE

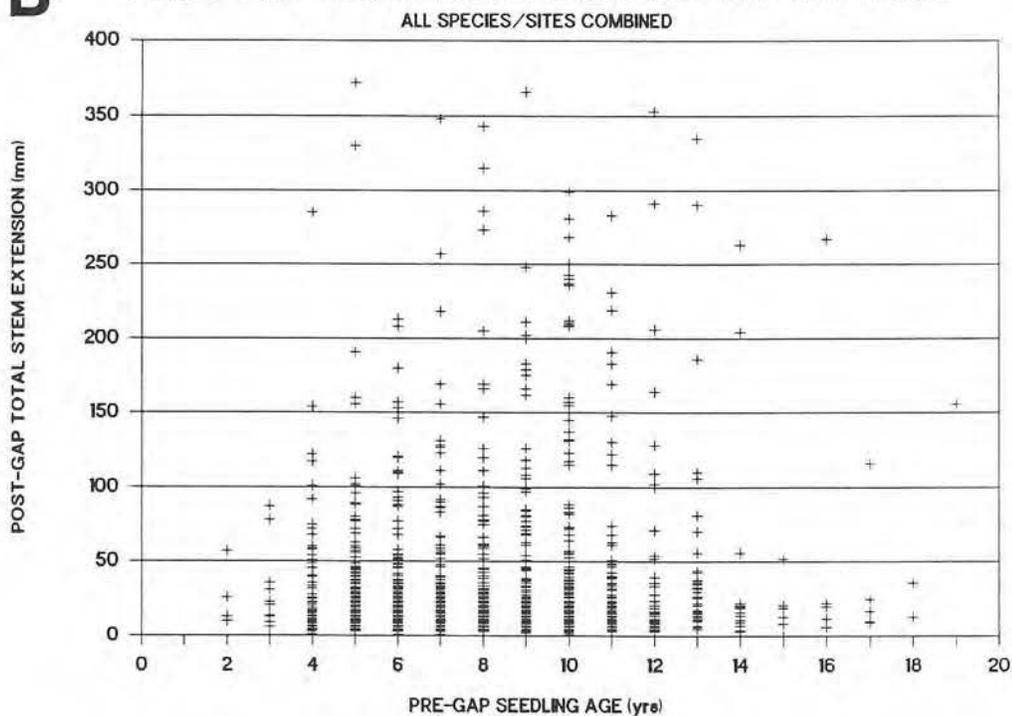
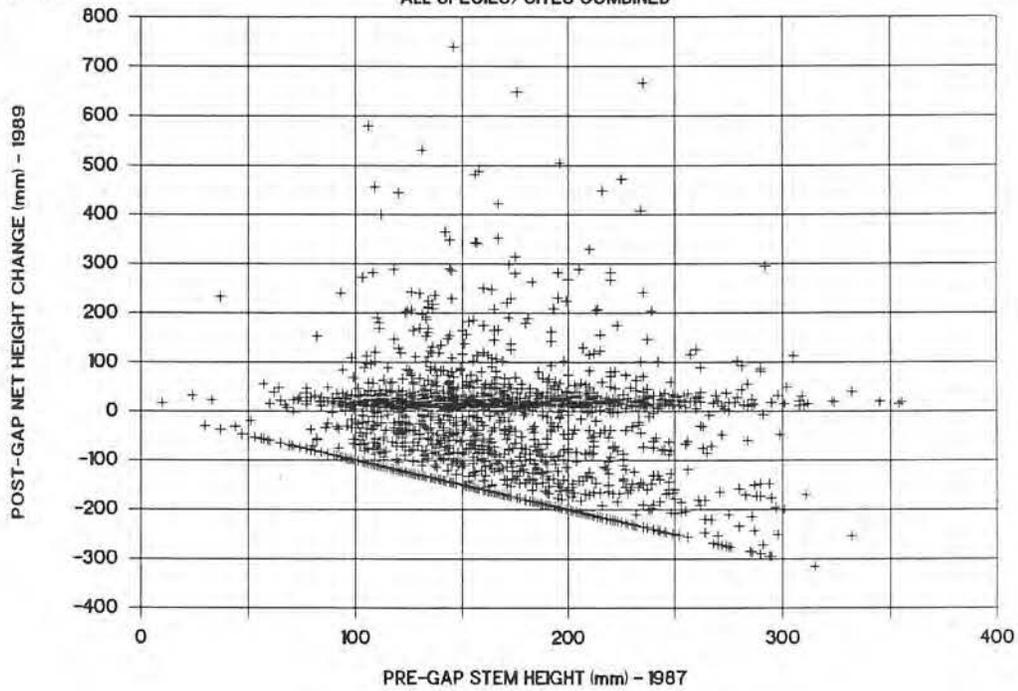


Figure 4-18. Post-gap cumulative height change (A) and basal diameter change (B) over 1987-89 versus pre-gap seedling height. Data are for all seedlings (n=2160), including those dead by October 1989. Points on the lower straight line are seedlings that died and lost all initial height.

A**POST-GAP HT GROWTH vs. PRE-GAP HT**

ALL SPECIES/SITES COMBINED

**B****POST-GAP BDIAM CHANGE vs. PRE-GAP HT**

ALL SPECIES/SITES COMBINED

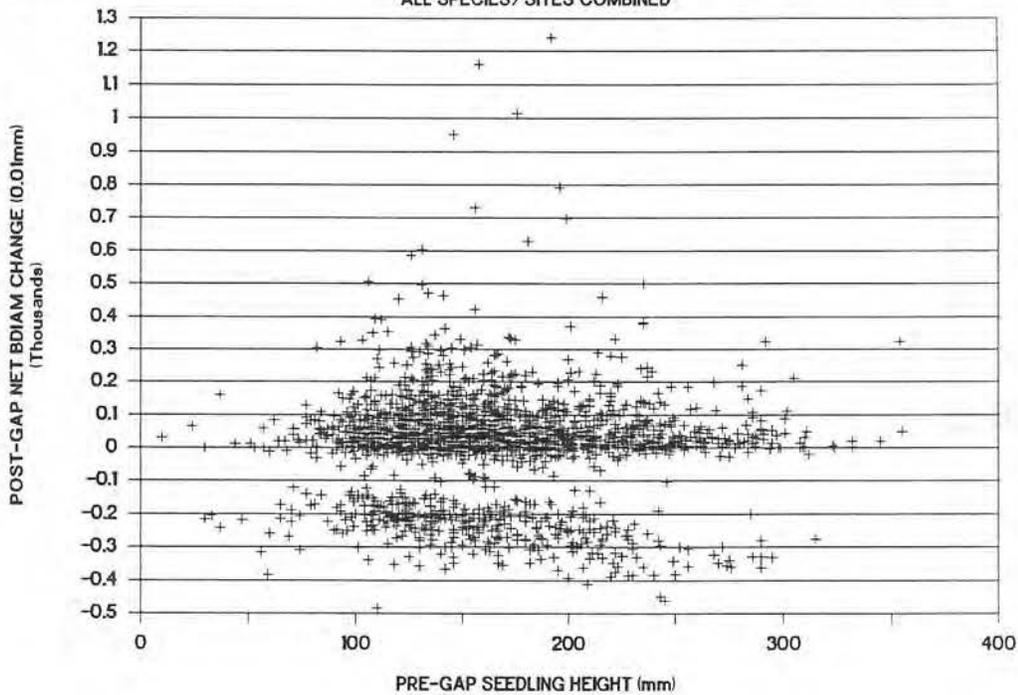


Figure 4-19. Post-gap leader extension (A) and total stem extension (leader plus branches) (B) over 1987-89 versus pre-gap seedling height. Data are for all seedlings (n=2160), including those dead by October 1989.

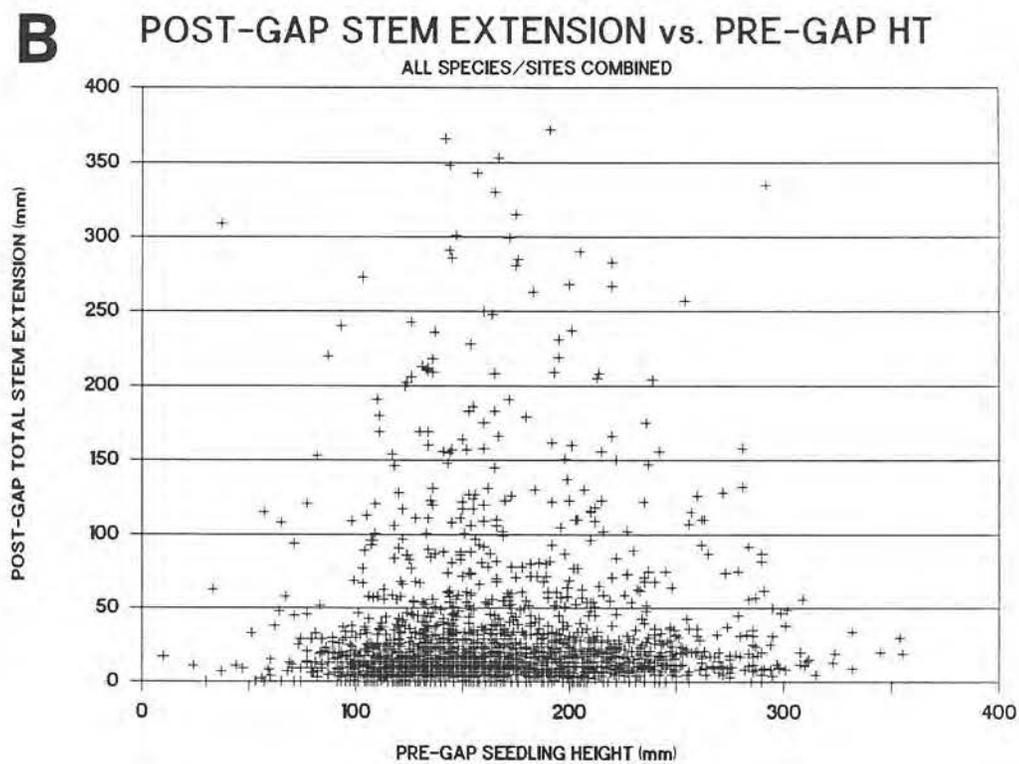
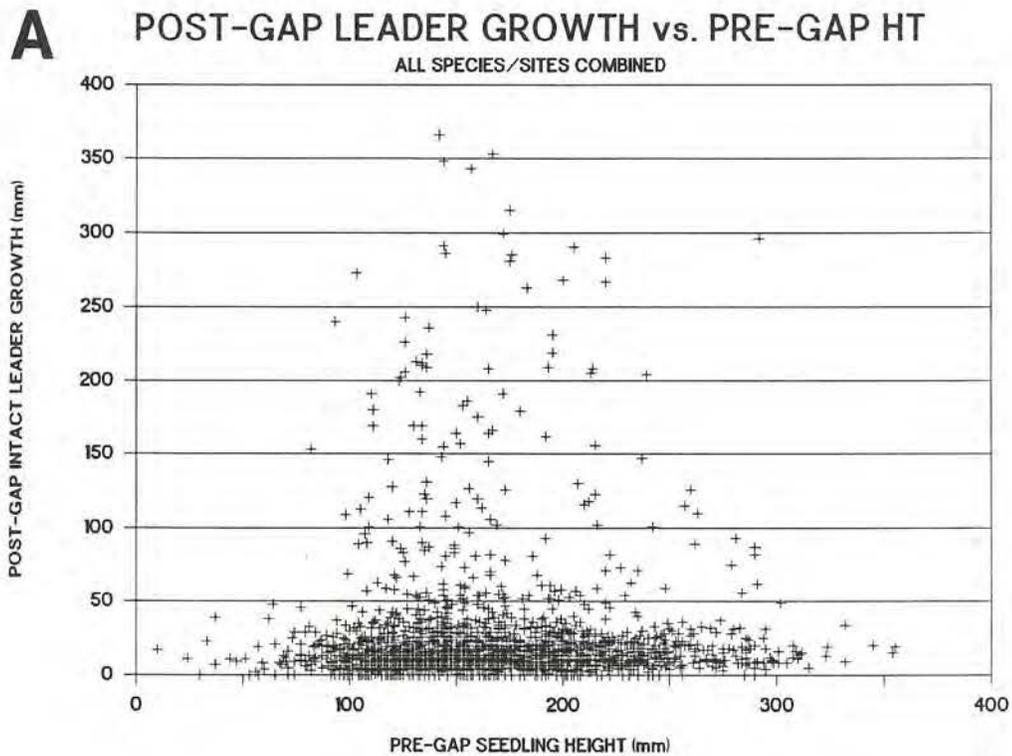
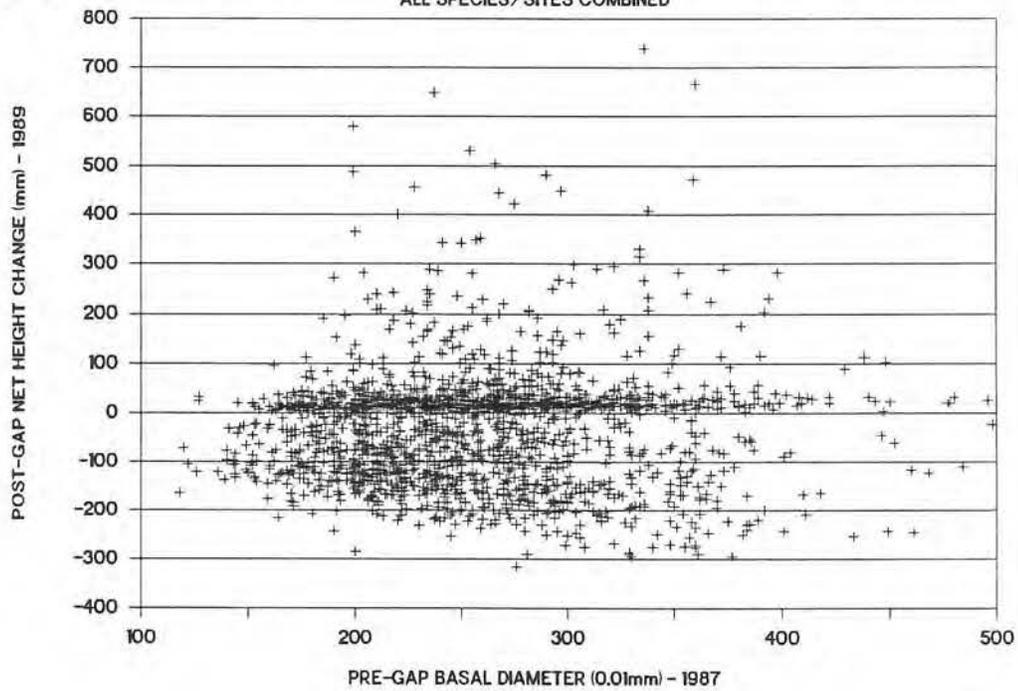


Figure 4-20. Post-gap cumulative height change (A) and basal diameter change (B) over 1987-89 versus pre-gap seedling basal diameter. Data are for all seedlings (n=2160), including those dead by October 1989. Points on the lower straight line are seedlings that died and lost all initial height.

A POST-GAP HT CHANGE vs. PRE-GAP BAS DIAM

ALL SPECIES/SITES COMBINED



B POST-GAP BDIAM CHANGE vs. PRE-GAP BDIAM

ALL SPECIES/SITES COMBINED

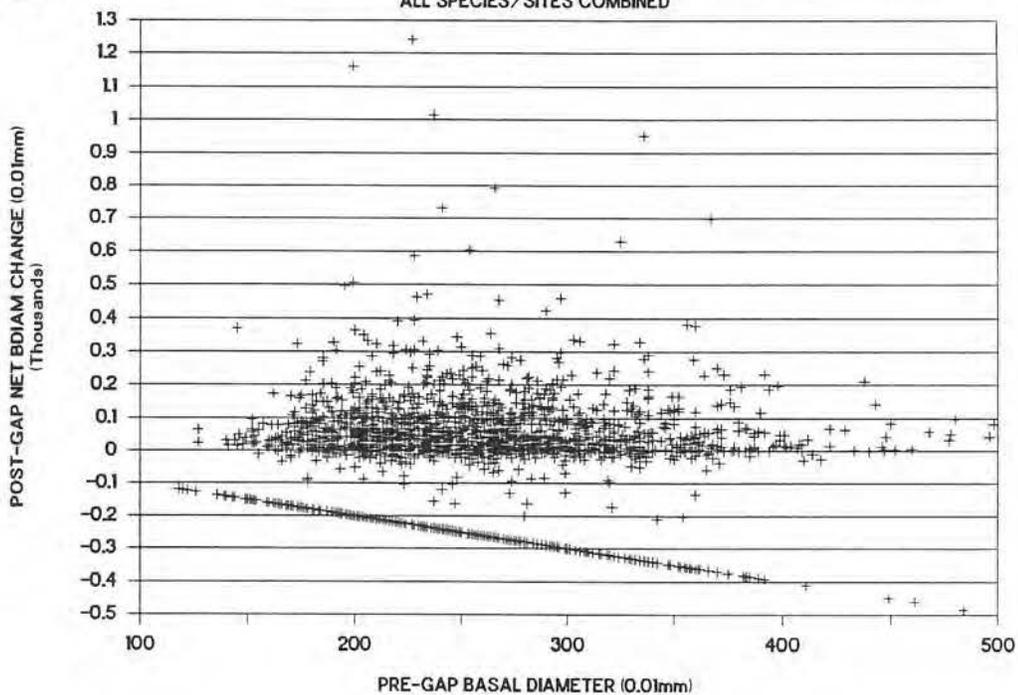
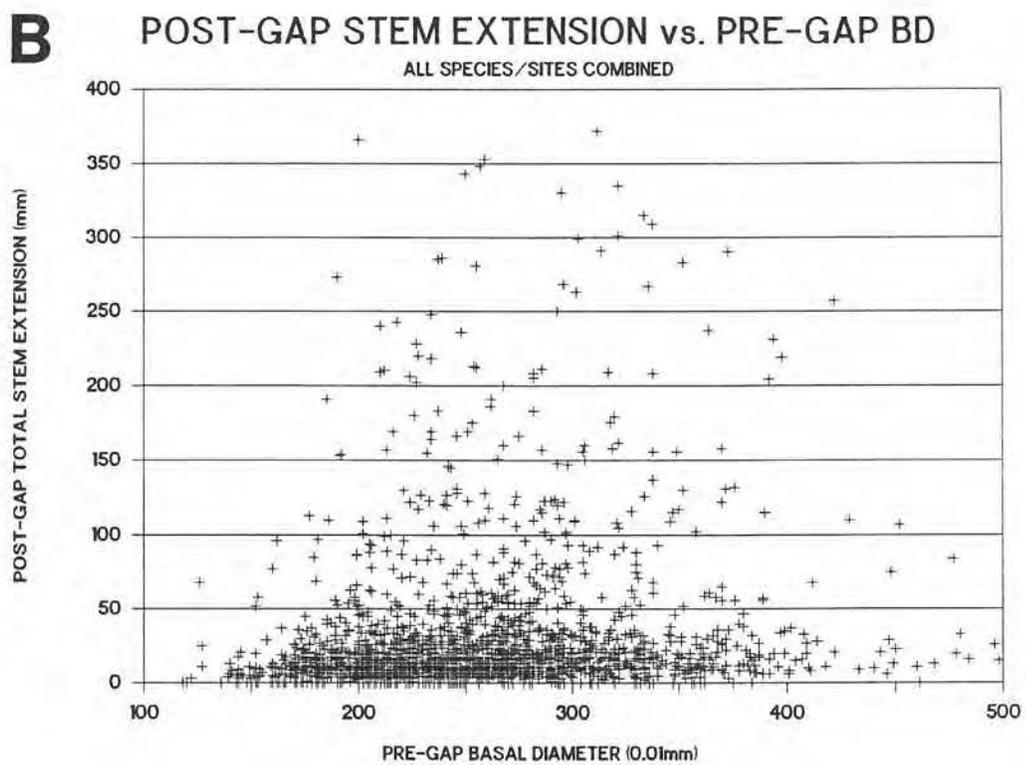
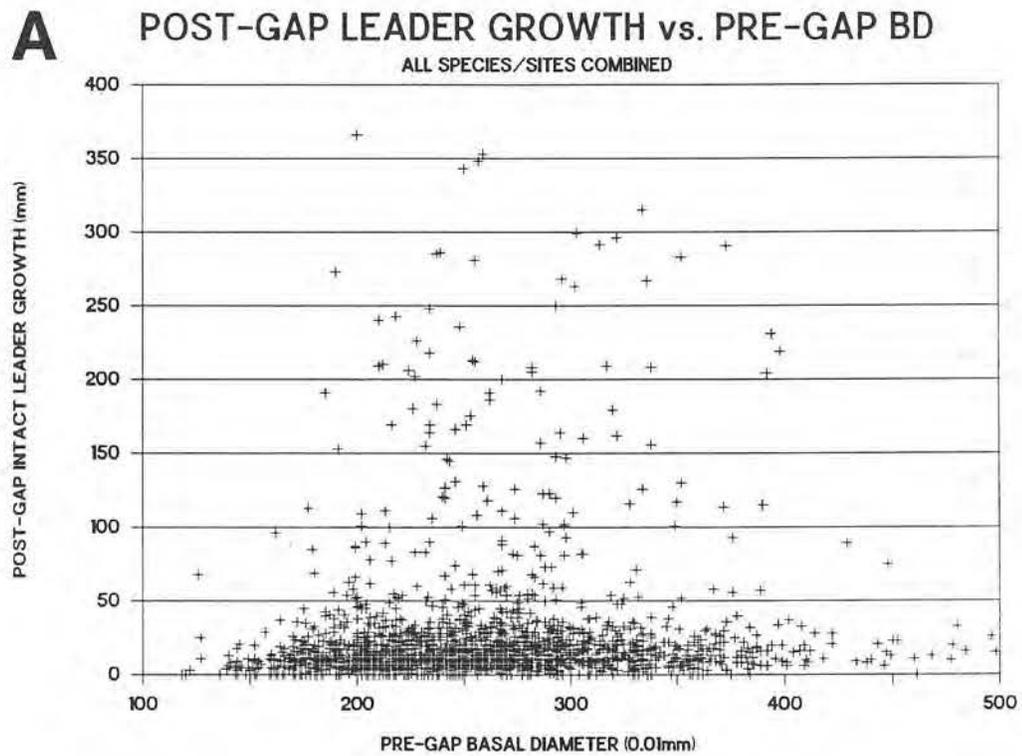


Figure 4-21. Post-gap leader extension (A) and total stem extension (leader plus branches) (B) over 1987-89 versus pre-gap seedling basal diameter. Data are for all seedlings (n=2160), including those dead by October 1989.



relationship between initial height and diameter.

A final point is worth noting. In all cases, the majority of non-negative data points are compressed toward the x-axis. This indicates that most positive gains were very modest, while perhaps only 100-200 exhibited large gains. In fact, an overall view of the 1987-89 growth graphs in Figures 4-6 through 4-15 supports this argument.

This presents an interesting problem. In general, outliers are detrimental to statistical analysis, especially ANOVA. The definition of an outlier is relative, in that it is a divergence from the average behavior of the remaining data points. In this experiment, it appears that the most interesting responses, and possibly those most influential for the ANOVA results, are the 100-200 individuals that appear as the divergent points in Figures 4-16 through 4-21. The options are to exclude many modest outliers, and risk losing the important distinctions between species and treatments, or accept the points as critical information and interpret the ANOVA with this in mind. The latter strategy was chosen here.

This point has significant bearing on the question of gap partitioning, since it appears that most sites and plots did not separate species behaviors well, producing the compressed scatterplots in this section. In effect, the large and small understory sites, as well as the small gap south plots, were quite similar in microenvironmental conditions and elicited comparable species behaviors.

4.4. SHOOT ARCHITECTURE

4.4.1. LEAF AREA:LENGTH RELATIONSHIPS

The quadratic functions of leaf laminar area (cm^2) on length (mm)

produced good fits for all individual pairs and pooled pairs within species (Table 4-10). All functions were tested with and without a forced zero intercept, and in all cases the forcing did not cause significant changes in curvilinear correlations. The functions with zero intercepts were used since they are biologically more meaningful. The addition of a linear term added usefully to the fits only in the case of the third pair for striped maple.

While pooling the pairs caused some loss of accuracy in estimating shoot leaf area, the resulting functions could be applied to any seedling for which the mean leaf length was known, regardless of the number of pairs. This was the primary goal of the curve-fitting, and the pooled correlations were judged acceptable.

4.4.2. ARCHITECTURAL CHANGES, 1987-1989

The 1987 architectural data consisted only of stem heights, number of leaf pairs, and total number of leaves. The uniformity of the transplanted seedlings had not changed much during the 1986-87 pre-gap year in the understory, and consequently much of the architectural difference as of October 1987 was due to inherent species-specific responses to suppressed understory conditions.

The species did differ significantly in height (discussed in Section 4.3.1.1.), with $SAC > RUB > PEN$, but the mean difference across the study area was no more than 31mm (Table 4-11). 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 $PEN = 2.1$). Since leaf lengths were not measured, leaf area data were not available. But the visual impression at this stage was that $PEN > SAC \Rightarrow$

Table 4-10. Leaf area versus length curvilinear regression parameters, by species and leaf pair number. All regressions have zero intercepts.

SPECIES	TERM(S)	LEAF PAIR #1	LEAF PAIR #2	LEAF PAIR #3	POOLED PAIRS
Acer pennsylvanicum	quadratic	0.006567	0.223454	0.005696	0.005646
	linear r-sqr	0.95	0.95	0.001474 0.76	0.84
Acer rubrum	quadratic	0.006317	0.004949	0.005355	0.005843
	r-sqr	0.85	0.96	0.96	0.89
Acer saccharum	quadratic	0.007828	0.007302	0.006845	0.007564
	r-sqr	0.98	0.92	0.83	0.94

Table 4-11. Fall 1987 (pre-gap) architectural status.

CATEGORY	STEM HEIGHT (mm)			NO. LEAF PAIRS			NO. LEAVES		
	N	MEAN	S.E.	N	MEAN	S.E.	N	MEAN	S.E.
TOTAL	2092	166	1.2	2012	1.8	0.02	2012	3.4	0.04
PEN	695	153	2.4	655	1.1	0.02	655	2.1	0.03
RUB	699	161	1.7	679	2.4	0.04	679	4.5	0.09
SAC	698	183	2.1	678	1.8	0.03	678	3.4	0.05
LGAP	523	162	2.1	501	1.8	0.04	501	3.3	0.08
SGAP	524	169	2.2	498	1.8	0.05	498	3.5	0.09
LUND	528	164	2.1	515	1.8	0.05	515	3.4	0.09
SUND	517	167	3.3	498	1.8	0.04	498	3.3	0.08
BLOCK 1	706	169	1.9	681	1.8	0.04	681	3.3	0.07
BLOCK 2	702	167	2.5	672	1.8	0.04	672	3.4	0.07
BLOCK 3	684	160	1.9	659	1.8	0.04	659	3.4	0.07
LGAP PEN	172	146	3.2	157	1.1	0.03	157	2.1	0.05
RUB	176	161	3.4	175	2.3	0.08	175	4.4	0.15
SAC	175	180	3.8	169	1.8	0.05	169	3.5	0.10
SGAP PEN	176	152	3.3	165	1.2	0.03	165	2.2	0.07
RUB	172	169	3.4	163	2.6	0.10	163	4.8	0.20
SAC	176	185	4.2	170	1.8	0.05	170	3.4	0.10
LUND PEN	176	154	3.3	172	1.1	0.03	172	2.1	0.06
RUB	178	156	3.2	174	2.5	0.10	174	4.6	0.19
SAC	174	184	4.1	169	1.7	0.05	169	3.4	0.10
SUND PEN	171	162	8.1	161	1.2	0.03	161	2.2	0.06
RUB	173	157	3.4	167	2.3	0.08	167	4.4	0.15
SAC	173	183	4.6	170	1.8	0.06	170	3.4	0.11
LGAP C	102	159	4.2	97	1.9	0.09	97	3.5	0.17
NE	104	155	4.4	99	1.7	0.10	99	3.2	0.20
NW	104	164	5.5	98	1.7	0.09	98	3.2	0.18
SE	106	163	4.9	103	1.7	0.08	103	3.3	0.15
SW	107	171	4.2	104	1.8	0.08	104	3.4	0.15
SGAP C	102	175	5.0	92	1.6	0.07	92	3.1	0.14
NE	103	170	5.2	100	1.9	0.12	100	3.6	0.24
NW	107	171	4.8	105	1.9	0.11	105	3.6	0.20
SE	105	166	4.5	97	1.9	0.12	97	3.6	0.22
SW	107	162	4.8	104	1.7	0.10	104	3.3	0.19
LUND C	107	163	4.8	105	1.8	0.09	105	3.4	0.18
NE	105	163	4.0	102	1.6	0.07	102	3.0	0.14
NW	107	157	5.0	104	1.7	0.07	104	3.2	0.14
SE	102	163	4.0	99	1.8	0.12	99	3.4	0.22
SW	107	176	5.3	105	2.1	0.14	105	3.9	0.27
SUND C	106	178	12.3	102	1.8	0.10	102	3.3	0.18
NE	97	162	5.6	94	1.8	0.09	94	3.2	0.18
NW	106	165	4.6	102	1.7	0.07	102	3.1	0.14
SE	105	167	5.4	102	1.9	0.10	102	3.7	0.19
SW	103	163	5.8	98	1.7	0.08	98	3.2	0.16

RUB.

As Table 4-11 indicates, the sites and plots within sites did not show consistent differences for any of these three variables, and the relative order among species was maintained in all sites. Thus the overall conclusion for 1987 is that stem heights varied by species due to experimental transplant selection, while leaf pair and total leaf numbers differed due to inherent species' architectures in understory environments.

The discussion of growth (Section 4.3.) indicated that tremendous architectural variation arose over the two seasons following gap creation. 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 was abundant site-induced branch initiation unrelated to shoot damage, some basal resprouts from dieback stems, and frequent secondary branching. The results of all these processes were 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 pre-gap seedlings. As will be seen, changes in shoot architecture, especially total leaf area, greatly affected estimated shoot photosynthesis in 1989 versus 1988 (Sections 5.3. and 5.4.).

Architectural data for 1989 are presented in Table 4-12. The ANOVA model applied to growth variables was also used on mean leaf length, mean leaf area, and total shoot area, and these results are in Table 4-9. Since 1989 stem height was already discussed in Section 4.3.3.3., it will not be presented here as well.

Table 4-12. Fall 1989 architectural status.

Table 4-12. Fall 1989 architectural status.

CATEGORY	HEIGHT (mm)			NO. BRANCHES			NO. LEAF PAIRS			NO. LEAVES			MEAN LEAF LENGTH (mm)			MEAN LEAF AREA (sqr cm)			TOTAL LEAF AREA (sqr cm)		
	N	MEAN	S.E.	N	MEAN	S.E.	N	MEAN	S.E.	N	MEAN	S.E.	N	MEAN	S.E.	N	MEAN	S.E.	N	MEAN	S.E.
TOTAL	1705	170	2.5	1106	2.1	0.04	1649	3.1	0.10	1573	5.8	0.20	1548	51	0.8	1548	22.2	0.68	1548	124.7	6.66
PEN	580	203	4.9	197	1.7	0.07	575	2.4	0.09	568	4.7	0.17	560	80	1.2	560	45.5	1.34	560	210.5	10.69
RUB	612	152	3.8	566	2.5	0.07	570	5.1	0.25	515	9.4	0.52	507	33	0.6	507	7.9	0.29	507	113.7	15.33
SAC	513	158	3.8	343	1.6	0.05	504	1.7	0.06	490	3.3	0.11	481	37	0.8	481	10.3	0.43	481	36.4	3.03
LGAP	339	194	7.7	253	2.3	0.10	334	5.8	0.41	323	11.0	0.80	322	46	1.4	322	17.5	1.05	322	235.4	26.90
SGAP	443	183	5.0	309	2.3	0.09	430	3.5	0.14	405	6.3	0.26	395	50	1.4	395	20.9	1.15	395	141.8	10.82
LUND	472	154	3.3	282	1.9	0.06	452	1.9	0.06	433	3.5	0.11	428	51	1.6	428	23.1	1.41	428	69.4	4.35
SUND	451	159	4.4	262	1.8	0.06	433	1.9	0.06	412	3.5	0.12	403	56	1.7	403	26.4	1.57	403	78.3	4.54
BLOCK 1	540	167	4.2	356	2.0	0.07	524	3.1	0.17	521	5.5	0.31	513	50	1.4	513	20.1	1.16	513	102.4	8.69
BLOCK 2	596	172	4.4	395	2.0	0.07	569	2.7	0.11	543	5.0	0.20	538	54	1.3	538	22.7	1.12	538	110.5	7.84
BLOCK 3	569	174	4.4	355	2.2	0.08	556	3.6	0.23	509	6.9	0.47	497	49	1.3	497	23.9	1.25	497	163.1	16.54
LGAP PEN	96	248	15.4	38	1.9	0.16	96	4.2	0.29	96	8.1	0.56	96	73	2.4	96	37.8	2.21	96	353.9	40.76
RUB	144	200	12.1	140	2.7	0.15	140	9.6	0.84	130	18.6	1.71	130	37	1.2	130	10.3	0.71	130	297.0	55.99
SAC	99	133	9.6	75	1.6	0.11	98	2.0	0.25	97	3.7	0.45	96	30	1.5	96	6.9	0.70	96	33.4	12.12
SGAP PEN	156	231	10.5	72	1.8	0.14	152	3.3	0.19	151	6.4	0.37	146	76	2.1	146	40.9	2.12	146	282.9	23.78
RUB	155	157	5.6	146	2.9	0.16	148	5.2	0.29	128	9.1	0.58	126	32	1.1	126	7.4	0.47	126	79.0	9.04
SAC	132	157	7.0	91	1.7	0.10	130	1.8	0.09	126	3.5	0.18	123	38	1.6	123	11.0	0.94	123	38.7	4.05
LUND PEN	167	170	5.0	50	1.8	0.11	167	1.4	0.06	163	2.8	0.11	162	80	2.4	162	46.9	2.77	162	127.2	9.23
RUB	161	128	4.9	146	2.2	0.10	143	2.9	0.14	132	5.0	0.25	130	31	1.1	130	6.9	0.51	130	36.2	3.34
SAC	144	165	6.8	86	1.6	0.08	142	1.6	0.06	138	2.9	0.12	136	37	1.5	136	10.3	0.76	136	32.2	3.06
SUND PEN	161	181	9.0	37	1.4	0.10	160	1.5	0.07	158	2.8	0.13	156	88	2.5	156	53.1	2.89	156	141.1	8.60
RUB	152	126	5.0	134	2.0	0.09	139	2.8	0.14	125	4.9	0.27	121	30	1.2	121	6.8	0.51	121	36.1	3.58
SAC	138	170	7.1	91	1.6	0.08	134	1.6	0.08	129	3.1	0.15	126	41	1.7	126	12.2	0.89	126	41.0	4.76
LGAP C	61	291	27.7	51	2.8	0.29	61	11.7	1.79	60	22.0	3.49	60	54	3.2	60	22.4	2.69	60	597.1	119.18
NE	51	174	14.4	42	2.4	0.21	50	5.9	0.63	50	11.1	1.21	50	45	3.0	50	15.0	2.28	50	179.8	34.08
NW	32	177	24.6	30	2.9	0.34	30	7.3	1.00	29	13.4	2.00	29	37	4.0	29	12.3	3.30	29	212.1	75.25
SE	98	174	11.6	67	1.9	0.14	97	4.1	0.33	95	7.8	0.62	95	45	2.6	95	17.1	18.28	95	162.9	24.04
SW	97	170	9.4	63	1.9	0.16	96	3.4	0.34	89	6.3	0.67	88	45	2.8	88	17.6	2.10	88	106.3	15.91
SGAP C	81	178	9.4	51	2.5	0.30	80	3.1	0.31	76	5.3	0.47	74	48	3.2	74	18.9	2.40	74	98.5	17.80
NE	81	152	9.4	56	2.2	0.18	78	3.1	0.30	70	5.5	0.54	68	44	3.3	68	17.0	2.72	68	94.6	15.31
NW	94	198	11.1	69	2.4	0.18	92	3.8	0.24	89	7.2	0.46	87	53	2.9	87	23.2	2.56	87	190.1	29.82
SE	92	187	12.7	64	2.2	0.18	90	3.5	0.29	85	6.2	0.53	85	50	3.2	85	21.4	2.56	85	147.0	22.10
SW	95	196	11.1	69	2.3	0.22	90	3.9	0.40	85	7.2	0.78	81	55	3.1	81	23.1	2.57	81	163.5	27.11
LUND C	97	163	6.8	55	2.1	0.15	93	1.9	0.13	87	3.4	0.24	86	48	3.0	86	19.5	2.48	86	58.4	7.73
NE	89	142	6.5	56	1.9	0.13	87	1.9	0.13	83	3.4	0.22	83	47	3.4	83	19.3	2.65	83	56.6	7.88
NW	98	147	6.9	52	1.9	0.13	94	1.9	0.12	91	3.5	0.22	88	51	3.3	88	22.3	2.93	88	66.2	8.09
SE	90	155	8.4	58	1.9	0.13	85	2.0	0.16	83	3.5	0.27	83	55	3.8	83	26.7	3.76	83	84.2	14.57
SW	98	162	8.0	61	1.9	0.15	93	2.0	0.13	89	3.7	0.24	88	56	3.7	88	27.7	3.68	88	81.4	8.80
SUND C	87	161	16.3	52	1.8	0.14	84	2.1	0.15	83	3.8	0.29	82	55	4.0	82	26.2	3.46	82	76.1	9.07
NE	82	148	8.1	45	1.7	0.14	79	1.8	0.13	77	3.3	0.23	77	55	4.1	77	26.4	3.76	77	71.4	9.17
NW	96	144	6.5	59	1.6	0.13	95	1.9	0.14	92	3.6	0.27	91	52	3.6	91	23.8	3.56	91	66.3	8.21
SE	97	175	7.1	52	2.0	0.14	94	2.0	0.14	85	3.7	0.26	83	62	3.7	83	30.1	3.28	83	101.1	11.87
SW	89	167	8.3	54	1.7	0.11	81	1.8	0.12	75	3.2	0.23	70	55	4.0	70	25.7	3.54	70	76.9	12.27

Red maple had 50% more branches than either striped or sugar maple (2.5 vs. 1.7 vs. 1.6, respectively) and this pattern held across all sites. Both gap sizes (2.3, 2.3) had seedlings with more branching than the understories (1.9, 1.8) when all species were combined. For plots within sites, the only notable differences occurred in the large gaps, where seedlings in the north and center plots had 25-50% more branches than the south plots. This corresponded to the more frequent leader loss in these plots. Somewhat surprisingly, the large gap south plots were more like the understories than they were like the small gaps. The 1987 data did not include branch numbers, but notes were taken on the presence of any branches, and the total of 1106 plants in 1989 with branches far exceeded that for 1987.

The results for leaf pair and total leaf numbers paralleled each other, as would be expected, so only total leaf numbers are discussed here. However, it was not unusual for complexly branching seedlings to not have a complete leaf pair at many nodes. So the correspondence was less tight than it was in 1987.

As in 1987, the species differed in both the number of leaves and leaf pairs, but the order was changed from RUB > SAC > PEN in 1987 to RUB > PEN > SAC in 1989. This new rank order held across all sites, although the relative differences among species varied. Red maples in large gaps had over twice as many leaves (18.6) as any other species in any site, mostly due to the center plots.

For combined species, the sites also differed in leaf numbers, with LGAP > SGAP > LUND = SUND. On average the large gap plants had three times as many leaves as the understory and 75% more leaves than the small gaps. Again, the comparison of plots within sites showed dramatic

numbers of leaves in the C (22.0), NW (13.4) and NE (11.1) plots of large gaps. These values were at least 50% greater than any plot in the remaining three sites. In general the large gap south plots were like the small gap plots and greater than the understories.

The ANOVA results (Table 4-9) show that the species differed greatly in mean lamina length ($F=585.68$, $p<0.001$). This was mostly due to striped maple leaves being over twice as long (80mm) as either sugar (37mm) or red (33mm). With one exception (large gap, where $PEN > RUB > SAC$), this rank order held in all sites. Due to this exception and slightly variant relative differences among species across sites, the site x species term was significant ($F=5.61$, $p<0.001$).

The sites did not differ significantly in mean lamina length ($F=0.15$, n.s.), which is rather surprising. The general dogma surrounding sun-shade syndromes suggests that species should increase mean leaf size in shaded environments. As it turns out, this was true for striped and sugar maple, which showed monotonically increasing lamina lengths from the large gaps to small gaps to understories. In contrast, red maple monotonically declined along this gradient. The result of the counter-behaving species was a cancellation of any overall site difference. In keeping with the lack of differences at the site level, the site x plot interaction was also nonsignificant ($F=1.27$, n.s.), and a perusal of Table 4-12 confirms the lack of variation across site/plot combinations when all species are combined.

Since leaf area is strongly related to lamina length, the results for mean leaf area paralleled those for mean leaf length across species, sites, and plots. The quadratic allometry increases the absolute values, but maintains the relative differences in a consistent fashion. In fact,

the ANOVA F-values for the two variables (Table 4-9) were remarkably similar, reflecting this allometry. Again, red maple declined across the large gap/small gap/understory gradient, running counter to the other species and the predictions of sun-shade theory, and the results were nonsignificant site and site x plot terms.

Total leaf area results are shown in Tables 4-9 and 4-12. The species differed significantly ($F=353.34$, $p<0.001$), with striped maple (210.5cm^2) nearly twice that of red maple (113.7cm^2) and over five times that of sugar maple (36.4cm^2). This rank order held across all sites but the large understory, where $\text{PEN} > \text{SAC} > \text{RUB}$. The site x species term was also significant ($F=11.66$, $p<0.001$), since the relative differences among species changed across sites. Red maple was much closer to striped maple in the large gaps (297.0 vs. 353.9cm^2 , respectively), but was less than one-third of striped maple in all other sites. The differences between these two species in large gaps would have been greater had it not been for one red maple seedling in the center plot of the Block 3 large gap, which amassed a total leaf area of 5560cm^2 through multiple basal sprouts of a dieback stem. This was over twice that of any other plant. Red and sugar maple were quite similar in both understories.

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. This generally concurs with sun-shade theory and with garden or glasshouse experiments on tree growth under light gradients. However, sugar maple inexplicably showed a different site preference for total leaf area, with $\text{SGAP} > \text{UND} > \text{LGAP}$. The differences were not large, only 5.3cm^2 overall, so it is likely that they were not significant.

Surprisingly, the seemingly large differences among site values for total leaf area did not yield a significant ANOVA term ($F=1.15$, n.s.). The rank order was LGAP > SGAP > LUND > SUND, with mean values of 235.4cm^2 , 141.8cm^2 , 78.3cm^2 , and 69.4cm^2 , respectively. The divergent means and the lack of a site effect may have been due to the unusually high leaf area in large gap center plots (597.1cm^2), which was almost three times that of any species in any other site/plot. This was partly due to the red maple seedling with 5560cm^2 in the center plot of large gap 3. This divergence was apparently responsible for the significant site x plot interaction ($F=2.11$, $p<0.05$).

In summary, the three species differed significantly in mean leaf length (PEN > SAC > RUB), mean leaf area (PEN > SAC > RUB), and total leaf area (PEN > RUB > SAC). Striped maple leaves were larger in length and area than red and sugar maple in all sites. Red maple generally had more leaves than either striped or sugar maple, and thus the interaction between leaf number and mean area led to the overall ranking in total leaf area. There were several monotonic patterns across the large gap/small gap/understory site gradient for all species combined: the number of leaves and total area declined, while mean length and area increased. But none of the differences were statistically significant due to the reversed patterns among the species.

As compared to 1987, the changes in architecture were enormous. But the consistent results were that striped and red maple increased their numbers of leaves and total leaf area much more than sugar maple, and the divergences among species were greater in the gaps (LGAP > SGAP usually) than in the understories. These changes paralleled the results for growth discussed in Section 4.3.

4.5. SHOOT DAMAGE AND RESPONSE

It has been suggested already that differential leader loss among the study species played a prominent role in growth and architectural patterns. This section presents an analysis of the effect of leader loss by partitioning the October 1989 cumulative growth and architecture data into two groups, those with and those without intact leaders. The primary motivation was to determine the degree to which leader loss was negative (or positive) and how species responded to this form of shoot damage. The most important criteria are cumulative height and basal diameter, since these variables represent ultimate success.

The reason for the extensive leader losses is not clear. Several biotic and physical factors may have been responsible. In general, the terminal buds were not removed by herbivores, but died in place. Bud miners are known to occasionally cause substantial leader dieback (Tubbs 1977). If such insects were present, their activity was certainly not obvious. Unidentified pathogens may also have been responsible.

However, two facts concerning the 1987-89 macroclimatic patterns may be most relevant here. As mentioned in Section 3.2., all three years following seedling transplant in 1986 showed unusually low mean daily minimum temperatures in February. Since snowfall and sustained snow cover were also below average in all three years, it is possible that the seedlings suffered cold damage, through freezing and/or dehydration. Of the three study species, red maple's range is the most southerly, and both sugar and striped maple occur in regions with colder winters than central New England. Therefore, it is possible that all species were affected by freezing damage, and that red maple was more susceptible

than the other two species. Freezing damage is more likely to occur in canopy openings than under intact canopy (Spurr 1957; Rasche 1958). The leafless forest provides enough buffering against heat loss such that ground-level temperatures do not fall as low as in openings, where re-radiation to space is unrestricted at night. Therefore, the large gaps in the present study may have been expected to show greater freezing damage, even by small seedlings.

A final point on this argument is that elevated soil nutrients, especially nitrogen, are known to delay normal schedules of frost hardening by trees in late autumn (Friedland et al. 1984). The manner in which the transplant plots were prepared eliminated external root competition and probably increased decomposition and mineralization rates, thereby raising nutrient levels, at least temporarily. Nutrient concentrations were not measured in the plots, but the occurrence of increased frost damage in red maple has been observed by other ecologists in experimental plots to which nitrogen fertilizers were added (Marianne Burke, personal comm.).

No data are available for testing whether or not leader loss in the experimental sites was paralleled by comparable loss rates outside the study area. It is impossible to say whether or not the high loss rates in the study area were due to experimental handling as opposed to the new microsite conditions. Two observations support the general argument that leader loss is not unusual. First, naturally-established seedling populations of these species at the Harvard Forest typically show significant proportions with damaged architecture, such that the task of locating suitable seedlings for transplant into the study plots was not easy. Second, the three maple species experienced differential

overwinter leader loss in simulated small and large gap irradiance regimes during a 1989-90 common garden experiment in Cambridge, MA. Red maple showed high losses that were greater than either striped or sugar maple (J.S. Coleman, personal comm.).

Table 4-13 summarizes mean values for eight variables according to the leader status dichotomy. Several points are immediately suggested by the totals for each category. First, leader loss was detrimental. Seedlings without leaders showed negative cumulative height change (-28mm) while those with leaders were positive (47mm). Leaderless seedlings also showed lower cumulative basal diameter change (50mm vs. 81mm) and 1989 height (141mm vs. 211mm). So regrowth during the two year period could not compensate for the losses. This was true in spite of the fact that leaf number rose due to increased branching, branch extension more than doubled, and total shoot extension increased by more than half for leaderless seedlings. Notable is the fact that total leaf area dropped by more than a third, in spite of the increased leaf numbers.

Among the species, all showed increased leaf number, branch extension, and total extension, but decreased cumulative height growth and 1989 height for leaderless plants. Striped and sugar maple declined in total leaf area and cumulative basal diameter growth as well, while red maple showed increases in these variables. Red maple also more than doubled its total extension, while the other species managed no more than 68% increase. So red maple appeared to be slightly better at compensating for leader loss.

With leaders intact, the species rank order was PEN > RUB > SAC for all variables but 1989 height, where PEN > SAC > RUB. Without leaders,

Table 4-13. Mean growth and architectural values for intact versus leaderless seedlings as of October 1989.

CATEGORY	1989 LEADER STATUS	1989 NO. LEAVES	1989 TOTAL LEAF AREA (sq. cm)	1989 STEM HEIGHT (mm)	1987-89 HEIGHT GROWTH (mm)	1987-89 BAS DIAM CHANGE (0.01mm)	1987-89 LEADER EXTENSION (mm)	1987-89 BRANCH EXTENSION (mm)	1987-89 TOTAL EXTENSION (mm)
TOTAL	Y	4.2	159	211	47	81	47.2	28.9	52.2
	N	7.0	98	141	-28	50	16.6	71.6	87.9
PEN	Y	4.5	221	218	61	105	61.5	37.9	67.1
	N	5.3	176	151	-3	43	12.5	61.5	73.1
RUB	Y	6.4	74	193	42	63	43.8	24.7	53.5
	N	9.8	119	146	-16	70	21.0	103.4	124.0
SAC	Y	2.9	45	202	17	34	17.0	14.2	19.3
	N	3.5	31	129	-60	20	10.8	21.3	32.1
LGAP	Y	6.9	251	248	88	131	88.7	50.6	100.7
SGAP	N	13.2	227	167	-2	106	23.4	157.8	181.0
	Y	5.6	220	239	73	122	73.8	26.4	81.9
LUND	N	6.9	77	141	-32	60	15.7	75.4	90.2
	Y	2.7	97	185	23	44	23.1	23.4	25.3
SUND	N	4.2	47	130	-39	20	14.0	31.3	45.3
	Y	2.9	114	192	24	52	24.2	13.5	25.6
	N	4.1	44	131	-37	21	13.5	31.9	45.4
	Y	7.7	361	279	124	180	124.2	90.2	139.4
LGAP PEN	N	9.4	333	162	10	72	15.5	136.2	151.7
	Y	11.3	91	202	50	66	56.9	22.8	73.6
RUB	N	19.3	318	200	35	158	32.5	234.9	265.7
	Y	3.0	31	196	16	43	15.9	8.5	17.1
SAC	N	4.0	34	108	-75	25	11.1	26.3	37.4
	Y	6.5	310	259	101	162	101.8	30.5	111.1
SGAP PEN	N	6.1	119	144	3	63	10.7	70.9	77.8
	Y	8.0	100	232	64	91	64.1	34.8	82.5
RUB	N	9.2	77	148	-21	78	19.1	105.1	123.5
	Y	3.2	56	198	18	46	17.7	10.2	20.2
SAC	N	3.7	26	126	68	24	11.9	23.9	35.9
	Y	2.4	130	176	25	55	24.6	18.0	25.4
LUND PEN	N	3.6	121	154	-3	28	13.9	32.0	45.8
	Y	4.4	64	182	32	48	31.8	23.4	38.9
RUB	N	5.1	32	119	-40	20	16.3	40.3	56.6
	Y	2.7	42	203	17	24	17.4	27.1	20.3
SAC	N	3.2	25	134	-58	16	10.1	15.3	25.4
	Y	2.8	148	189	26	62	26.2	16.2	27.6
SUND PEN	N	3.3	102	143	-23	15	9.6	30.3	39.9
	Y	4.1	52	168	31	55	31.1	4.7	31.8
RUB	N	5.0	34	119	-36	26	16.4	39.5	55.9
	Y	2.8	43	207	17	28	16.6	12.7	18.2
SAC	N	3.2	40	146	-43	15	10.2	20.5	30.7

PEN > RUB > SAC in cumulative height change, 1989 height, and total leaf area, but RUB > PEN > SAC in leaf number, branch extension, total extension, and cumulative basal diameter change. This partial reversal of order underscores again the ability of red maple to recover relative to other species.

Among the four sites, all showed increases in branch and total extension but declines in all other variables when leaders were lost. The large gap plants showed the least reductions, and therefore the best compensation, possibly due to the addition of more leaves and maintenance of leaf areas close to or greater than that for intact seedlings. In general, seedlings in both gap sizes compensated better than in the understories.

Species comparisons in sites showed trends that support the statements above. In large gaps, the species rank order for intact plants was PEN > RUB > SAC for all variables, while leaderless plants showed RUB > PEN > SAC for all variables but leaf area, where red and striped maples were similar. Red maple exhibited the best compensation, maintaining 1989 height and increasing cumulative basal diameter change by 2.5-fold over intact plants. Red maple showed a three-fold increase in leaf area, a ten-fold increase in branch extension, and a four-fold increase in total extension. This was probably mostly due to the center plots where, as discussed in Section 4.3., the most dramatic growth occurred. It appears that red maple actually benefitted from leader loss in some large gaps plots. This is not true for the other species, which lost comparable fractions in cumulative height and basal diameter change as well as 1989 height, even though they recovered leaf area close to intact levels.

In small gaps, all species showed net decreases in leaf area, cumulative height and basal diameter change, and 1989 height. All species increased leaf numbers and branch extension; red and sugar maple also increased total extension, while striped maple did not. With intact leaders, $PEN > RUB > SAC$ in all variables but branch extension and leaf number, where $RUB > PEN > SAC$. The results were mixed for leaderless plants, with $PEN > RUB > SAC$ in leaf area and cumulative height change, but $RUB \Rightarrow PEN > SAC$ in all other variables, including the two most important ones, 1989 height and cumulative basal diameter change. Like the large gaps, red maple compensated better than the other species when leaders are lost, although its dominance of the growth variables was not as complete.

The overall results for the large understory were similar to small gaps, although the rank orders among species for different variables were even more mixed. All species exhibited decreased leaf area, cumulative height and basal diameter change, and 1989 height when leaders are lost. With intact leaders, $PEN > RUB > SAC$ in leaf area and cumulative basal diameter change, $RUB > PEN > SAC$ in cumulative height change and total extension, and $SAC > RUB > PEN$ in 1989 height and branch extension. Without leaders, $PEN > RUB > SAC$ in leaf area and cumulative height and basal diameter change, $PEN > SAC > RUB$ in 1989 height, and $RUB > PEN > SAC$ only in branch and total extension.

The question of relative success versus leader status in the understory is curious as compared to large and small gaps. With leaders intact, striped maple was not as dominant over the other species in the understory as it was in both gap sizes. In the gaps, the loss of leaders caused striped maple to finish second behind red maple, which

compensated well for losses. In contrast, striped maple increased its dominance over the other species for leaderless plants in the understory, with highest rankings in all but branch and total extension.

Thus in all sites the loss of leaders resulted in changes in species relative dominance, but red maple was the beneficiary in the gaps while striped maple benefitted in the understory. Sugar maple was almost always last. These statements are in relative terms, however, and it is worth noting again that leader loss was detrimental overall. The one exception was red maple in large gaps, due to the unusual nature of the large gap center plots.

4.6. DISCUSSION

This discussion is divided into two parts. First, a brief synopsis of the survival, growth, architecture, and damage results will be given to draw together the many points presented throughout the above sections. Then comparisons to the literature will be made, in which the focus will be on research that involve the responses of the three study species to forest understory and gap conditions.

Red maple survived better overall across the study, but this was due mostly to its greater persistence over striped and sugar maple in large gaps, particularly the north and center plots. The small gaps and understories showed no differences among the species. Survival rates overall were fairly high, with low values only in the exposed plots of large gaps. There was no relationship between post-gap survival and previous age, height, or basal diameter for any species, site, or species x site combination. The apparent interaction between physical stress and a pathogen (suspected to be the root-rot fungus *Armillaria*

mellea) caused dramatic site- and species-specific mortality, concentrated in the north and center plots of large gaps, where up to 60% of the seedlings died.

Patterns of growth among the three species diverged over the two years following gap creation. All species showed signs of initial adjustment to the treatments and/or lingering effects of transplanting in 1988, with reduced height and growth rates as compared to pre-gap rates. The delay in response is probably due to the relatively determinate shoot development characteristic of these species, where bud development for the subsequent year is determined by the environment of the previous year, and leaf and stem expansion in the present year is based on stored carbohydrates.

By the end of 1989, both gap sizes induced greater distinctions among the species in all growth variables than the understory. Striped maple exhibited greater leader extension, stem height, and basal diameter than red maple and sugar maple (in that order) in nearly all sites and plots. The only exception was large gap center and north plots, where red maple equalled or exceeded striped maple in basal diameter growth. Sugar maple was the least responsive of the species to the gap-understory gradient.

The species differed little in pre-gap initial height, age, or basal diameter, although all variables yielded significant differences. There was no composite bias in favor of any species. Surprisingly, there were no significant relationships whatsoever between pre-gap age or size and post-gap growth variables, except that the extremes (very young or old, small or large) may have been less likely to exhibit high growth rates. This was true for survival as well, suggesting that pre-gap

status is a poor indicator of gap release potential, at least for seedlings in the size and age ranges used here.

The species differed little in shoot architecture prior to gap creation due to experimental selection of undamaged seedlings in constrained size classes and to inherent architectural tendencies in suppressed understory conditions. However, architectural variation increased enormously in the two years following release. Species-specific patterns varied among the several architectural variables, but the overall trend was that striped and red maple increased branch numbers, leaf numbers, and total leaf areas greatly in gaps, especially large gaps, and sugar maple 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.

Much of the architectural variation by 1989 was due to the extensive occurrence of leader dieback, lateral bud release, and basal resprouting. Red maple was most likely to die back, followed by sugar maple and then striped maple. The analysis of performance by intact versus leaderless seedlings showed that leader loss was detrimental for all species in all sites, except for red maple in large gaps (especially center plots). In fact, due to dieback, only striped maple showed net increases in mean height across the entire study area and in every site. Red and sugar maple both declined on average. The exception was red maple in large gap center plots, which managed to show net increases in height through rapid growth of resprouts following dieback.

Neither the survival nor the growth results support gap partitioning. The species did differ in survival in large gaps, but striped and sugar maple were essentially equivalent, and both differed

from red maple only in the north and center plots. In nearly all growth variables, particularly for seedlings with intact leaders, the rank order among species was consistently $PEN > RUB > SAC$. As before, the exception was red maple in large gap centers. Red maple did show a considerable ability to recover from leader loss, with branch and total shoot extension values greater than the other species in most site/plot combinations. But the net effects of leader loss relegated red maple to the number two ranking in net growth over 1987-1989.

The large gap center plots produced the greatest height and basal diameter growth for all species. The north plots of large gaps are exposed to direct beam irradiance the entire growing season, and such irradiance levels were clearly inhibitive. Survival and growth in the large gap south plots were much better than in the north. Although survival in the center was not as high as in the south, growth was much greater, suggesting that the center plots represent the optimal growth environment for these species. The center plots receive the highest diffuse light levels on both clear and overcast days, and it may be that seasonal and diurnal periods of direct beam are not as inhibitive as in the north. Direct beam shines on 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 (approximately the third week of August) reduces radiation stress more than in the north plots, where direct beam continues through September. It may also be true that bud primordial development in the latter half of the season is differentially affected by the direct beam durations in such a way as to trigger greater shoot extension the following spring in center plots. If true, this would

involve an important interaction between site- and plot-specific seasonal microenvironmental sequences and plant developmental timing.

The conclusions from controlled, cleared gaps are supported by data from a companion experiment in natural gaps (Sipe, unpublished data). In June 1986, 297 naturally-established seedlings of the three maple species (99 per species, 15-30cm tall, leader intact, unbranched, undamaged) were transplanted (bare-rooted) from several locations into 10" clay pots buried to ground level near three natural gaps in the Tom Swamp 1 Compartment of the Harvard Forest. The forest in this compartment is the oldest, least disturbed mixed hardwood stand in the three Harvard Forest tracts. The soil catena in this site (Charlton stony loam/Sutton silt loam/Whitman silt loam), derived from schistose glacial till, is finer textured and generally more fertile than the Glouster/Acton/Whitman catena in the experimental gap study area. Consequently, the overstory and understory are more diverse taxonomically, but the relative dominance by overstory species is not widely divergent from the experimental gap stand. An important difference is that sugar maple is more abundant in Tom Swamp 1 than in Prospect Hill 7.

The three natural gaps were all less than 5 years old and ranged in size from 62m^2 to 107m^2 (based on ellipse formula). They were thus comparable to the small (75m^2) experimental gaps in Prospect Hill 7. Initial data on height, age, and basal diameter were recorded after transplanting. The seedlings remained in the understory near the three gaps until May 1988. Then three seedlings per species were moved into five plot locations (C and NW, NE, SW, SE edges) in each gap and reburied (with pots). The survival, growth, and architecture of the 45 seedlings

in the gaps and the remaining seedlings in the understory were measured during the two seasons (1988, 1989) following simulated "gap release". The downed biomass and regrowing community in the gaps were disturbed as little as possible during the transplanting.

Results from the Tom Swamp 1 experiment make it possible to extrapolate from the cleared gaps in Prospect Hill 7 to unmanipulated natural gaps. The rank order of species for leader and basal diameter growth in 1988 (the first year after gap release) was the same in both understory and gaps, and this order matched the 1987-89 pattern for the experimental gaps: PEN > RUB > SAC. Striped maple's height growth in gaps was 2.5 times that of red maple and over 6.0 times that of sugar maple. For basal diameter, striped maple grew 74% more than red maple and 2.3 times as much as sugar maple. In the understory, striped maple's height and basal diameter growth were over twice as much in 1988 as either red or sugar maple. The 1989 data are not yet analyzed, but observations during October 1989 measurements strongly suggest that the relative differences among the species were magnified in the second year following release. Therefore, as with the experimental gaps, sugar maple showed little differential response to gap release, red maple showed an intermediate response, and striped maple was the superior species. There was no evidence of understory versus small gap partitioning.

Having established this synopsis of results, it is now useful to compare them to published research. Both ecological and silvicultural studies exist in which the responses of one or more of the study species to understory and gap environments were measured. In a few cases, all three species were included. It is worth noting here that the ecological studies tended to be non-manipulative measurements in natural gaps,

while the silvicultural studies were usually experimental studies of regeneration management in harvest cuts of varying style (e.g., clearcut versus shelterwood) and geometry (e.g., opening size and shape). In terms of gap geometry and method of creation, the experimental gaps produced by the author were intermediate between natural and silvicultural gaps. They were in the size range of most natural gaps in temperate deciduous forests but smaller than the majority of silvicultural cuts. However, the author's small gaps mimicked selection cuts while the large gaps mimicked group selection or small patch cuts (P. Hannah, personal comm.). This is especially true because they were created by basal cutting and stump resprouts have been cut back, unlike natural treefalls.

Canham (1985, 1988b) has produced some of the most useful comparative data for sugar maple. In his studies of maple and beech sapling growth in the understory and gaps in western New York, he has concluded that both species typically experience multiple periods (1-5, mean >2.5) of suppression and release before final attainment of canopy codominance. This is due to the relatively slow growth rates of saplings released in gaps (mean ~30cm/yr), which, although an order of magnitude greater than in understories, are not enough to outcompete other faster-growing species. Canham (1985) showed that sugar maple responds to gaps as small as 15-75m² with significant height and lateral growth increases, but mean height growth was not correlated with gap size beyond this. This insensitivity to gap size also occurred in the present research, and has been noted by other authors for both field and simulated (Logan 1965) environments. Basal diameter growth of sugar maple saplings increased three-fold in the small gaps studied by Canham

(1985), from 0.22mm/yr to 0.69mm/yr.

Canham (1988b) elaborated on the morphological mechanisms of gap response by sugar maple and beech. He concluded that, although both species were small-gap specialists, they nonetheless differed in their responses in a way that suggested gap-understory partitioning. One of the reasons was that sugar maple was more flexible in shoot architecture than beech (also see Steingraeber 1982), producing more branches and a greater leaf area index, while doing so efficiently with respect to the amount of stem length needed to support the higher leaf area. The allometric relationships between leaf area and either stem length or stem surface area were constant for sugar maple saplings up to 4 meters tall, suggesting a tight control over architecture. He also noted that although absolute height growth was not correlated with gap size, lateral growth was correlated for both species. Based on Canham's results, sugar maple should have responded more than it did to both the small gaps and the south sides of large gaps in the present study.

Hibbs (1979) and Hibbs et al. (1980) studied striped maple distribution and performance in the forests of western Massachusetts, while Wilson and Fischer (1977) reported on striped maple shoot development and growth in garden and glasshouse experimental light gradients. All three studies emphasized the characteristics that seem to favor striped maple for exploiting small canopy gaps. Hibbs (1979) noted the nearly zero mortality of suppressed striped maple seedlings from 2-15 years old, and Hibbs et al. (1980) observed that seedlings as old as 35 years are capable of gap release, with height growth rates that can exceed 1.0m/yr. Such growth rates were not achieved in the course of the present study, but many individuals showed leader extensions of over

0.50m during the second post-gap year, especially in the small gaps. Hibbs et al. (1980) also noted that striped maple is inhibited by high irradiances, which likewise agrees with the present study. The best leader extension occurred in small gaps (south plots!) and the south plots of large gaps.

Wilson and Fischer (1977) demonstrated that striped maple's ability to capitalize on small canopy gaps was in part due to developmental switching in the fate of rudimentary preformed leaf primordia in dormant buds that could develop into either bud scales or new leaves, depending on the light environment during bud expansion. Using 10 irradiance levels from 6% to 82% of full sun, they determined that the switching occurred between 6% and 18% full sun. Maximum height growth occurred at slightly higher irradiances (30-60%).

This developmental shift was noticed in several sites and plots in the present study. But the shift in many cases appeared to be only partially successful, in that the morphology of the resulting leaves was negatively altered. The leaves resulting from rudimentary inducement often failed to develop fully, with deformed apical meristematic regions on the lamina and significantly reduced sizes. The overall appearance suggested hormonal imbalance.

Sakai (1987) distinguished variable levels of shoot indeterminacy among Japanese species of *Acer*, and specifically referenced striped maple as being of the indeterminate class due to the inducible primordial shift. He also emphasized the difference among species tending toward monopodial-spread, elongate, or sympodial-spread shoot development, and suggested that these categories represent architectural adaptations to large, intermediate, and small gaps, respectively.

Several silvicultural studies reported survival and growth rates for the three maple species. Leak and Solomon (1975) observed that red maple had higher establishment densities than either striped or sugar maple under four levels of overstory thinning and a 0.67A circular patch cut in north-central New Hampshire. Marquis (1964) reported that striped maple exceeded sugar maple in height growth in 0.1-0.3A (400-1200m²) circular patch cuts in the same experimental forest. Striped maple seedlings greater than 10 years old were capable of release and growth rates of 0.6-1.0m/yr in full sun. Bicknell (1982) followed regrowth on a clearcut watershed at the Hubbard Brook Experimental Forest in New Hampshire. Advance regenerants of sugar maple and beech were the tallest trees in the first season, but by the end of the sixth year, advance-regenerated striped maple ranked second only to pin cherry (*Prunus pennsylvanica*) in average height, while sugar maple fell behind. Notable here is the fact that striped maple outgrew such fast-growing intolerant species as trembling aspen (*Populus tremuloides*) and yellow birch (*Betula allegheniensis*).

In one of the most comparable studies, Marquis (1982) explored the effects of initial age, height, size, and number and size of leaves on release from understory to large gap conditions by several species in north-central Pennsylvania. A study of naturally-established seedlings of all three maple species was complemented by an experimental study of clay-potted red and sugar maple seedlings switched from understory to clearcut conditions. Several results are pertinent. First, unlike the present research, Marquis found significant positive correlations between initial size and age and subsequent survival. The number of leaves was not correlated with survival, but maximum leaf size was. Pre-

release height growth rates were significantly correlated with post-release growth, but the relationship was positive for red maple and negative for sugar maple.

The sizes of the potted seedlings (grown from seed) at the time of switching to the clearcut were mostly smaller (6-21cm tall, 50-2.54mm basal diameter) than the transplants used in the present research. Nonetheless, Marquis calculated that the minimum height and basal diameter required for insuring up to 100% survival by both red and sugar maple were only 21cm and 2.54mm. This result, if potted conditions can be extrapolated, suggests that survival in even the center and north plots of large gaps at the Harvard Forest should be high. However, the actual ground-level conditions of the clearcut area were not described by Marquis, and it is safe to assume that debris and regrowth ameliorated the conditions at the small seedling level somewhat. Marquis noted browning and some defoliation on seedlings exposed to full sun in the middle of the growing season. Such individuals survived, although they grew less.

Several authors have cited the frequency of dieback by shade-tolerant advance-regenerating species, as well as the ability of dieback individuals to grow rapidly (Godman and Tubbs 1973; Tubbs 1977; Hibbs et al. 1980; Bicknell 1982; Clark and Clark 1985; Uhl et al. 1988). These reports collectively include all three of the maple species, and thus confirm the observations of dieback and regrowth in this study.

In broad terms, published research supports many of the results found in the present research. Striped maple is clearly capable of prolonged understory survival and rapid growth in gap sizes ranging from $<100m^2$ to full watershed clearcuts. It is therefore not surprising that

it dominated growth patterns across the sites in this study. Red maple is known to be capable of rapid release and growth rates as well, and its survival and persistence following dieback were predictable. Sugar maple's general lack of differential response to the two gap sizes concurs with the literature, but its slight increases in growth rates for intact seedlings and net losses in height for all (intact and leaderless) seedlings do not mirror the more prominent responses to small gaps noted by Canham (1985). The architectural flexibilities exhibited by red and striped maple were expected (Wilson and Fischer 1977; Wallace and Dunn 1980), but the morphological adjustment and efficiency in small gaps observed by Canham (1988b) for sugar maple were not observed for the smaller seedlings used in this study.

The lack of response by sugar maple and its poor ranking in understory growth compared to red and striped maples are the most unexpected feature of species differences in this study. One possible reason may be that the soils of the Prospect Hill 7 study site are not favorable enough to permit sugar maple to express its potential in response to gap 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 drainage positions. This corresponds to the patterns studied more extensively by Leak (1975, 1978, 1979) in New Hampshire, where sugar maple is preferentially abundant on finer soil textures and tills dominated by schistose rather than granitic parent materials.

The Gloucester-Acton-Whitman catena in the experimental gap study area is derived principally from granitic tills, and although sugar maple is abundant as a dominant species on other sites in the Harvard

Forest mapped as the Gloucester catena, there may be subtle fertility differences within the mapped catena that represent interactions between the overriding till and underlying bedrock types (G.G. Whitney, personal comm.). Whether or not such differences are significant enough to disfavor small seedlings as well as mature-sized individuals is not known. But it is at least plausible that nutrient or other soil-related differences (e.g., mycorrhizal abundance) affected the performance of sugar maple in this study. However, as noted above in the discussion of the Tom Swamp 1 natural gap experiment, sugar maple did not perform any better relative to striped and red maple on the more fertile Charlton loam soils, which are derived from schistose glacial till. So if soil nutrient status is the key in sugar maple's low growth rates, it is true for both the Gloucester and Charlton series, and thus for much of the upland soils in this region.

The soil variable(s) that is (are) responsible for this result is unclear. Nitrogen and phosphorus are the most likely nutrient candidates. However, Aber et al. (1989) have measured wet deposition rates for anthropogenic nitrogen inputs to the Harvard Forest system and suggest that the levels may be high enough currently to offset natural nitrogen limitations in these soils. In addition, dry deposition may also be adding substantial amounts of nitrogen (Wofsy, personal comm.). The form of nitrogen may play a role, since the system is ammonium-dominated while nitrate is more abundant in deposition. The availabilities of phosphorus in these soils relative to sugar maple seedling requirements have not been studied.

There are two ways to view the possible nutrient limitation of sugar maple in this study, if indeed this is the key factor. It may be

regarded as experimental error in the selection of study site and species ill suited to each other. On the other hand, it may be interpreted as useful information; on the substrates used in this study, sugar maple does not perform as well as the other two species, and this limits the expression of understory or gap size preferences that might otherwise occur. This reinforces the point that many resources influence relative performance among plant species, and that responses to gap-understory microclimatic gradients on one site may not apply directly to other sites with varying soil resource availability. The only way to test for this would be comparable studies on different soil series in the Harvard Forest region.

Several final points will conclude this discussion. First, many of the widely-cited gap studies for both temperate and tropical forests are based on either (1) the growth of the tallest seedlings or saplings in natural gaps, often those individuals that are judged to be the likely "winners" of the scramble for canopy space (e.g., Barden 1979, 1980, 1981, 1983; Hibbs 1982), or on (2) trees larger than a specified height cutoff (usually 1m) (e.g., Runkle 1981, 1984; Brokaw 1985a, 1987). Such selective samples are suitable for comparisons of species-specific replacement tendencies, but they do not reveal species relationships at the entire population level, the level that includes suppressed, smaller individuals, individuals recovering from dieback, and those with no chance of outcompeting neighbors.

Second, the pervasiveness of damage and recovery in seedlings and saplings has earned forest ecologists' serious attention only recently (Clark and Clark 1985), even though foresters have been aware of various forms and results of damage for a long time (e.g., Tubbs 1977). The vast

majority of the tree architectural and ecophysiological literatures are focused on undamaged seedlings, and consequently may not be directly applicable to damaged and recovering plants. Since advance-regenerant seedlings of tolerant species are exposed to various agents of shoot damage for up to several decades before gap release, the probability of release as an undamaged seedling is not high. Furthermore, if the post-gap frequency of leader loss in natural gaps is even close to that observed in this study, then many more seedlings incur damage before successful attainment of overstory space and/or reproductive maturity. The apparent prevalence of leader loss during both pre-gap and post-gap periods argues that we need to know more about the occurrence of architectural damage and the ways in which it may distinguish species' regeneration potentials before and after gap release.

Third, the complete lack of any relationship between pre-gap status and post-gap survival and growth places even greater emphasis on the microsite conditions in which released seedlings find themselves, since microenvironmental variability appears to override previous age and size. The lack of any age effect for seedlings in the age range used here suggests that conclusions on age structures in seedling populations be interpreted with caution, particularly in the understory, since age may have little to do with the ability to respond to gap release and grow to reproductive maturity.

Finally, species growth relationships in this study were seen to be consistent across most sites and plots, with $PEN > RUB > SAC$. The nearly complete absence of a significant site x plot x species term in the ANOVA results supports this consistency. Had relative differences among species differed predictably across various site x plot combinations,

the three-way interaction with species would have been significant. This would imply gap partitioning, or at least significant differences among species related to sites and plots in some fashion. The absence of the three-way interaction is instead confirmation that species relationships are relatively constant across site x plot combinations, and that gap partitioning does not occur.

CHAPTER 5

PHOTOSYNTHETIC PERFORMANCE IN GAPS AND UNDERSTORY

5.1. METHODS AND INSTRUMENTATION

One of the most difficult problems historically for physiological ecologists has been bridging the chasm between (1) a precise understanding of steady-state responses by a limited number of plants in controlled environments and (2) the behavior of diverse populations in spatially and temporally variable field conditions. Technical improvements in portable instruments over the last decade have made it possible to collect large numbers of leaf-level physiological samples in the field for analysis of water relations and photosynthetic gas-exchange. Nonetheless it is still difficult to connect instantaneous spot samples of photosynthetic behavior to whole-plant success over 2-3 years, particularly at the population level.

Understanding the physiological mechanisms for gap partitioning (or its absence) requires this kind of connection across spatial and temporal scales. There are at least four major scaling problems involved: (1) from unit leaf area rates to whole plant (or at least shoot); (2) from individuals to population; (3) from one microsite to the entire gap-understory gradient; and (4) from one sample point (hour or day) to seasonal patterns. In spite of the remarkable capabilities of field gas-exchange systems, it is still impossible to span all four scales at once. Compromises are involved.

The strategy used in this research always employed simultaneous comparative sampling across species and microsites on carefully selected seedlings. All measurements were done on plants with intact leaders and

normal architecture. Samples were always replicated ($n=3$ in most cases) for any diurnal representation of photosynthesis by each species. Since microsite comparisons were made at the plot level, this typically meant sampling 9 seedlings per plot per diurnal data point. As much as possible, measurements among plot positions were repeated across the course of a day to yield 4-5 points per species per day. This provided diurnal patterns at the leaf level. Two days were selected for presentation of diurnal photosynthetic patterns across large gap, small gap, and large understory microsities: (1) 6.25.88, when the NW plots of the three sites were sampled, and (2) 8.8.88, when the SE plots of all sites were sampled.

Leaf-level gas-exchange rates are useful for many physiological questions, but physiological ecologists have strongly emphasized the importance of shoot-level photosynthesis because of the way in which whole-shoot carbon balance depends on leaf number, area, orientation, and water and nutrient status (e.g., Küppers 1985; Chazdon and Field 1987; Field 1988). Measuring all leaves on even architecturally simple plants with a portable gas-exchange system is time-consuming and precludes diurnal, multiple microsite comparisons. So the strategy here was to secure enough measurements of photosynthesis within and across leaf pairs so that shoot-level net photosynthesis could be estimated with acceptable accuracy.

The data for calculating shoot-level scaling factors came from four sample days in 1988 and 1989. The goal was to provide a scaling factor that would estimate unit area photosynthetic rates within and across leaf pairs based on measurements of one leaf per plant. This was done by regressing rates between paired samples on each other. The linear

regression of leaf #2 on leaf #1 was used to calculate the predicted rate for leaf #2. The predicted leaf #2 rate was then averaged with leaf #1 measured rate, and this average was divided by the leaf #1 rate to produce the scaling factor.

This method was used within leaf pairs (leaf #2 regressed on leaf #1) and across leaf pairs (i.e. mean rates for pair #2 regressed on mean rates for pair #1, where pair #1 was the lowest, oldest leaf pair on the shoot). The within- and across-pair scaling factors were then multiplied to yield a single combined shoot scaling factor for each species.

Shoot estimates also depend on total shoot leaf area. Section 4.1. described how estimates of total leaf area in 1989 were derived for all seedlings by applying leaf length:area regressions to end-of-season leaf length data. These data were unsuitable for the photosynthetic scaling because they included all the architecturally complex seedlings that had diverged from the normal state due to leader loss and variable regrowth. So shoot leaf areas for photosynthetic scaling were calculated from phenological data taken biweekly on a subset of seedlings in all sites and plots during 1988 and 1989. These 540 plants (3 per species per plot x 60 plots) were selected before leafout in April 1988 as representative of mean age, height, and basal diameter for each species. They were initially undamaged and not obviously stressed (i.e., their subjective 1987 condition rating was >3.0 on a 1-5 scale).

Mean laminar lengths for each leaf pair were taken at each biweekly sample, thus providing a seasonal course of individual and total shoot leaf areas. Since multiple (biweekly) estimates of total leaf area were available for both 1988 and 1989, the samples closest to the dates of diurnal photosynthetic sampling were selected, so that scaled shoot

photosynthesis estimates were as accurate as possible. Thus shoot leaf areas were derived for the appropriate dates in both 1988 and 1989. The north (NW plus NE) and south (SW plus SE) plot pairs were each pooled for the large gap, small gap, and large understory sites in Block 1 of the experiment where most of the photosynthetic sampling was done. This yielded six microsite positions - large gap N and S, small gap N and S, and large understory N and S - across which species' net assimilation rates were compared at the leaf and shoot levels.

Estimates of shoot photosynthesis were then calculated by multiplying the single leaf unit area rate by the shoot photosynthesis scaling factor (also per unit area) and then by total leaf area. This technique yields maximum potential shoot photosynthesis since it does not take into account the effects of differential leaf orientation or self-shading by the species. Essentially every portion of the total shoot leaf area is regarded as receiving the same quantity of light and photosynthesizing at a rate equal to that predicted by the shoot photosynthesis scaling coefficients. For species of substantially different shoot architectures, this would be a serious problem. However, the three maple species do not differ greatly in phyllotaxy or leaf display angles. All tend to hold their leaves horizontally except during periods of water stress. Furthermore, they are all relatively determinate in their leaf flushing within any given year, such that leaf ages do not vary widely on the shoot, particularly in understory conditions.

Consequently, the estimates of net shoot photosynthesis calculated here were regarded as sufficiently accurate to make useful comparisons among the species across various microsites. As will be seen, these

estimates provided important data supporting survival and growth patterns that leaf-level photosynthesis data did not explain as clearly.

The diurnal leaf- and shoot-level photosynthesis patterns presented in Section 5.3. give actual assimilation on specific days, from which inferences may be drawn on species relationships. Without repeated diurnal sampling across the season, it is difficult to say whether or not the relative differences among species hold across longer time scales than those covered in diurnal sampling.

Another strategy was used here to span the longer time scale. Photosynthetic light response curves (net carbon assimilation versus irradiance) are the traditional analytical tool used by plant physiologists to understand how species differ in their responses to the availability of light. Since photosynthetic carbon gain provides the primary currency of plant metabolism and growth (Mooney 1972; Reekie and Bazzaz 1987), and since light is the dominant limiting factor for photosynthesis in moist terrestrial ecosystems, the emphasis attached to this relationship is justified. However, this relationship is usually studied under steady-state controlled conditions. While the resulting information is relatively precise, it is difficult to relate such data to field performance in the long term (Field 1988).

Therefore a new, relatively simple method was developed here to produce population-level light response curves that span seasonal scales and are much more representative of actual population behavior under real field conditions than controlled environment data. All diurnal sample days in 1988 were pooled for this analysis. Since all samples were comparative among species for each day and time, we have equivalent representation by the species in the pooled data. Also, since

temperatures, air pressures, and humidities varied across the sample days, the analysis spanned a range of environmental conditions. The only exception to this is that most of the sampling was done on clear to hazy days, limiting the extrapolation to overcast weather.

The data were screened carefully for deviant measurements. These were cases in which either the coefficient of variation of $[CO_2]$ drawdown exceeded a specified cutoff, usually 5%, or other errors (such as elevated initial $[CO_2]$ due to the experimenter's exhalation) obviously altered assimilation rates. The measurements were then partitioned into PPFD intervals that provided the best breakdown of numbers of samples across the PPFD continuum. Since average irradiance levels during photosynthesis measurements were much greater in large gaps than small gaps and understory, two overlapping PPFD breakdowns were used. There were enough measurements for sufficient representation across PPFD levels in the six microsites discussed above: large gap N and S, small gap N and S, and large understory N and S.

Net assimilation ($\mu\text{mol C/m}^2/\text{s}$) and PPFD from the samples were averaged within each PPFD interval. Assimilation means were plotted against PPFD means for each species. The results were photosynthetic light response curves at the population/seasonal level. The initial curves were for unit area assimilation rates. Then shoot scaling factors were applied in the same manner as for the diurnal curves to yield estimated shoot-level assimilation versus PPFD response curves for 1988 and 1989.

The results for both diurnal patterns and population-level light response curves apply primarily to undamaged, architecturally simple seedlings (intact leader, 2-4 pairs of leaves), since nearly all the

field measurements of photosynthesis and the estimates of shoot leaf area and photosynthesis scaling factors were based on such plants. The results are not expected to apply to the architecturally diverse plants that by 1989 had exhibited leader loss and extensive regrowth, especially in the large gap centers.

All measurements of gas-exchange in the field were done with a Lambda Instruments LI-6200 photosynthesis system, operating in absolute mode. The infrared gas analyzer (IRGA) was calibrated against an independently tested CO₂ standard in the laboratory twice on each day of sampling, in the morning before sampling commenced and at midday. The LI-6200 is a closed system, with net assimilation based on the rate of drawdown of [CO₂] in the cuvette. With the exception of relative humidity, environmental conditions are not held steady-state within the cuvette and therefore air and leaf temperatures can rise quickly in high irradiance environments, requiring that the samples last no longer than about two minutes. Relative humidity is maintained near steady-state during measurements by diverting an adjustable portion of the total system air flow through a magnesium perchlorate dessicant. The LI-6200 system simultaneously measures PPF, air temperature (in the cuvette), leaf temperature, and relative humidity and calculates stomatal conductance and transpiration along with assimilation.

The LI-6200 system allows the user to record several sequential measurements on the same leaf. The typical sampling scheme used in this research was to take three 30-second measurements per leaf. This interval was determined to be long enough to get repeatable assimilation rates and short enough to avoid elevated cuvette and leaf temperatures. The three measurements were averaged to provide mean net assimilation

for that seedling at each temporal data point in the diurnal comparisons. The multiple measurements per seedling were treated independently for the population-level light response curves to increase sample sizes.

5.2. SHOOT-LEVEL SCALING FACTORS

Table 5-1 presents the results of the shoot-level measurements and calculations of scaling factors. Non-zero intercepts produced better fits for the regressions in all cases. The correlation coefficients were acceptable, although the within-pairs values for sugar maple (0.52) was low. It is interesting to note that all scaling factors were greater than 1.00. This was expected for across-pairs data, where upper leaf pairs are developmentally slightly younger than the first (lowest) pair, and where the relationship of declining photosynthetic capacity with leaf age (Field and Mooney 1986) would generally apply. It was surprising that the within-pairs factors also exceeded 1.00 uniformly, implying that the second leaf within pairs had, on average, a higher net assimilation rate. Furthermore, the factors for within-pairs were all larger than factors for across-pairs. The reason for this is unknown.

In general, we would expect the correspondence within leaf pairs (as measured by the correlation coefficient) to be greater than across pairs. But this varied across species, with striped maple following this expectation, red maple having approximately equal values, and sugar maple exhibiting a much tighter relationship across pairs than within pairs. Again, the reason is not clear.

The estimates of shoot leaf area for the photosynthetic scaling are summarized in Table 5-2. The relationships among species changed

Table 5-1. Regression results and scaling factors for estimating shoot assimilation from unit leaf area assimilation data. Factors were calculated within and across leaf pairs. The combined scaling factor is the product of the within- and across-pairs factors.

VARIABLE	PEN	RUB	SAC	TOTAL
WITHIN PAIRS				
N	48	33	35	116
SLOPE	0.775	0.744	0.770	0.760
INTERCEPT	0.304	0.260	0.234	0.275
R-sqr	0.72	0.89	0.52	0.81
SCALING FACTOR	1.044	1.039	1.061	1.052
ACROSS PAIRS				
N	6	16	15	37
SLOPE	1.215	1.342	1.192	1.324
INTERCEPT	0.015	-0.018	-0.145	-0.143
R-sqr	0.64	0.87	0.92	0.91
SCALING FACTOR	1.114	1.160	1.015	1.082
COMBINED SCALING FACTOR	1.163	1.205	1.077	1.138

Table 5-2. Shoot architectural summary for a subset of seedlings in the north and south plots of the Block 1 large gap, small gap, and large understory sites. The leaf areas for 1988 and 1989 in this table were used to scale upward from assimilation per unit leaf area to estimated shoot assimilation.

SPECIES	SITE/ PLOT	1988						1989					
		N	NO. LF PAIRS	NO. LEAVES	MEAN LF LGTH (mm)	MEAN LF AREA (cm ²)	TOTAL LF AREA (cm ²)	N	NO. LF PAIRS	NO. LEAVES	MEAN LF LGTH (mm)	MEAN LF AREA (cm ²)	TOTAL LF 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
	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
	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
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
	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
	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
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
	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
	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

dramatically between 1988 and 1989. In 1988, PEN => RUB > SAC in total leaf area (79.5cm², 78.3cm², and 49.7cm², respectively). But by 1989, striped maple had gained significantly (+94%), red maple gained modestly (+34%), and sugar maple lost significantly (-48%).

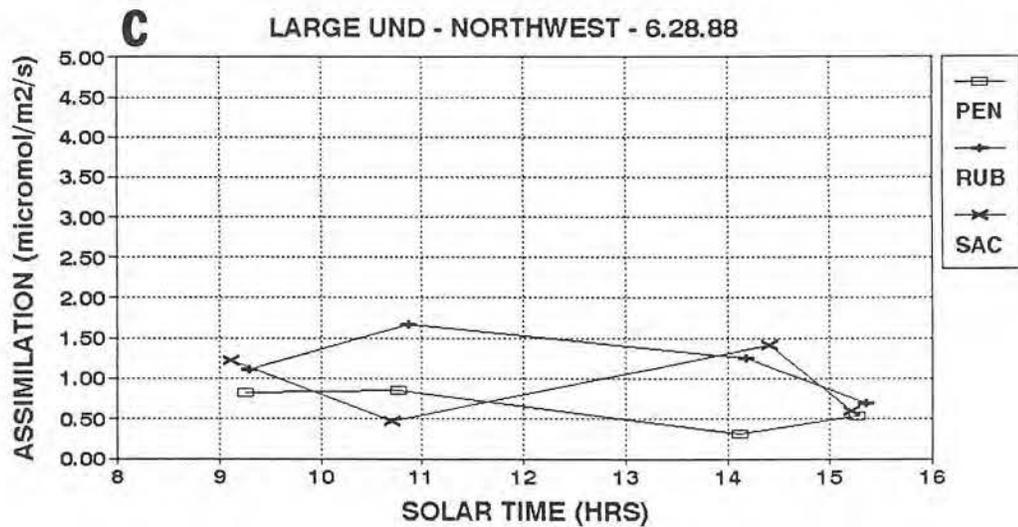
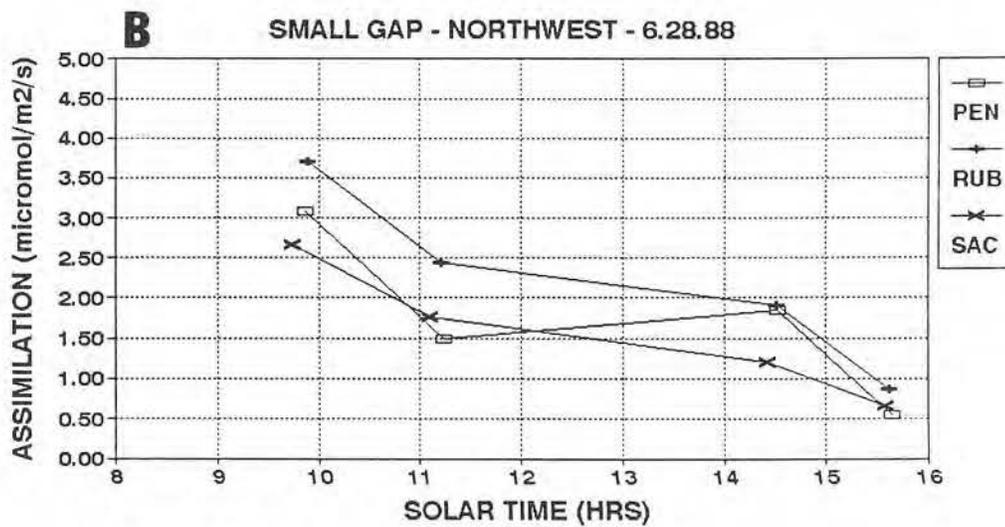
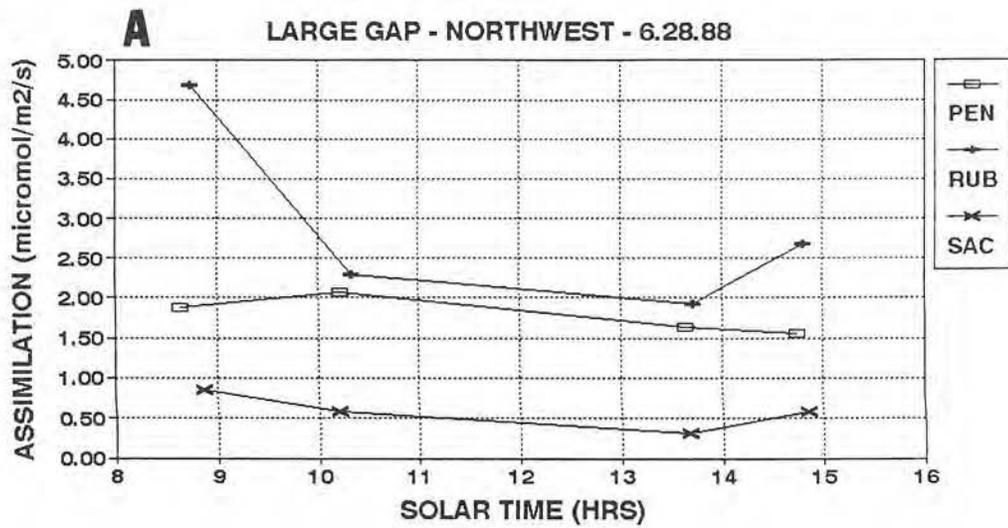
There were notable site/plot related differences in this pattern. First striped maples declined in large gap and large understory north plots while gaining in all others, especially the small gaps. Red maple gained in all plots except the large understory north, but not at the same pace as striped maple. Finally, sugar maple declined in all sites and plots.

These differences in total leaf area are controlled by leaf number and mean leaf area, and again the species showed variations. Both red and sugar maple increased the mean number of leaves overall, 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 5 out of the 6 site/plots, with red maple the greatest in the large gap north. Sugar maple was last in all but the large understory north and small gap south. These results are in general agreement with the 1987-1989 trends in architecture across the entire study area discussed in Section 4.4.2.

5.3. DIURNAL LEAF AND SHOOT ASSIMILATION

Figure 5-1 shows diurnal leaf-level assimilation in the NW plots of the three site types on 6.25.88. The overall rank order of total assimilation across the day (estimated visually) was RUB > PEN > SAC in large gaps, RUB > PEN => SAC in small gaps, and RUB > SAC > PEN in the large understory.

Figure 5-1. Diurnal patterns of net assimilation per unit leaf area on a clear day (6.28.88) by the three study species in the northwest plots of the large gap (A), small gap (B), and large understory (C) in Block 1 (n=3 seedlings and 1-9 assimilation measurements per data point).



The clearest differences were in the large gap, where red maple showed its greatest advantage in the early morning and late afternoon, with an apparent midday depression. Sugar maple exhibited a similar pattern, but at rates only one-fourth that of red maple. Striped maple showed steady rates, 3-4 times that of sugar, with no midday depression. All species showed mid-morning peak rates in the small gaps, corresponding to the period of direct beam irradiance, and declined more or less steadily throughout the day. Red and striped maples showed fairly clean differences in the understory, but sugar maple fluctuated more between the second and third data points, producing an intermediate total daily assimilation. The species showed different site preferences in terms of peak assimilation: red maple in large gaps and the other two species in small gaps.

Scaling to the shoot level in 1988 produced a slightly better distinction among species in the large gaps, but not in small gaps or understory (Figure 5-2). In fact, due to its lower shoot leaf area, red maple dropped down into the range of the other two species in the understory.

Shoot assimilation in 1989 exhibited striking shifts due to species changes in shoot leaf area (Figure 5-3). There was a dramatic separation in the large gaps, where red maple doubled its assimilation rates over 1988 while striped and sugar maple declined substantially (note the scale differences compared to Figure 5-2). The species were cleanly separated in the small gaps, where the rank order was PEN > RUB > SAC, due to striped maple doubling, red maple staying the same, and sugar maple declining. There were essentially no differences from 1988 to 1989 in the understory, although striped maple gained slightly.

Figure 5-2. Diurnal patterns of estimated maximum net shoot assimilation in 1988 by the same seedlings portrayed in Figure 5-1 (n=3 seedlings and 1-9 assimilation measurements per data point).

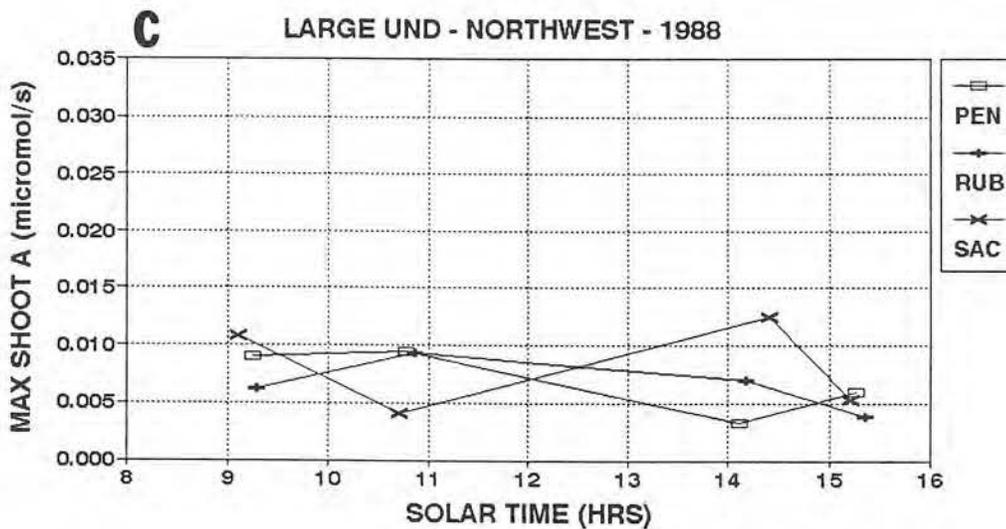
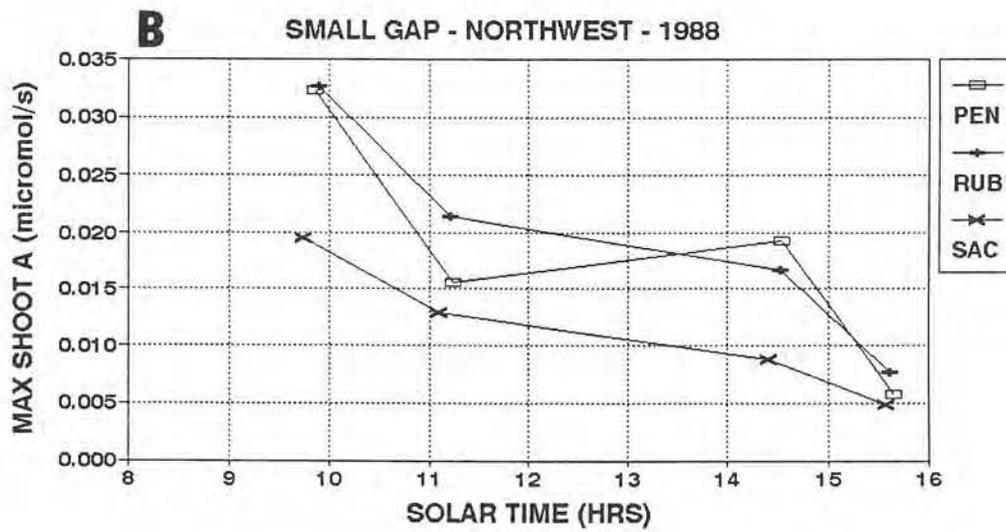
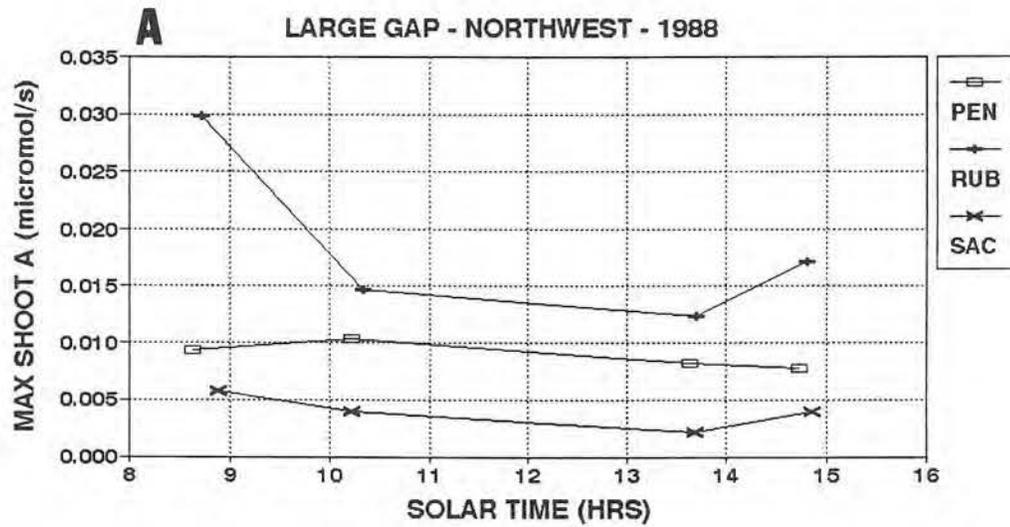
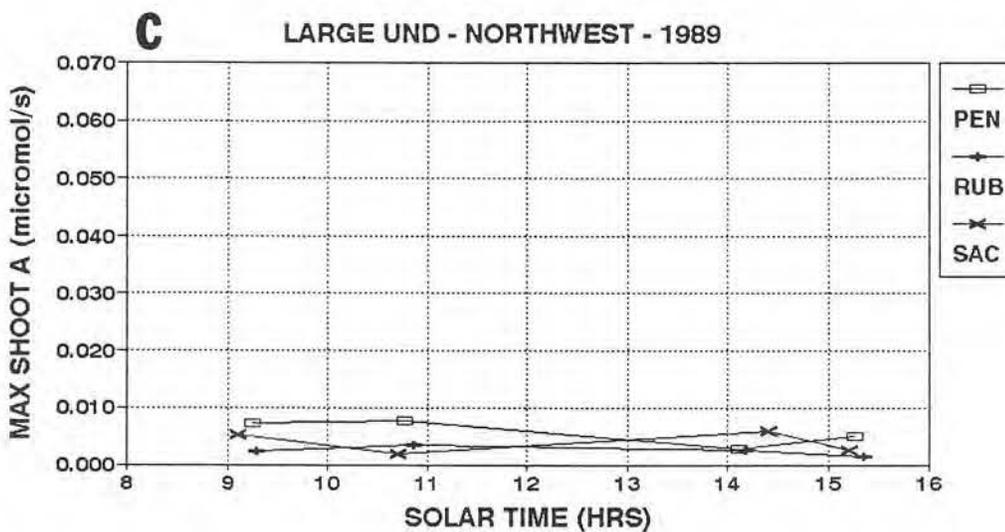
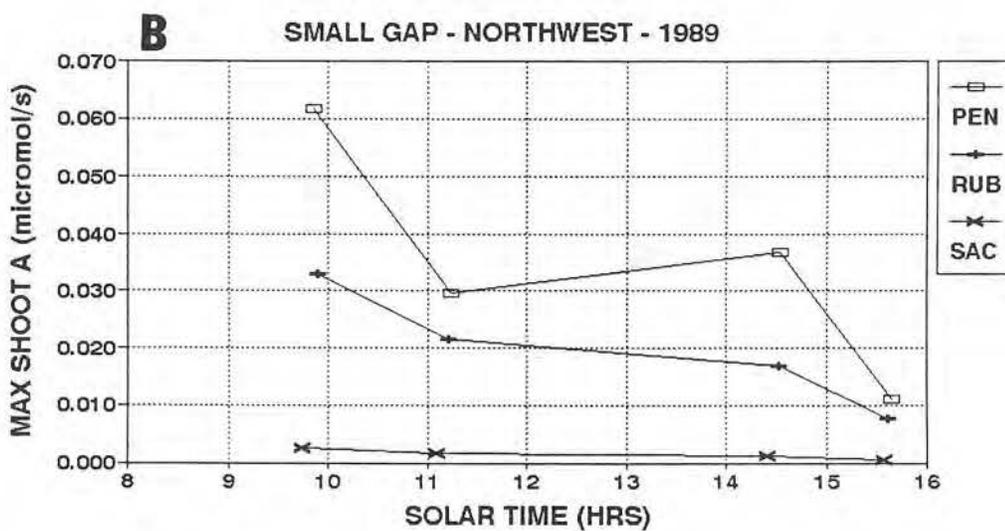
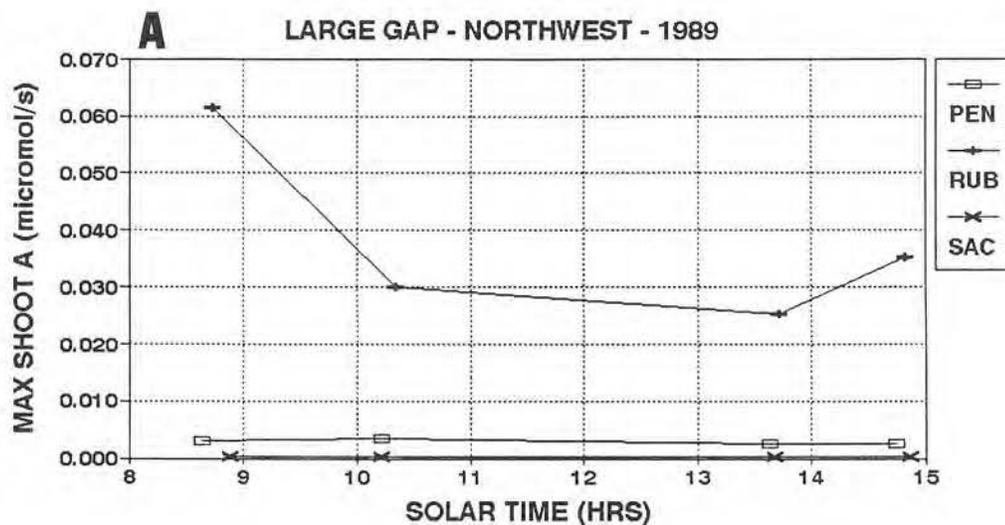


Figure 5-3. Diurnal patterns of estimated maximum net shoot assimilation in 1989 by the same seedlings portrayed in Figure 5-1 (n=3 seedlings and 1-9 assimilation measurements per data point).



In summary, diurnal comparisons in the NW plots show that the leaf-level rates (Figure 5-1) distinguished species only in the large gaps. Shoot-level assimilation in 1988 distinguished species only in large gaps, but divergence in leaf areas during the following year led to clear shoot-level separation among species in both gap sizes as of 1989. Overall, red maple showed the best shoot level assimilation in large gaps, striped maple was the best in small gaps, and the three species were indistinguishable in the understory. Sugar maple was therefore competitive only in the understory environment.

Leaf-level assimilation for the SE plots of the three sites are graphed in Figure 5-4. In comparison to the NW plots, there was a cleaner separation among species across sites, though the magnitudes of the differences were not great. The rates were much more comparable across sites than for the NW plots, as expected, since PPFD differences were also less divergent.

The rank order among species was $PEN \Rightarrow RUB > SAC$ in large gaps, $RUB > PEN > SAC$ in small gaps, and $RUB > SAC > PEN$ in the understory. All species in the large gap and understory showed peaks in midday, while the pattern in the small gap was variable.

The rank orders among species shifted noticeably for shoot-level estimates in 1988 (Figure 5-5). The species were cleanly separated in the large gap, where $PEN > RUB > SAC$. Sugar and striped maple now exceeded red maple in the small gap. The differences between striped and sugar maple were small, although it would appear that sugar maple had a slightly higher daily assimilation in the small gap while striped maple was higher in the understory. The three species were not very distinctive in the understory.

Figure 5-4. Diurnal patterns of net assimilation per unit leaf area on a clear day (8.8.88) by the three study species in the southeast plots of the large gap (A), small gap (B), and large understory (C) in Block 1 (n=3 seedlings and 1-9 assimilation measurements per data point).

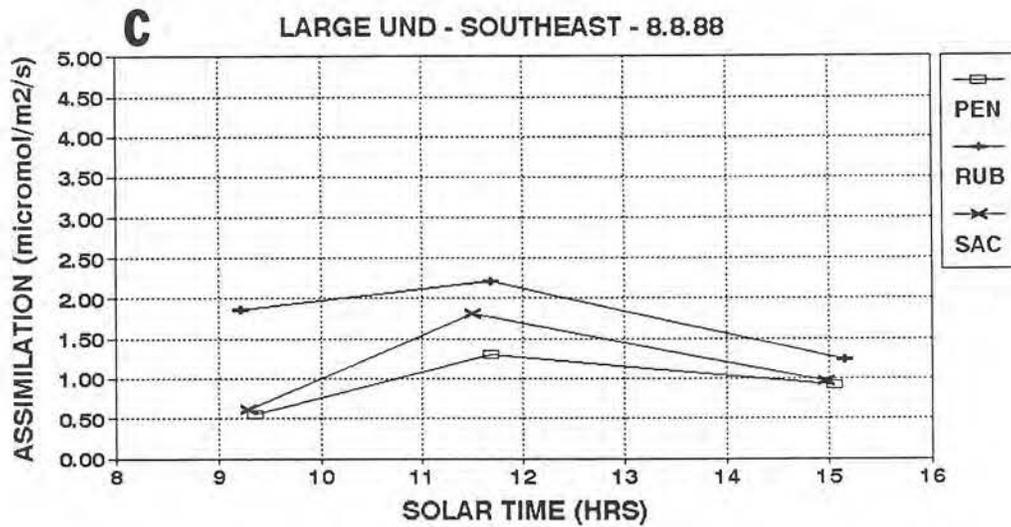
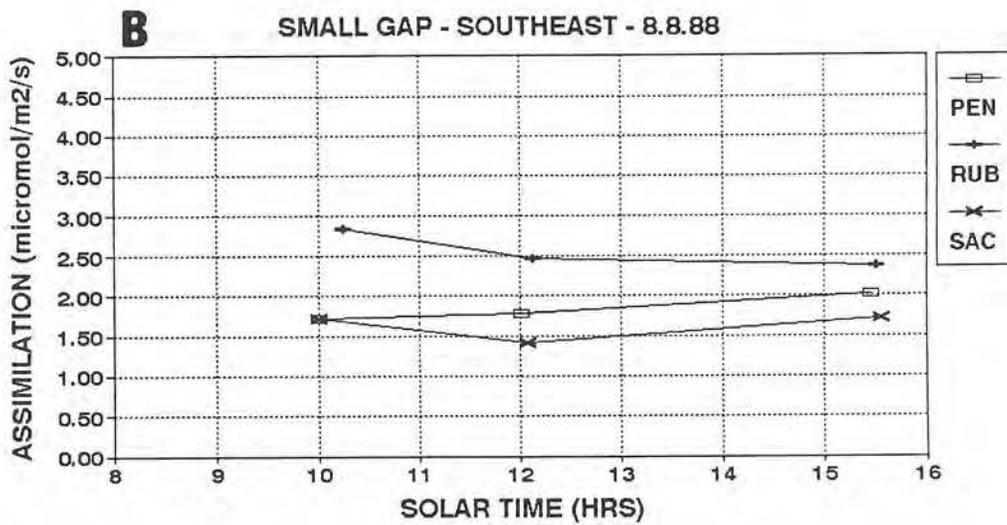
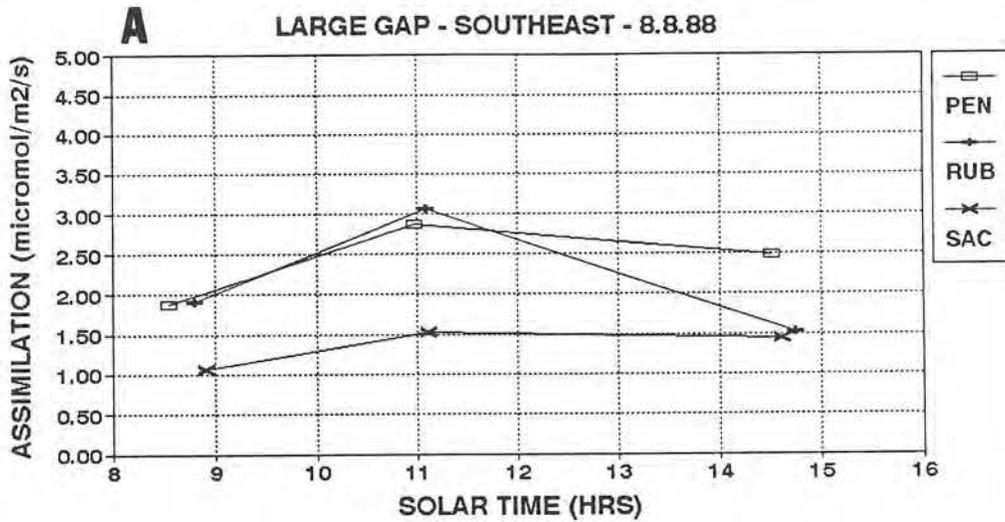
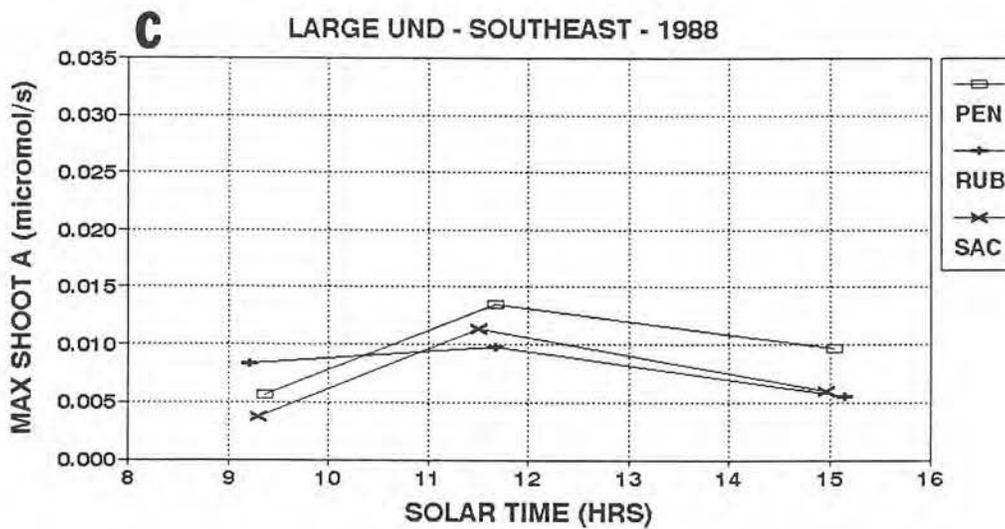
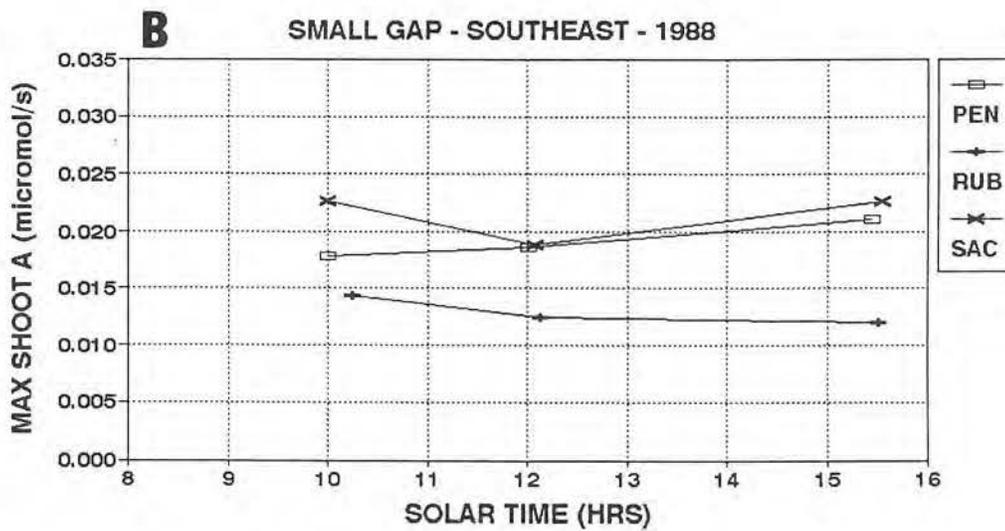
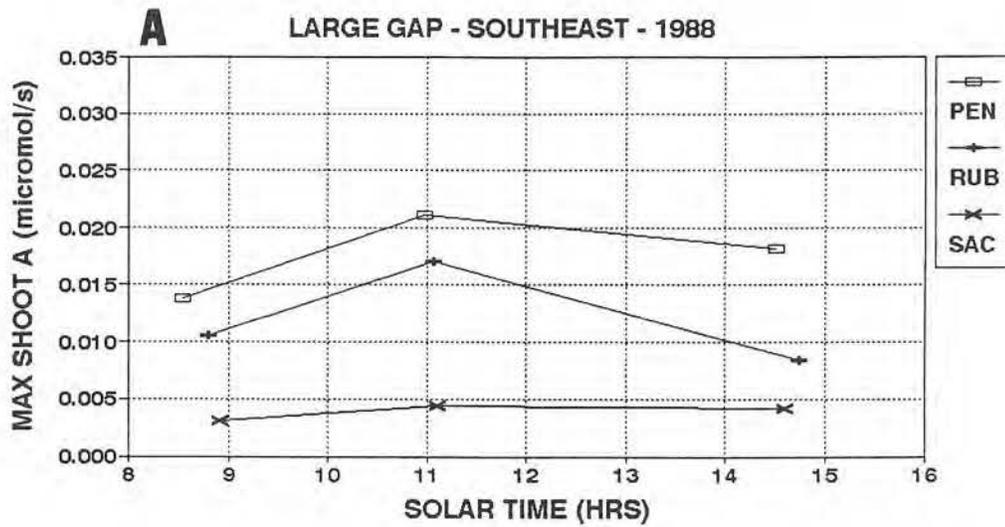


Figure 5-5. Diurnal patterns of estimated maximum net shoot assimilation in 1988 by the same seedlings portrayed in Figure 5-4 (n=3 seedlings and 1-9 assimilation measurements per data point).



The following year yielded even greater divergences among the species (Figure 5-6). There was a very clear separation in large gaps, with the same rank order as in 1988 (PEN > RUB > SAC). Striped maple doubled its assimilation, while red increased modestly and sugar maple showed no change. The small gap distinctions increased greatly, such that PEN > RUB > SAC. Striped maple tripled its rates, red maple doubled, and sugar declined slightly. There was some clarification in the understory, with PEN > RUB > SAC. Striped and red maples essentially held steady, while sugar maple declined.

The SE plot summary is similar to the NW plots, in that the leaf-level data did not distinguish the species as well as shoot-level rates, particularly for 1989. In both cases, scaling to the shoot level not only clarified species relationships, but in some cases reversed rank orders (small gap in 1988, small gap and understory in 1989). This was most often true because red maple had higher unit area rates but smaller shoot leaf areas.

5.4. POPULATION-LEVEL LIGHT RESPONSE CURVES

Much of the ecophysiological literature gives the impression that photosynthetic light responses follow nicely predicted trends, based as they are on steady-state measurements of carefully selected plants. Field conditions are different. Figures 5-7 through 5-9 are included here to emphasize how variable photosynthetic rates can be at the same PPFD, depending on the genetic identity of the plant, its phenotypic status, the time of season, spatial variability in soil resources, and short-term microenvironmental conditions. All figures show the data points used in the analysis of population-level curves presented in this

Figure 5-6. Diurnal patterns of estimated maximum net shoot assimilation in 1989 by the same seedlings portrayed in Figure 5-4 (n=3 seedlings and 1-9 assimilation measurements per data point).

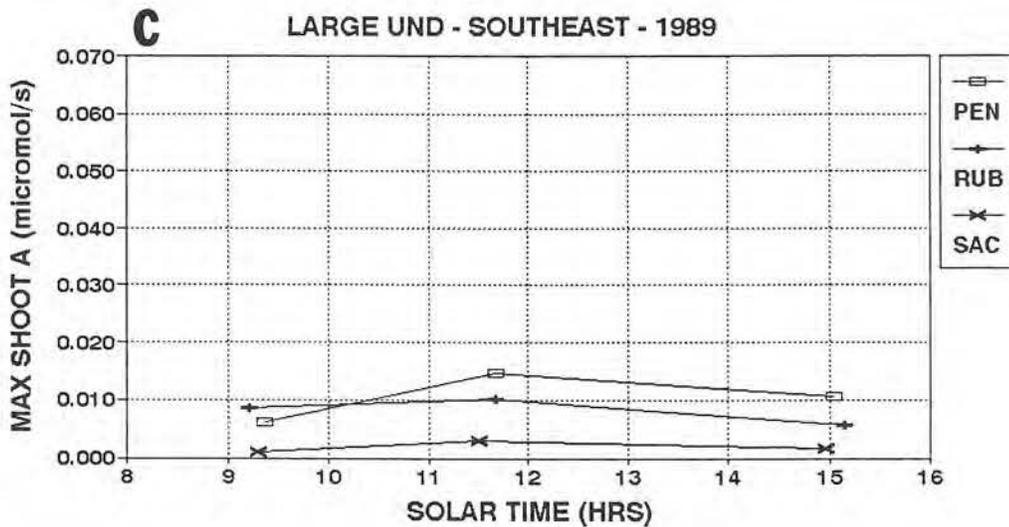
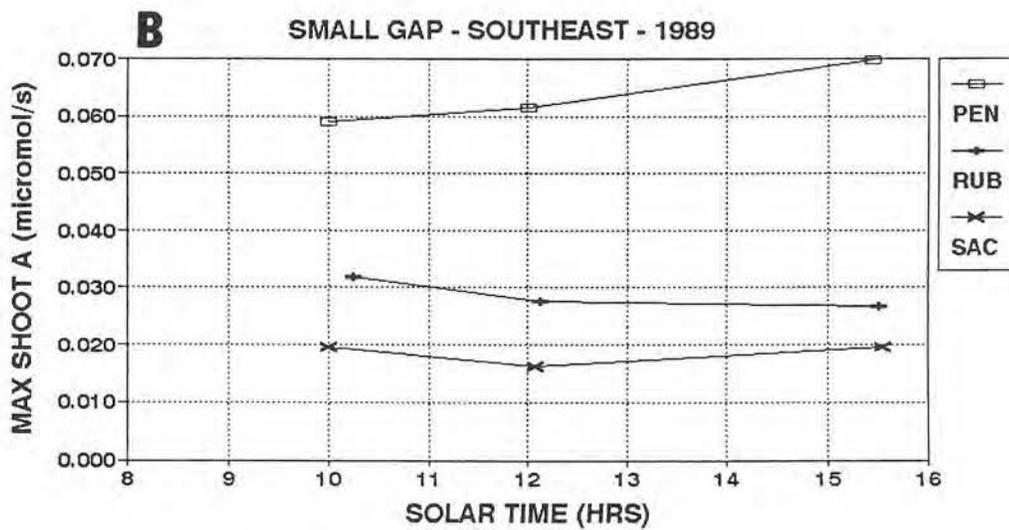
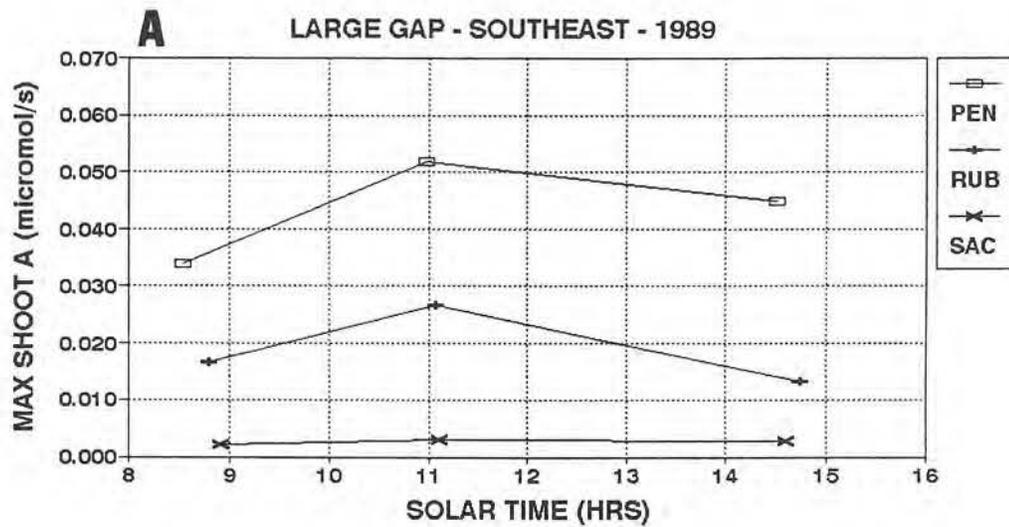


Figure 5-7. Scatterplot of net assimilation versus PPFD for *Acer pensylvanicum*. This figure includes all data points from several diurnal sampling periods across the 1988 season, which were used for the analysis of population-level light response curves. (A) Entire PPFD range, (B) Enlargement of lower left portion of (A).

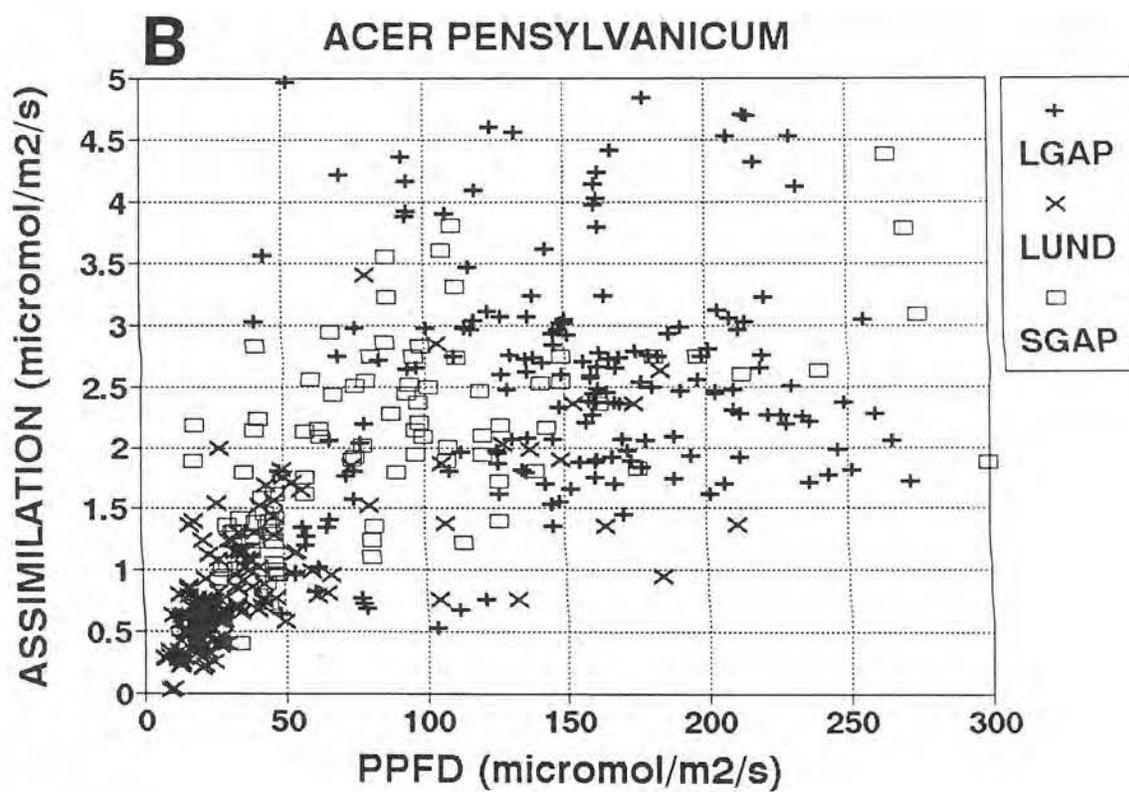
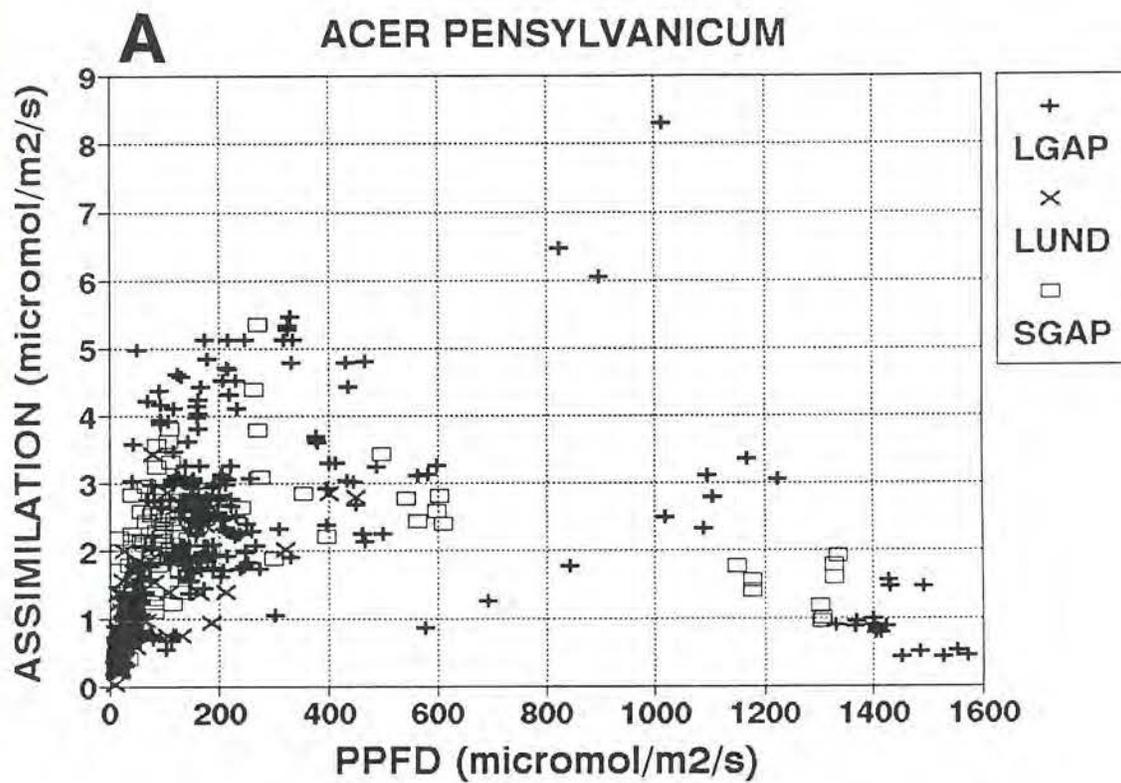


Figure 5-8. Scatterplot of net assimilation versus PPFD for *Acer rubrum*.

This figure includes all data points from several diurnal sampling periods across the 1988 season, which were used for the analysis of population-level light response curves. (A) Entire PPFD range, (B) Enlargement of lower left portion of (A).

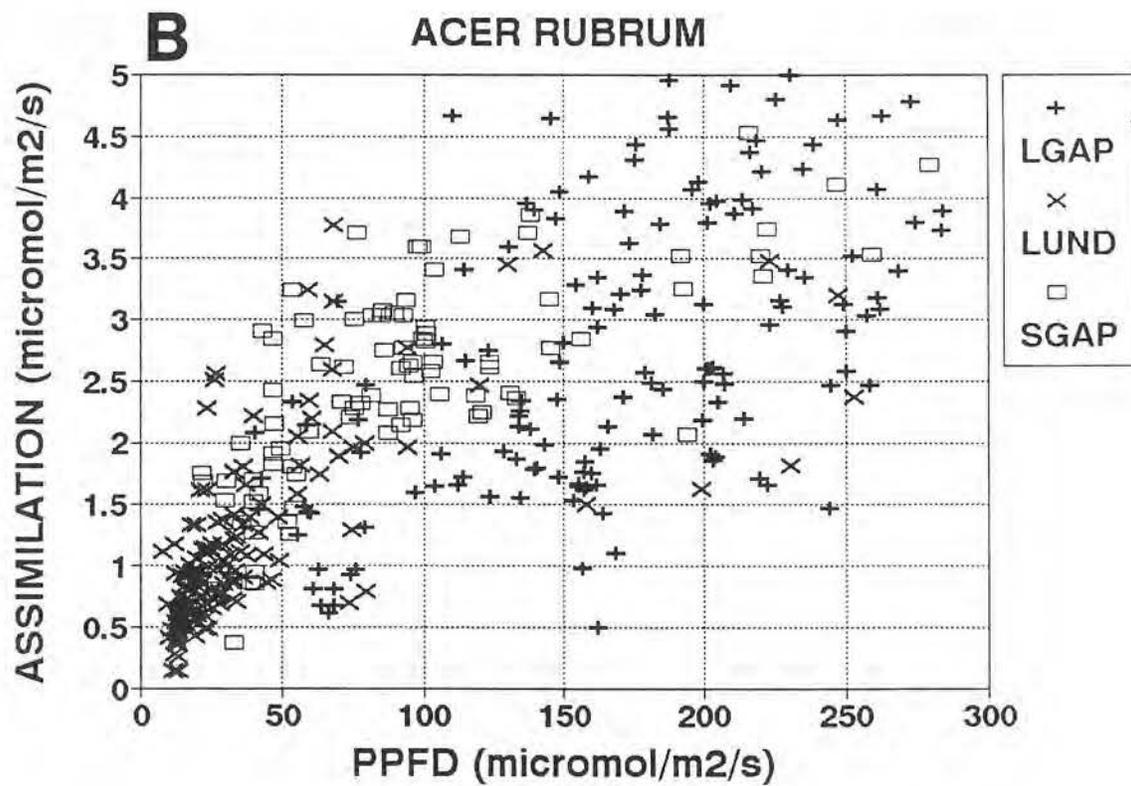
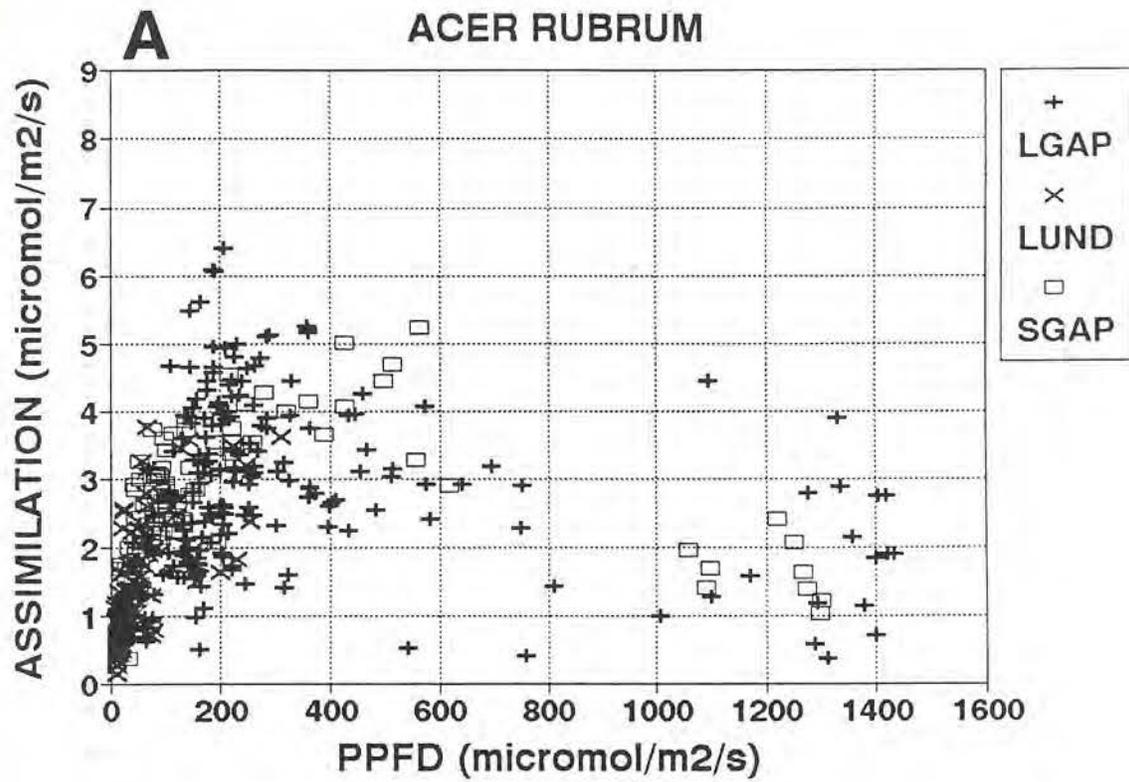
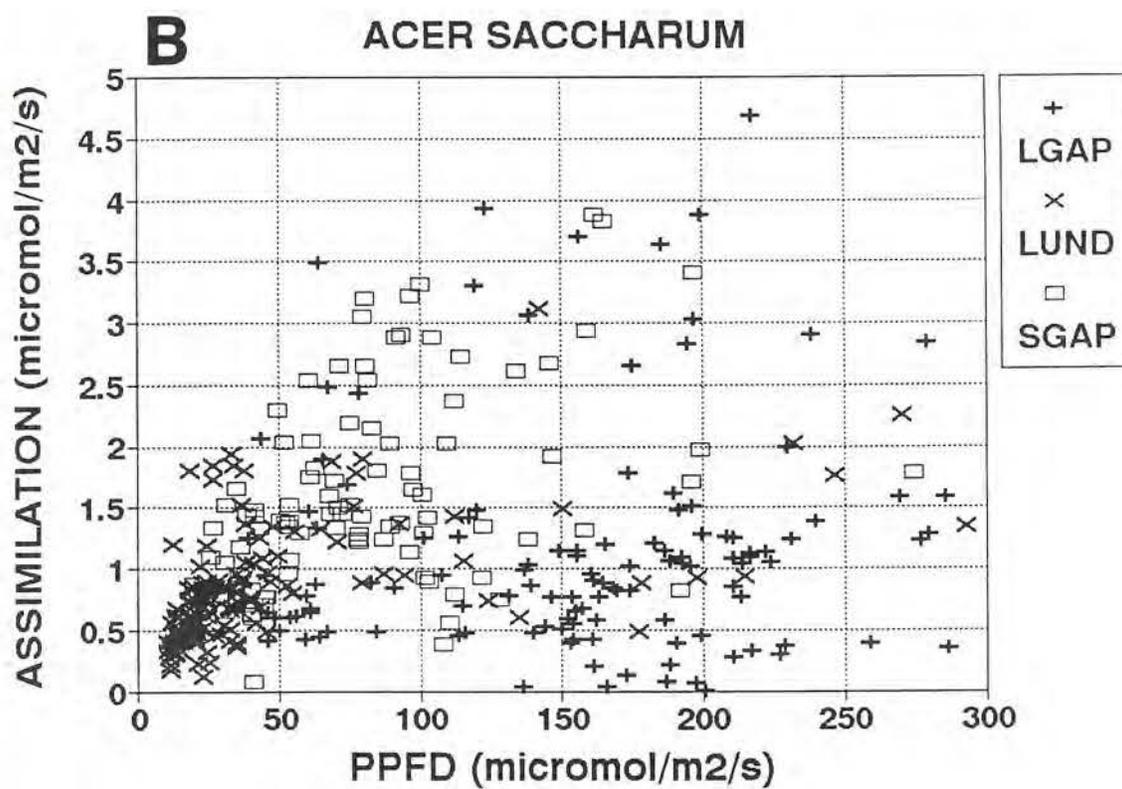
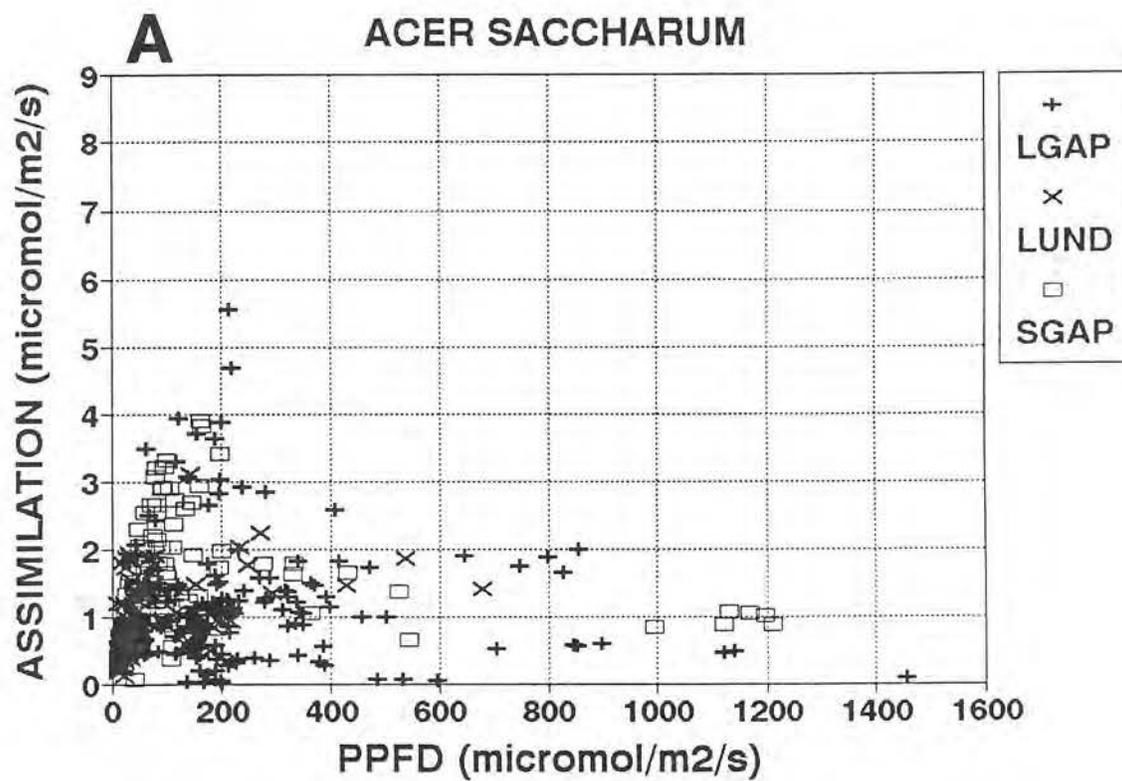


Figure 5-9. Scatterplot of net assimilation versus PPFD for *Acer saccharum*. This figure includes all data points from several diurnal sampling periods across the 1988 season, which were used for the analysis of population-level light response curves. (A) Entire PPFD range, (B) Enlargement of lower left portion of (A).



section. The second panel of each figure is an enlargement of the lower left corner to clarify relationships in this PPF_D range. It is worth emphasizing again that the data are truly comparative across species due to the sampling scheme.

Several useful points emerge from these scatterplots beyond the five-fold variability in net assimilation that can occur at any given PPF_D. First, over 90% of the samples had PPF_D less than 800 micromol/m²/s. This was true even though most of the sampling was done on clear to hazy days, with peak PPF_D values above 1500 micromol/m²/s in the large and small gaps. Second, there was an obvious separation among the three sites in average PPF_D during measurements. The large gaps produced the widest range of PPF_D values due to early morning and late afternoon conditions, while the understory values were nearly all restricted to less than 300 micromol/m²/s. Small gap PPF_D levels were intermediate between these two regions.

Third, striped and red maple were roughly comparable except that red maple showed higher rates in the 150-300 micromol/m²/s range, especially by the large gap plants. Sugar maple was suppressed at all PPF_D above 300 micromol/m²/s, especially the large gap plants. The other species declined in net assimilation above 800 micromol/m²/s as well.

Based on visual impressions, the site preferences for the three species were as follows: (1) striped maple, SGAP ~ LGAP > LUND; (2) red maple, LGAP > SGAP > LUND; and (3) sugar maple, SGAP > LGAP ~ LUND. These preferences are relative within species across sites and not across species within sites.

Tables 5-3 through 5-5 summarize the assimilation data used to produce the population-level light response curves. Each table includes

Table 5-3. Data on net assimilation versus PFD used to construct population-level light response curves for large gaps.

SITE/PLOT	SPECIES	VARIABLE	PPFD INTERVALS (micromol/m2/s)								
			0-50	51-100	101-150	151-200	201-300	301-400	401-600	601-1000	1001-1600
LARGE GAP NORTH	PEN	LEAF-LEVEL MEAN		0.65	0.88	1.45	1.81	1.47		1.51	0.88
		S.E.		0.05	0.22	0.00	0.11	0.43		0.25	0.14
		N		3	4	1	5	2		2	11
		MAXIMUM SHOOT A - 1988		0.0033	0.0044	0.0073	0.0091	0.0074		0.0076	0.0044
		MAXIMUM SHOOT A - 1989		0.0011	0.0014	0.0024	0.0030	0.0024		0.0025	0.0014
	RUB	LEAF-LEVEL MEAN		0.78			2.68	2.26			2.35
		S.E.		0.06			0.61	0.31			0.33
		N		6			3	5			12
		MAXIMUM SHOOT A - 1988		0.0050			0.0171	0.0145			0.0150
		MAXIMUM SHOOT A - 1989		0.0103			0.0352	0.0297			0.0308
SAC	LEAF-LEVEL MEAN			0.48	1.04	1.30	1.45			0.09	
	S.E.			0.03	0.23	0.23	0.19			0.00	
	N			2	5	4	3			1	
	MAXIMUM SHOOT A - 1988			0.0033	0.0071	0.0088	0.0098			0.0006	
	MAXIMUM SHOOT A - 1989			0.0002	0.0004	0.0006	0.0006			0.0000	
LARGE GAP SOUTH	PEN	LEAF-LEVEL MEAN	2.26	2.35	2.70	2.66	2.96	4.13	3.26	4.40	3.63
		S.E.	0.65	0.24	0.11	0.11	0.17	0.34	0.27	0.76	0.79
		N	4	26	45	53	35	12	12	5	7
		MAXIMUM SHOOT A - 1988	0.0166	0.0172	0.0198	0.0195	0.0217	0.0302	0.0239	0.0322	0.0266
		MAXIMUM SHOOT A - 1989	0.0408	0.0423	0.0487	0.0480	0.0533	0.0744	0.0588	0.0793	0.0654
	RUB	LEAF-LEVEL MEAN	1.55	1.75	2.67	2.95	3.50	3.63	2.99	2.18	1.08
		S.E.	0.24	0.17	0.18	0.20	0.15	0.30	0.24	0.44	0.36
		N	4	14	33	46	49	13	15	6	3
		MAXIMUM SHOOT A - 1988	0.0086	0.0097	0.0148	0.0164	0.0194	0.0201	0.0166	0.0121	0.0060
		MAXIMUM SHOOT A - 1989	0.0135	0.0152	0.0232	0.0256	0.0304	0.0315	0.0259	0.0190	0.0094
SAC	LEAF-LEVEL MEAN	0.92	1.23	1.29	1.14	1.41	0.98	1.04	1.27	0.47	
	S.E.	0.22	0.20	0.24	0.16	0.28	0.10	0.34	0.22	0.01	
	N	7	18	19	41	24	16	8	9	2	
	MAXIMUM SHOOT A - 1988	0.0027	0.0036	0.0037	0.0033	0.0041	0.0028	0.0030	0.0037	0.0014	
	MAXIMUM SHOOT A - 1989	0.0018	0.0024	0.0025	0.0022	0.0027	0.0019	0.0020	0.0025	0.0009	

LEAF-LEVEL UNITS = micromol/m2/s MAXIMUM SHOOT A UNITS = micromol/s

Table 5-4. Data on net assimilation versus PPFD used to construct population-level light response curves for small gaps.

SITE/PLOT	SPECIES	VARIABLE	PPFD INTERVALS (micromol/m ² /s)										
			0-50	51-100	101-150	151-200	201-300	301-400	401-600	601-1000	1001-1600		
SMALL GAP NORTH	PEN	LEAF-LEVEL MEAN	0.68	1.24	1.45		4.51	2.51	2.81	2.59	1.47		
		S.E.	0.14	0.07	0.15		0.45	0.32	0.22	0.22	0.12		
		N	3	3	3		3	2	4	2	9		
		MAXIMUM SHOOT A - 1988	0.0071	0.0129	0.0151		0.0472	0.0263	0.0294	0.0271	0.0154		
		MAXIMUM SHOOT A - 1989	0.0136	0.0247	0.0290		0.0901	0.0502	0.0561	0.0518	0.0294		
		RUB	LEAF-LEVEL MEAN	0.76	2.27	2.54	3.26	4.11	3.89	4.41	2.89	1.64	
		S.E.	0.13	0.07	0.10	0.00	0.21	0.25	0.58	0.00	0.15		
		N	4	3	4	1	4	2	3	1	9		
		MAXIMUM SHOOT A - 1988	0.0067	0.0199	0.0223	0.0286	0.0362	0.0342	0.0387	0.0254	0.0145		
		MAXIMUM SHOOT A - 1989	0.0068	0.0202	0.0226	0.0290	0.0367	0.0347	0.0393	0.0258	0.0147		
	SAC	LEAF-LEVEL MEAN	0.49	1.34	1.43	3.17		1.78	1.51	0.31	0.98		
		S.E.	0.14	0.03	0.44	0.23		0.00	0.14	0.53	0.04		
		N	4	9	4	2		1	2	2	5		
		MAXIMUM SHOOT A - 1988	0.0036	0.0098	0.0104	0.0232		0.0131	0.0111	0.0022	0.0072		
		MAXIMUM SHOOT A - 1989	0.0005	0.0013	0.0014	0.0031		0.0017	0.0015	0.0003	0.0009		
			PPFD INTERVALS (micromol/m ² /s)										
			0-10	11-20	21-30	31-40	41-50	51-100	101-150	151-200	201-300	301-400	401-600
SMALL GAP SOUTH	PEN	LEAF-LEVEL MEAN			1.09	1.51	1.33	2.37	2.52	2.42	2.55		
		S.E.			0.19	0.51	0.35	0.46	0.61	0.44	0.50		
		N			4	12	14	28	16	4	4		
		MAXIMUM SHOOT A - 1988			0.0114	0.0158	0.0139	0.0248	0.0264	0.0254	0.0267		
		MAXIMUM SHOOT A - 1989			0.0376	0.0521	0.0458	0.0819	0.0871	0.0837	0.0881		
		RUB	LEAF-LEVEL MEAN			1.39	1.54	2.17	2.60	2.91	2.81	3.54	3.99
		S.E.			0.43	0.27	0.46	0.60	0.59	0.73	0.19	0.00	0.48
		N			6	6	9	36	13	3	3	1	3
		MAXIMUM SHOOT A - 1988			0.0070	0.0078	0.0110	0.0132	0.0147	0.0142	0.0179	0.0202	0.0228
		MAXIMUM SHOOT A - 1989			0.0156	0.0172	0.0243	0.0292	0.0326	0.0315	0.0397	0.0447	0.0504
	SAC	LEAF-LEVEL MEAN		0.88	1.07	1.18	1.21	2.00	1.58	2.26	1.78	1.34	0.64
		S.E.		0.00	0.22	0.38	0.53	0.68	0.81	1.30	0.00	0.41	0.00
		N		1	4	7	9	33	15	6	1	2	1
		MAXIMUM SHOOT A - 1988		0.0117	0.0141	0.0156	0.0161	0.0265	0.0209	0.0299	0.0236	0.0177	0.0085
		MAXIMUM SHOOT A - 1989		0.0102	0.0123	0.0136	0.0140	0.0231	0.0182	0.0260	0.0205	0.0154	0.0074

LEAF-LEVEL UNITS = micromol/m²/s MAXIMUM SHOOT A UNITS = micromol/s

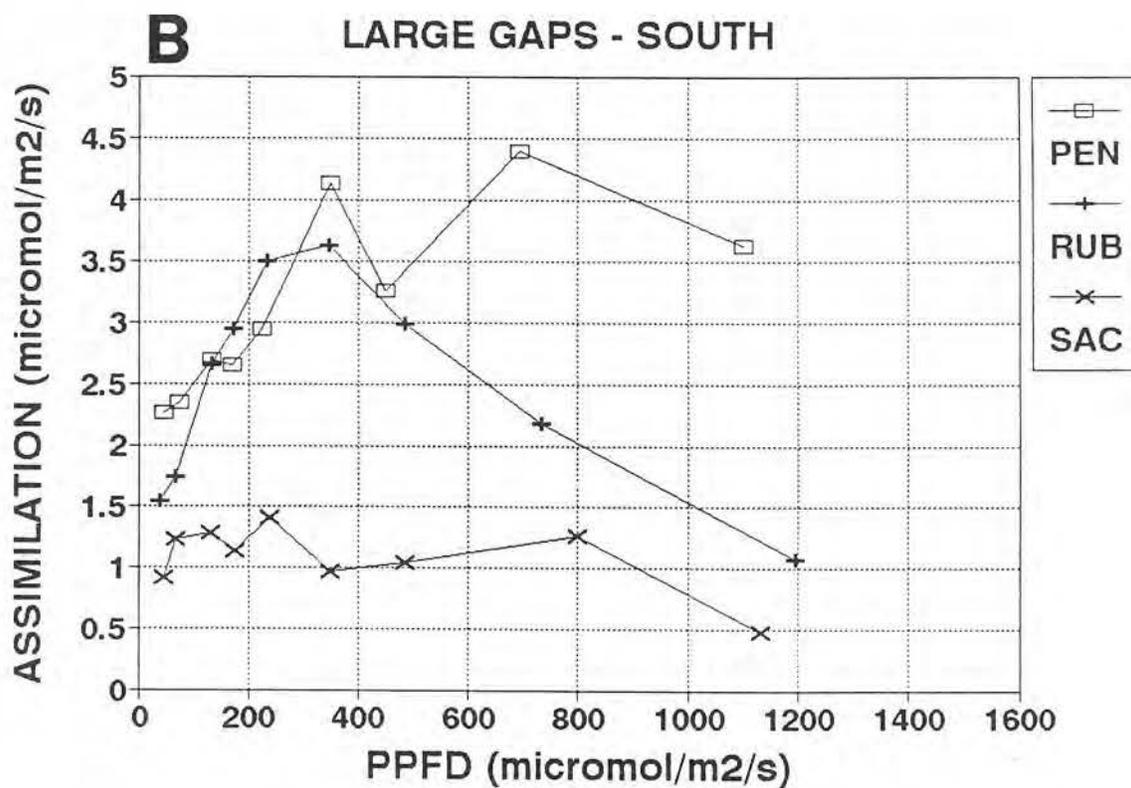
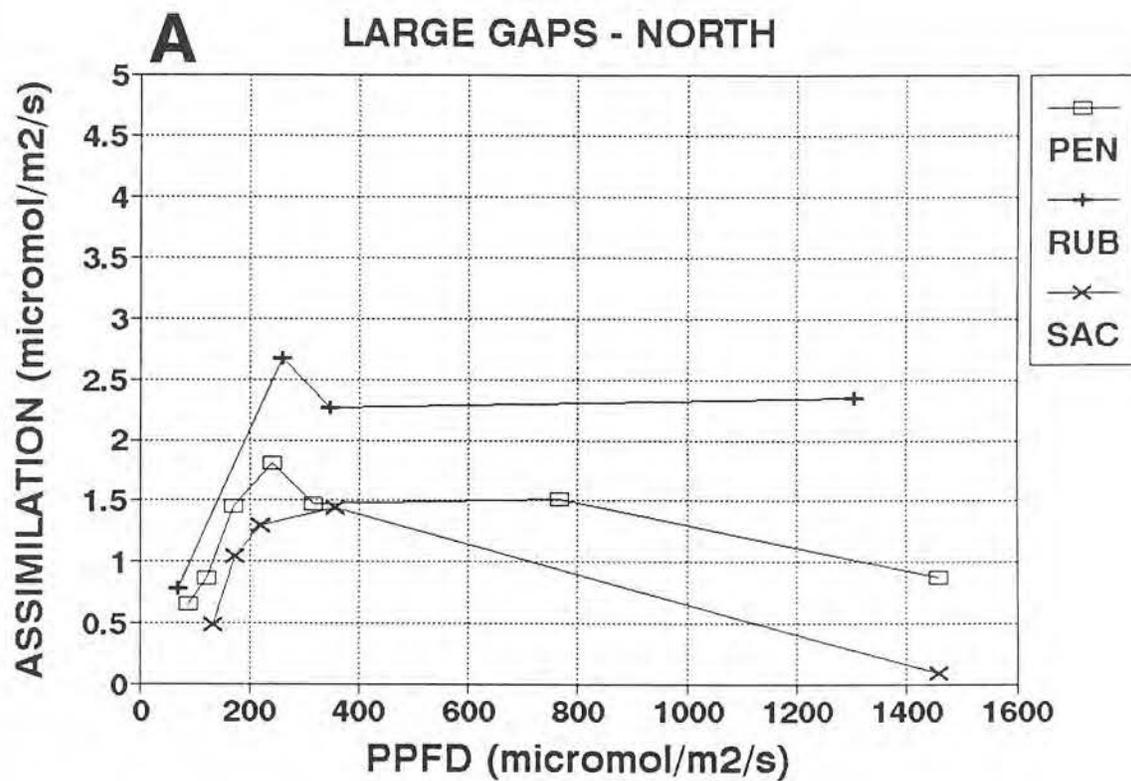
Table 5-5. Data on net assimilation versus PPFD used to construct population-level light response curves for large understories.

SITE/PLOT	SPECIES	VARIABLE	PPFD INTERVALS (micromol/m ² /s)										
			0-10	11-20	21-30	31-40	41-50	51-100	101-150	151-200	201-300	301-400	401-600
LARGE UND NORTH	PEN	LEAF-LEVEL MEAN	0.02	0.42	0.52	1.02	0.64	0.79	0.76	0.95			
		S.E.	0.16	0.16	0.17	0.07	0.09	0.00	0.00	0.00			
		N	4	26	14	3	2	1	2	1			
		MAXIMUM SHOOT A - 1988	0.0020	0.0046	0.0057	0.0113	0.0071	0.0088	0.0083	0.0105			
		MAXIMUM SHOOT A - 1989	0.0016	0.0037	0.0047	0.0092	0.0058	0.0071	0.0068	0.0085			
		RUB	LEAF-LEVEL MEAN	0.42	0.63	1.06	1.32	1.01					
	S.E.	0.00	0.25	0.33	0.25	0.10							
	N	1	39	13	6	3							
	MAXIMUM SHOOT A - 1988	0.0023	0.0035	0.0059	0.0073	0.0056							
	MAXIMUM SHOOT A - 1989	0.0009	0.0013	0.0022	0.0027	0.0021							
	SAC	LEAF-LEVEL MEAN	0.33	0.45	0.76	0.81	0.90	1.21	1.43				
	S.E.	0.00	0.12	0.13	0.09	0.00	0.22	0.00					
N	1	35	13	3	1	3	1						
MAXIMUM SHOOT A - 1988	0.0029	0.0040	0.0067	0.0071	0.0080	0.0107	0.0127						
MAXIMUM SHOOT A - 1989	0.0014	0.0019	0.0032	0.0034	0.0038	0.0051	0.0060						
LARGE UND SOUTH	PEN	LEAF-LEVEL MEAN	0.40	0.73	0.85	1.04	1.04	1.63	2.15	2.49			2.81
		S.E.	0.20	0.27	0.41	0.23	0.42	1.19	0.47	0.20			0.03
		N	3	18	18	12	5	4	4	2			2
		MAXIMUM SHOOT A - 1988	0.0041	0.0075	0.0088	0.0107	0.0107	0.0169	0.0223	0.0258			0.0291
		MAXIMUM SHOOT A - 1989	0.0045	0.0082	0.0096	0.0117	0.0117	0.0184	0.0243	0.0281			0.0317
		RUB	LEAF-LEVEL MEAN	0.91	0.67	1.41	1.35	1.39	2.57	3.16		3.01	3.61
	S.E.	0.30	0.41	0.69	0.48	0.15	0.70	0.60		0.58	0.00		
	N	2	15	11	9	2	9	3		3	1		
	MAXIMUM SHOOT A - 1988	0.0040	0.0030	0.0063	0.0060	0.0062	0.0114	0.0141		0.0134	0.0161		
	MAXIMUM SHOOT A - 1989	0.0042	0.0031	0.0065	0.0062	0.0064	0.0118	0.0145		0.0138	0.0165		
	SAC	LEAF-LEVEL MEAN		0.71	0.71	1.23	1.04		1.89		1.85		1.66
	S.E.		0.40	0.51	0.54	0.38		1.08		0.39		0.27	
	N		13	16	10	4		3		4		2	
	MAXIMUM SHOOT A - 1988		0.0045	0.0044	0.0077	0.0065		0.0118		0.0116		0.0104	
	MAXIMUM SHOOT A - 1989		0.0012	0.0011	0.0020	0.0017		0.0031		0.0030		0.0027	
	LEAF-LEVEL UNITS = micromol/m ² /s MAXIMUM SHOOT A UNITS = micromol/s												

sample sizes, mean assimilation rates, standard errors of the mean, and maximum estimated shoot assimilation rates for 1988 and 1989 within each PPFD interval. Note that the small gap north intervals are identical to the large gaps, while the small gap south intervals are the same as the understory. Overall, the coefficients of variation were not distressingly large, indicating that the condensing of variable sample data from across the season is a viable method. Also note that very few plants (1-2) were occasionally represented in an interval, reducing confidence in these data points. These low sample sizes (and coefficients of variation, if large) are taken into account in the discussion that follows.

The three species showed fairly distinctive curves at the leaf level for both the north and south sides of large gaps (Figure 5-10). The rank order in the north was RUB > PEN > SAC. The order varied in the south, with PEN ~ RUB > SAC for PPFD in the 0-500 micromol/m²/s range and PEN > RUB > SAC for PPFD > 500 micromol/m²/s. All species declined in assimilation above 800 micromol/m²/s, except for red maple in the north, which maintained close to saturation values to at least 1300 micromol/m²/s. The species separated nicely in the north on the irradiance at which they begin to show inhibition of assimilation, with RUB > PEN > SAC. This order was not maintained in the south, where SAC > PEN > RUB. It is not clear why red maple showed such a steady decline after 400 micromol/m²/s in the south.

Saturation rates were greater in the south than in the north for striped and red maples, but about the same for sugar maple. Saturation irradiances were lower in the north for striped maple (300 vs. 600 micromol/m²/s), the same at both plots for red maple (300 micromol/m²/s)



and higher in the north for sugar maple (350 vs. 250 micromol/m²/s). It appears that light compensation points would be higher in the north for all species. Based on leaf-level assimilation, the south plots of large gaps were a more favorable environment than the north plots for all three species.

Shoot level results for these plots showed distinctions between the species not revealed by leaf-level data (Figure 5-11). In 1988, the species were still quite similar in the north plot (RUB > PEN ~ SAC), especially since sugar maple increased relative to striped maple via shoot scaling. The south plot showed a much better separation of species than at the leaf level. The species retained their rank order overall (PEN > RUB > SAC), but this order now held across all PPFD levels. Shoot-level gains were higher in the south than in the north for striped and red maple, but the reverse was true for sugar maple.

These patterns diverged even more in 1989 (Figure 5-11). The loss of leaf area by striped and sugar maple and the increase by red maple led to a huge advantage for the latter (RUB > PEN > SAC). Striped maple assimilation was greater than sugar maple across all irradiances, but both were very low and the differences were therefore not great in absolute terms. The south plot showed the best species distinctions overall, with PEN > RUB > SAC. Striped maple more than doubled, red maple increased by 50% and sugar maple was essentially unchanged. These curves show plainly that red and striped maple exhibited a tradeoff across the large gap in net shoot assimilation, while sugar maple showed little recognition of the gradient.

Leaf-level results for the small gap plots are shown in Figure 5-12. The species were very similar in the north up to about 200

Figure 5-11. Population-level light response curves (estimated maximum shoot assimilation versus PPFD in 1988 and 1989) for the three study species on the north and south sides of large gaps. (A) North - 1988, (B) North - 1989, (C) South - 1988, (D) South - 1989. Note differences in scale on the y-axis.

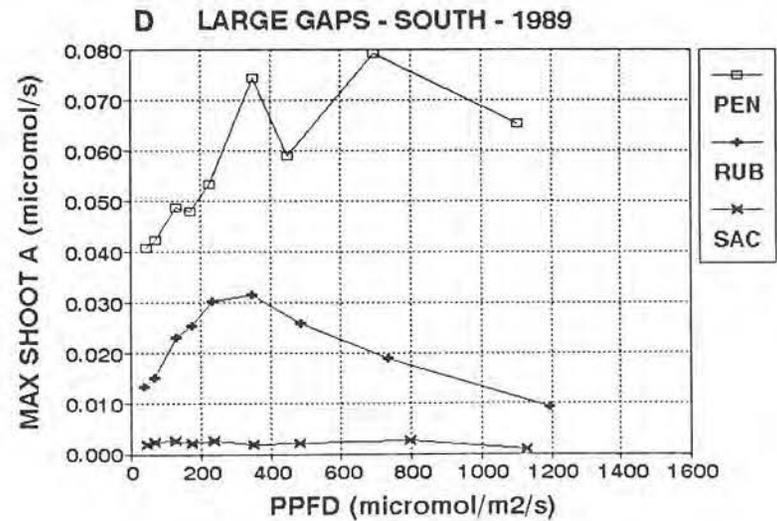
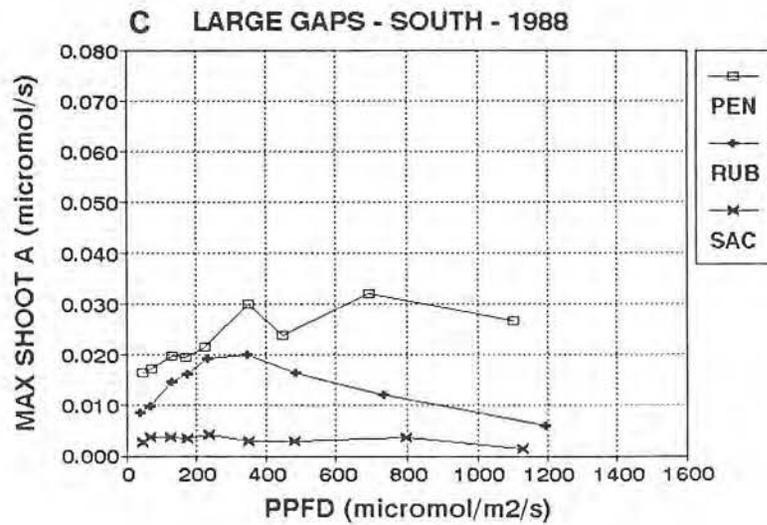
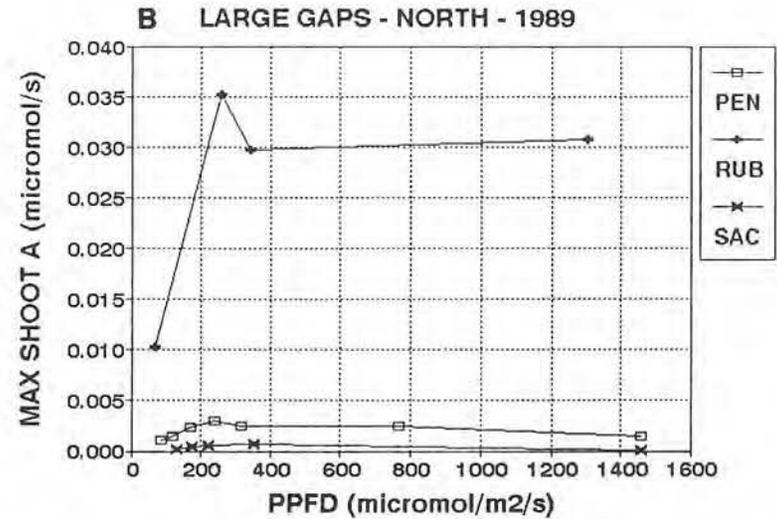
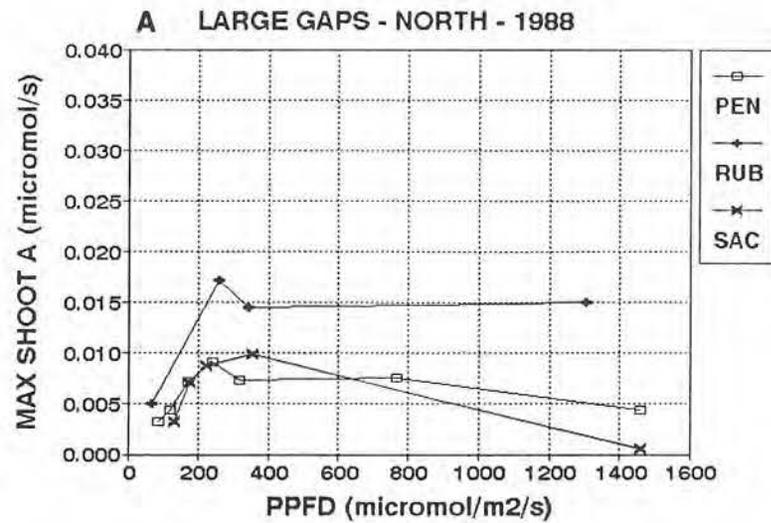
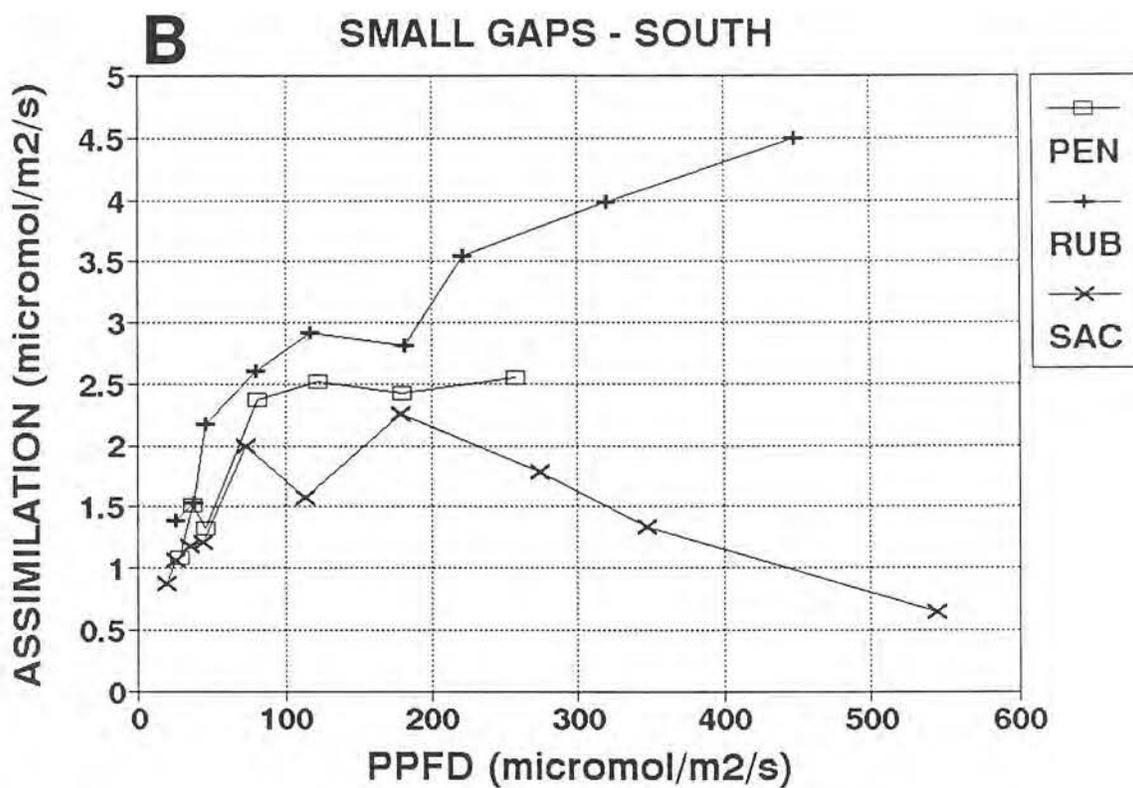
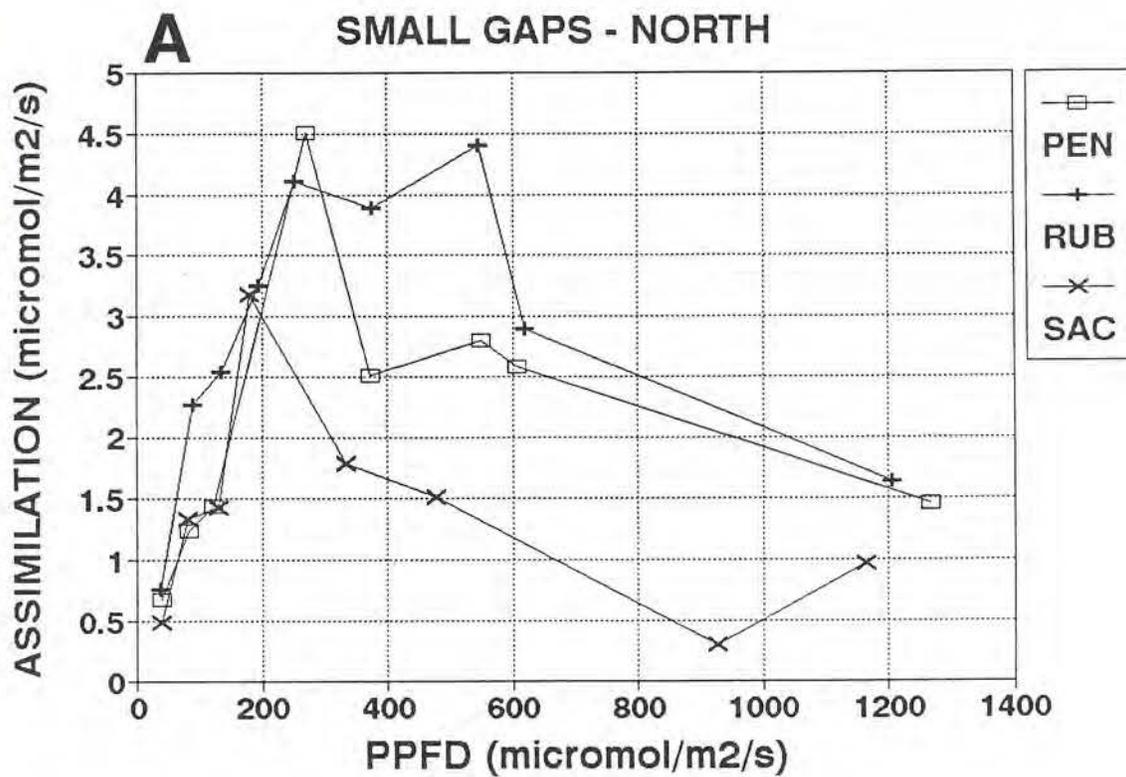


Figure 5-12. Population-level light response curves (assimilation per unit leaf area versus PPF) for the three study species on the north (A) and south (B) sides of small gaps (n=1-36 for each data point).



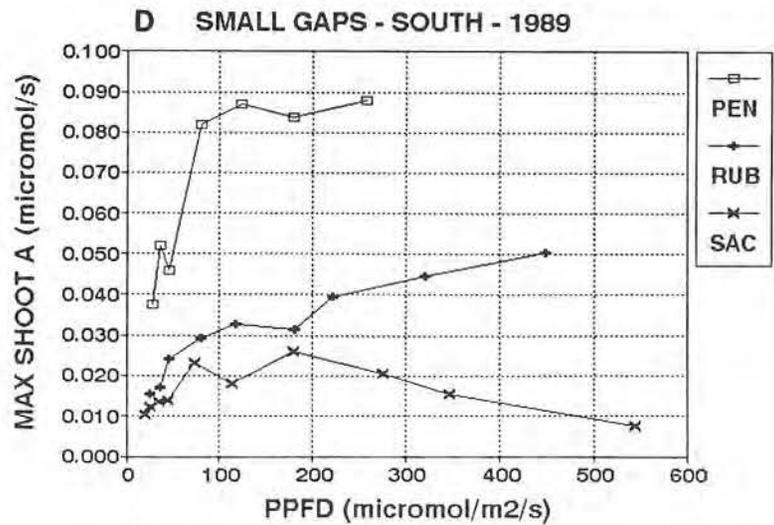
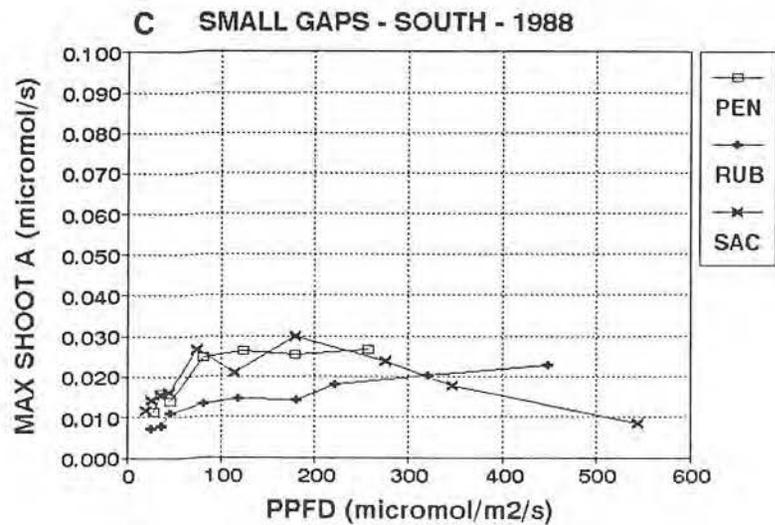
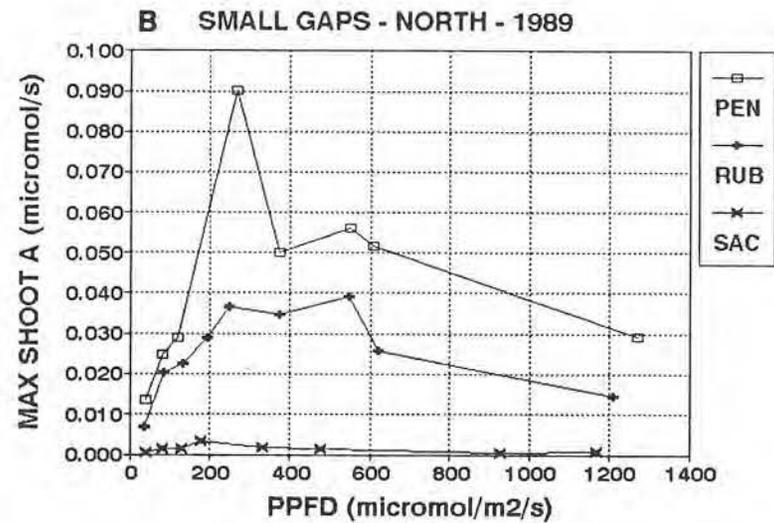
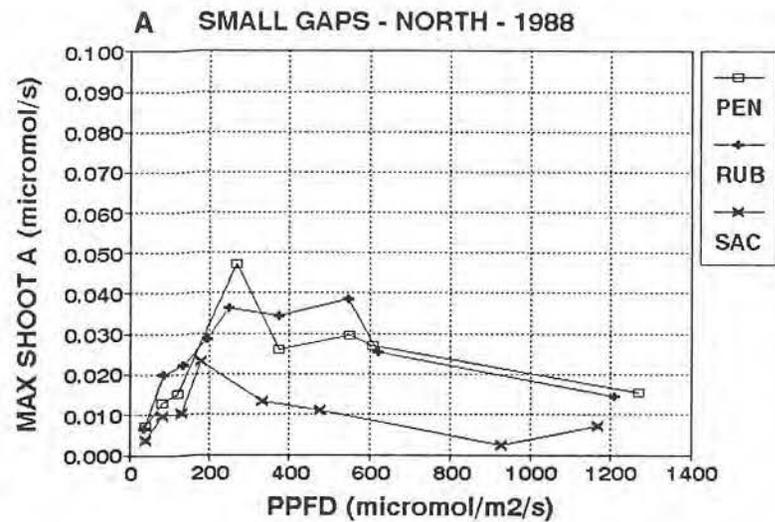
micromol/m²/s, where sugar maple began to decline. Red maple exceeded striped maple from 300-600 micromol/m²/s and then they converged again. Neither data point in the 200-400 micromol/m²/s range is spurious for striped or red maple, so their relative values are correct.

The pattern in the south plot was different from that for the north (note the scale differences on the x-axis). The species were similar to 75 micromol/m²/s, after which they diverged to RUB > PEN > SAC. The curves for red and sugar maple were like the north plot in most respects, except that both showed higher rates in the 0-100 micromol/m²/s region, and sugar maple maintained higher rates above 200 micromol/m²/s. Striped maple also showed higher rates in the 0-100 micromol/m²/s interval in the south, but did not exhibit the high peak at 200-300 micromol/m²/s as it did in the north.

Saturation rates were higher in the north for both striped and sugar maple, and about the same for red maple. Saturation irradiances were lower in the south for striped and sugar maple, and would likely have been the same for red maple. The compensation points did not show as clear a distinction between plots as in the large gaps. The best that could be said is that compensation was below 50 micromol/m²/s for all species in both plots.

The 1988 shoot-level data for the small gaps showed a pattern in the north comparable to leaf-level results (Figure 5-13). But the south plot had a complete species reversal, from RUB > PEN > SAC to SAC => PEN > RUB, in the 0-300 micromol/m²/s range. Both plots showed enhanced divergence by 1989. In the north, the clear separation was PEN > RUB > SAC at all PPF, due to the increase by striped maple, no change by red maple, and decline by sugar maple. The south plot likewise clarified,

Figure 5-13. Population-level light response curves (estimated maximum shoot assimilation versus PPFD in 1988 and 1989) for the three study species on the north and south sides of small gaps. (A) North - 1988, (B) North -1989, (C) South - 1988, (D) South - 1989. Note differences in scale on the y-axis.



but with another shift in species rank, with $PEN > RUB > SAC$ across all PPFD levels. Striped and red maple increased by different amounts and sugar maple declined.

Large understory curves for leaf-level assimilation are displayed in Figure 5-14 (PPFD = 0-600 micromol/m²/s) and Figure 5-15 (PPFD = 0-200 micromol/m²/s; note the scale differences on the y-axis). The north to south gradient in PPFD levels limits the interpretation of data above 200 micromol/m²/s due to the absence of data points above this in the north. So this discussion will focus on Figure 5-15. Assimilation rates were about the same across plots for each species in the 0-50 micromol/m²/s range. The clear rank order in the north plots in this range was $RUB > SAC > PEN$, while it was $RUB > PEN = SAC$ in the south.

Assimilation rates continued to rise above 50 micromol/m²/s in the south. Sugar maple was not seen to peak in the north, and reached assimilation rates only slightly lower than saturation rates in the south. The rank order for PPFD > 50 micromol/m²/s was $RUB > PEN > SAC$ in the south and $RUB ? SAC > PEN$ in the north.

As compared to the south, striped maple was apparently suppressed in the north, sugar maple was about the same, and it is unclear how red maple compared due to limited data. Saturation rates and irradiances were higher in the south for striped maple, but there weren't enough data points at higher PPFD levels in the north to compare red and sugar maple saturations. It is notable that the apparent compensation points were less than 20 micromol/m²/s (1% full sun) in the south and less than 10 micromol/m²/s (0.5%) in the north. These values are quite low, particularly for red maple, which would not be predicted to have such a low compensation point on the basis of its shade tolerance ranking. This

Figure 5-14. Population-level light response curves (assimilation per unit leaf area versus PPFD) for the three study species on the north (A) and south (B) sides of large understories (n=1-39 for each data point).

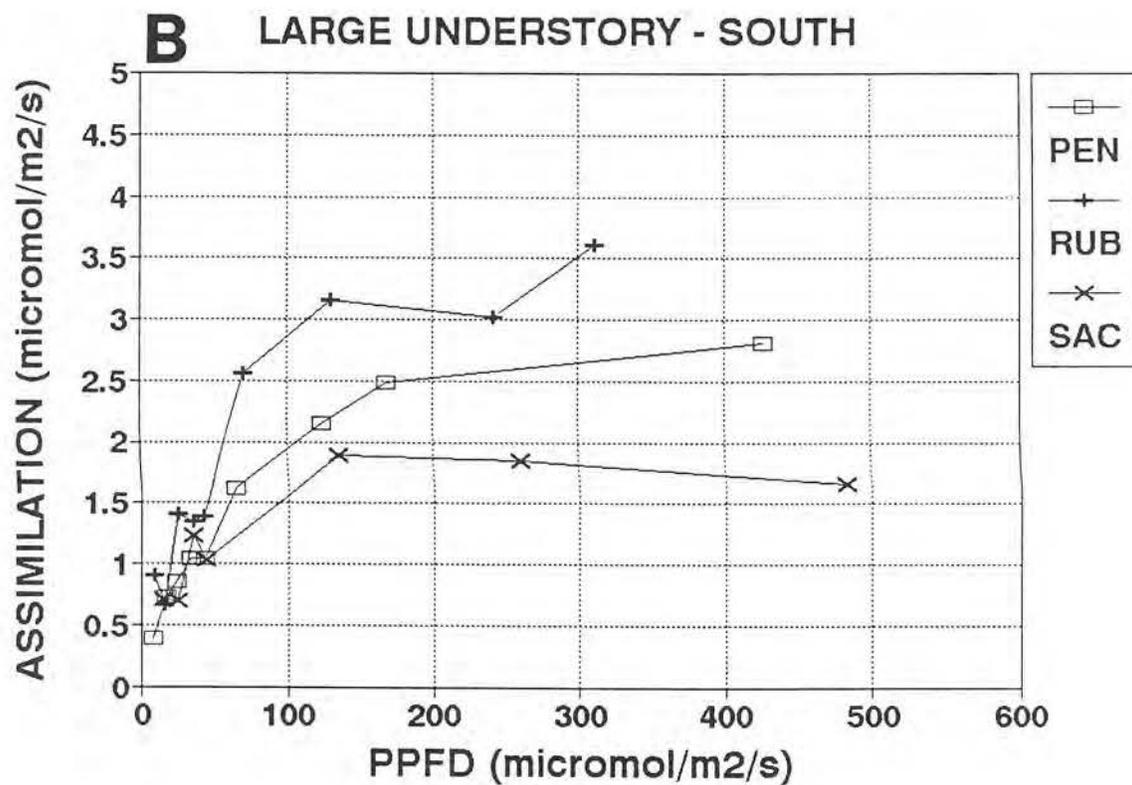
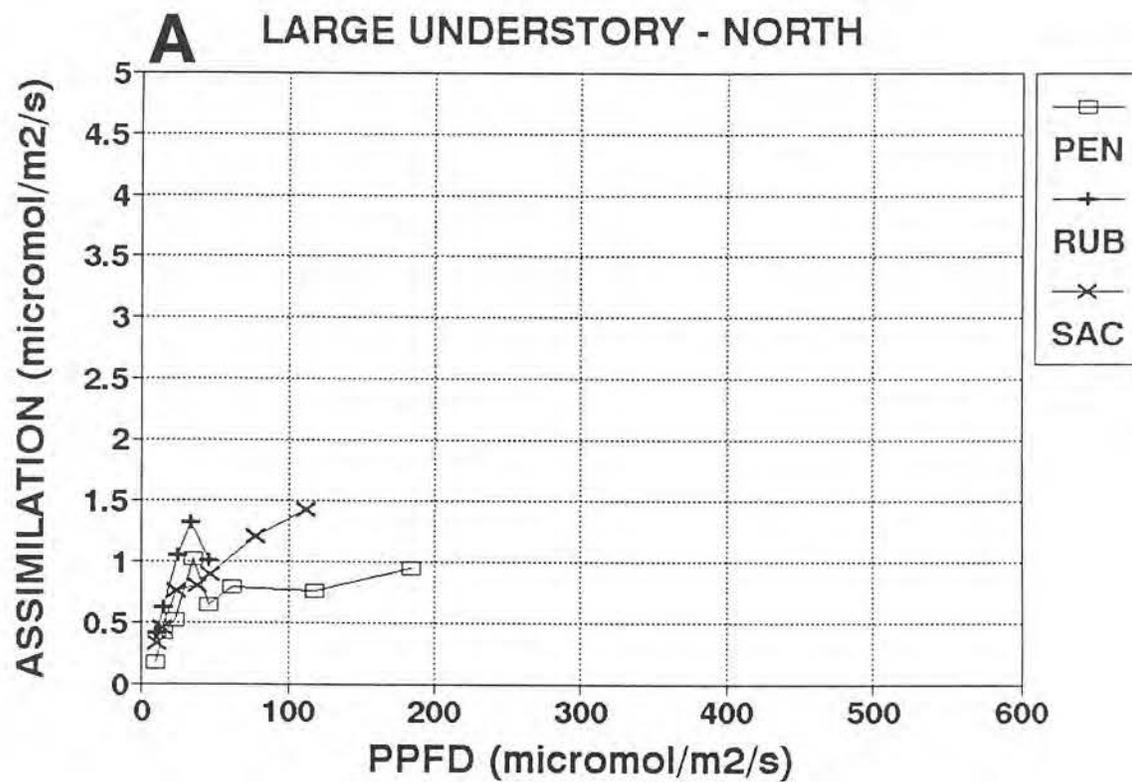
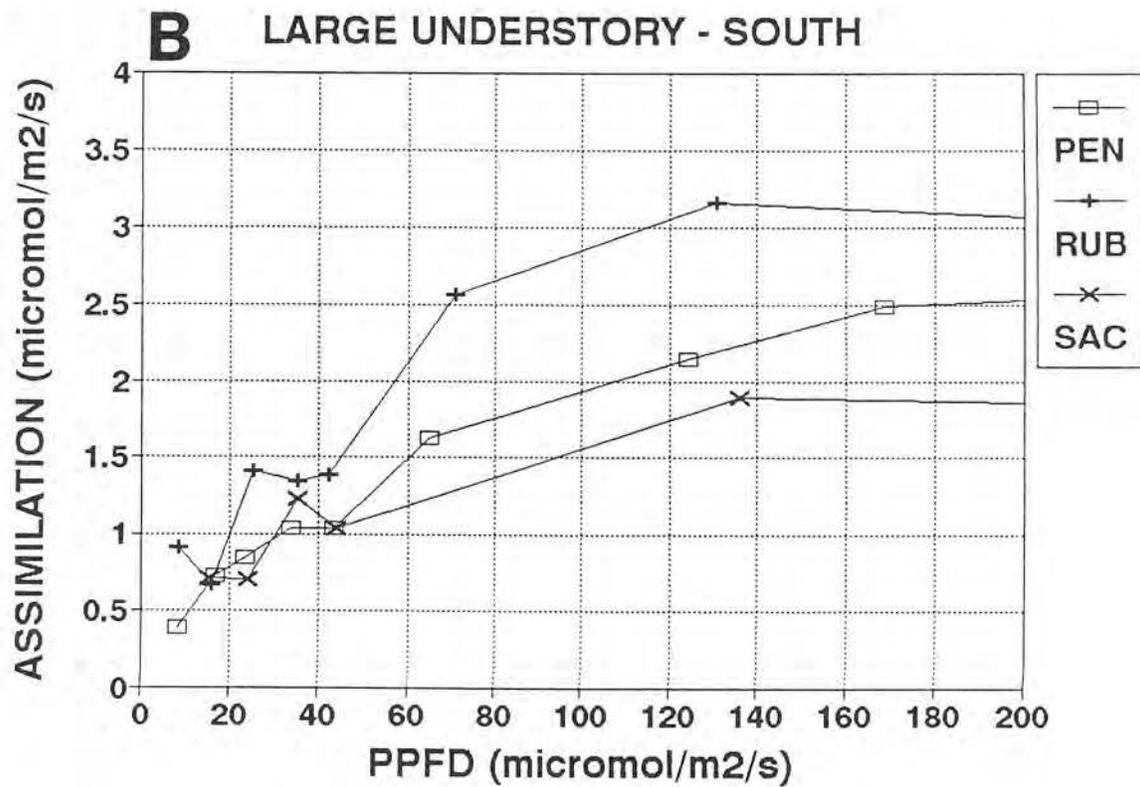
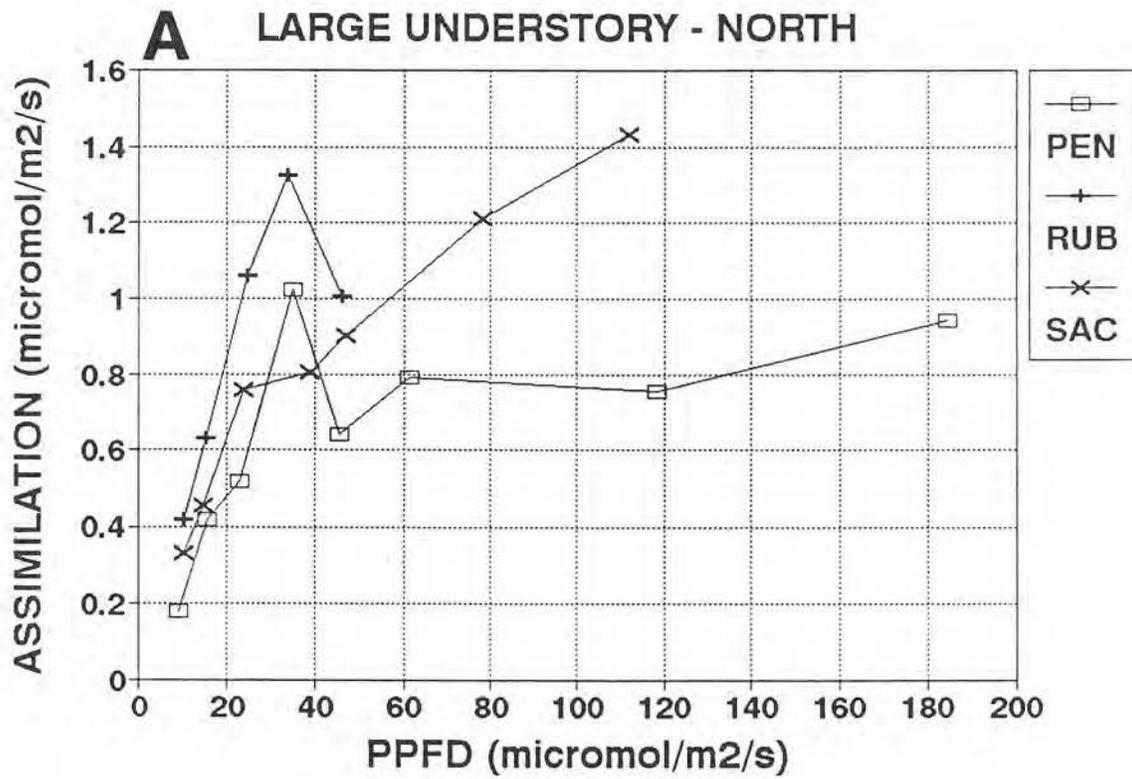


Figure 5-15. Enlargement of Figure 5-14 to clarify species relationships in the PPFD range of 0-200 micromol/m²/s.



is true for striped maple as well.

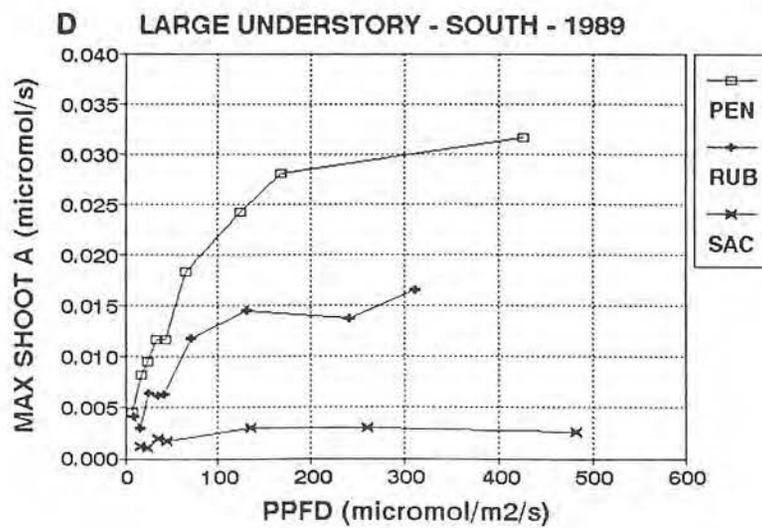
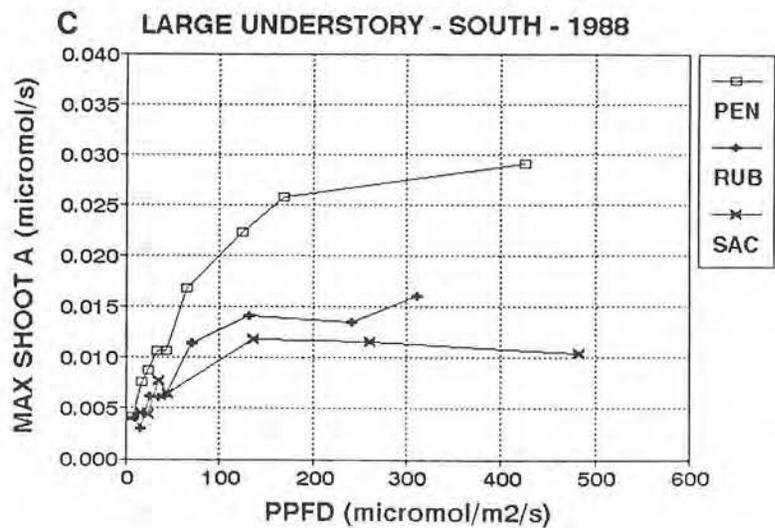
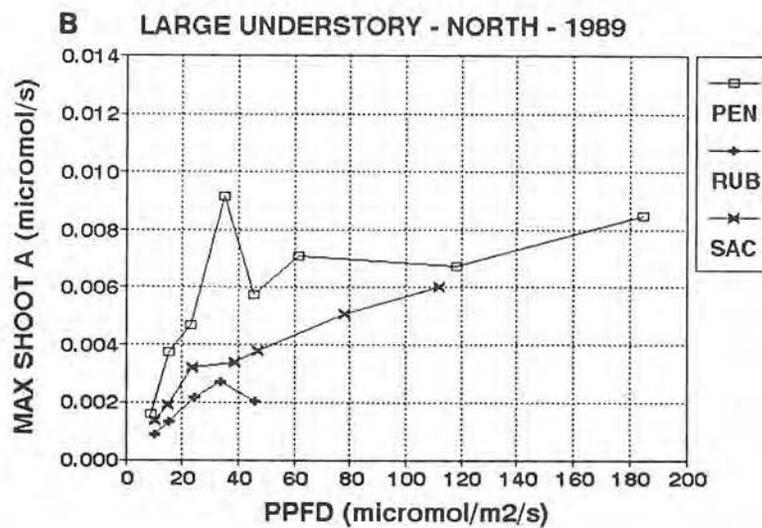
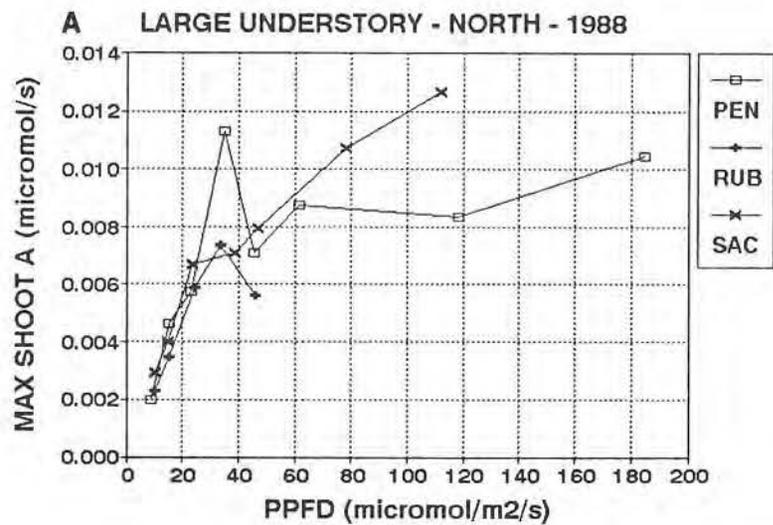
As with the large and small gaps, the shoot-level data showed trends not clear in the leaf-level curves (Figure 5-16). The north plot was not much different from leaf-level data in 1988, but the south plot showed a reversal of striped and red maples, so that $PEN > RUB > SAC$ for all PPFD levels above $50 \text{ micromol/m}^2/\text{s}$. By 1989, the pattern in the north plot was clearer, with $PEN > SAC > RUB$ for all sampled PPFD levels, and $PEN > RUB > SAC$ across the entire PPFD range in the south. The relative differences among species were much greater in the south plot than in the north (note y-axis scale differences). Also, it should be noted that all species showed reductions in the north plot from 1988 to 1989, even though the separation among species became clearer. The 1988-89 changes in the south plot were due to a slight increase by striped maple, no change by red maple, and a decline by sugar maple.

5.5. DISCUSSION

The following discussion is divided into three components: (1) a brief synopsis of the results presented in this chapter; (2) comparisons to published data on gas-exchange performance by the three study species; and (3) a broader consideration of the role of photosynthetic behavior in contributing to differential success by co-occurring tree species in response to disturbance in various temperate and tropical forest systems. For both (2) and (3), the focus is on performance in gap versus understory conditions, especially in the field but also including controlled-environment experiments that simulate forest conditions.

The diurnal patterns of photosynthesis by these species, and their population-level light curves, differed significantly within and between

Figure 5-16. Population-level light response curves (estimated maximum shoot assimilation versus PPFD in 1988 and 1989) for the three study species on the north and south sides of large understories. (A) North - 1988, (B) North -1989, (C) South - 1988, (D) South - 1989. Note differences in scale on both the X-axis and Y-axis.



gap and understory sites. In both cases, estimated shoot-level assimilation (particularly in 1989) differentiated species more than unit area assimilation rates, and in fact led to reversed conclusions on species success across the gap-understory gradient. Red maple surprisingly showed higher diurnal leaf area rates than striped and sugar maple in all site/plot combinations except the large gap SE, where striped maple exceeded red maple. Based on shade-tolerance categories, red maple would not have been expected to surpass sugar and striped maple in the understory. Population-level assimilation versus PPF response curves exhibited a similar pattern, with red maple dominating in all site/plots except large gap south, where $PEN > RUB$, and small gap north, where $RUB \sim PEN$. In contrast, when scaled to the shoot level in 1989, the rank order among species for both diurnal and light curve comparisons was $PEN > RUB > SAC$ in all site/plots except the large gap north, where $RUB > PEN > SAC$. Thus shoot-level estimates differed sharply with unit area measurements, and as will be discussed in Section 6.1., shoot-level assimilation patterns were strongly correlated with patterns of survival and growth.

Sugar maple photosynthesized at both leaf and shoot levels at rates lower than the other species, even in the understory. While its inferior performance in gaps may have been expected, it is not clear why it should perform so poorly in the understory as well, unless the possibility of limitation by soil nutrient status discussed in Section 4.6. is indeed accurate. Photosynthetic performance 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). It is possible that sugar maple is

affected more than the other species by suboptimal soil fertility on the study site.

It was clear from the presentation of growth results that the center plots of large gaps produced the greatest mean and individual growth rates by all species. Unfortunately, few measurements of gas-exchange were done in these plots, and thus the photosynthetic correlates of the enhanced growth are not available. Since architectural proliferation was intimately involved with the growth patterns, it would stand to reason that the large leaf numbers and leaf areas of both intact and recovering seedlings yielded even higher estimated shoot assimilation rates than those presented above for all other sites and plots along the gap-understory gradient.

It is important to recall that the photosynthesis results were derived from and apply mostly to undamaged, architecturally simpler seedlings of all species, since field sampling and shoot-level scaling factors were based on such plants. Hence the effects of rapid increase in leaf number and area on damaged and branched plants, and the variable chronological and physiological ages of leaves on fast-growing seedlings, were not included in the species comparisons.

Finally, the use of population-level light response curves is a new technique which captures species photosynthetic comparisons at biological (i.e., population) and temporal scales (across entire seasons) relevant to survival and growth not easily measured in any other way. The only reference to using repeated samples of assimilation to construct light response curves from field data is Weber et al. (1985). But in this case, the data points were taken in steady-state cuvettes held on a few seedlings for extended periods of time in the

understory. Thus they do not represent the microsite and population-level (genotypic/phenotypic) variation spanned here.

A number of published studies exist on gas-exchange behavior by the study species. But with the exception of Jurik et al. (1985), there are no published data in which more than one of the species was used. This limits species comparisons to cross-study measurements, involving the problems of variable growing conditions and measurement methods. Furthermore, the only reference for striped maple is the Jurik et al. study. Nonetheless, available data will be compared to the present study sequentially for red and sugar maple, and this part of the discussion will conclude with the Jurik et al. (1985) data.

Loach (1967) compared red maple to several other temperate tree species of varying shade tolerance grown under two different irradiance levels, reporting that red maple saturated at higher irradiances when grown at 100% full sun as opposed to in 17% full sun. This is consistent with the saturation irradiances reported here, although red maple expressed its highest saturation rates not in 100% full sun or even in the most exposed north and center plots of large gaps, but in the north plots of small gaps. Loach also commented that respiration rates were important in distinguishing the species.

Woods and Turner (1971) studied stomatal response times to step increases and decreases in irradiance for red maple and three other hardwood associates of varying shade tolerance (*Fagus grandifolia*, *Quercus rubra*, and *Liriodendron tulipifera*, in order of declining tolerance). Red maple was intermediate between the most shade tolerant (*Fagus*) and the least shade tolerant (*Liriodendron*) in speed of stomatal response. The suggestion by the authors was that such differences may

contribute greatly to the efficiency with which sunflecks are utilized.

Wallace and Dunn (1980) provide the data for red maple most relevant to the present research. They compared naturally-established 4- to 7-year old small saplings of red maple, *Liriodendron tulipifera*, and *Cornus florida* in understory and clearcut sites, as well as in a potted seedling glasshouse experiment involving switching from low to high irradiance to simulate gap release. The saturation assimilation rates and irradiances for the forest saplings were somewhat lower than those reported here: 1.9 micromol C/m²/s at PPFD = 37 micromol/m²/s in the understory, and 2.5 micromol C/m²/s at PPFD = 44 micromol/m²/s in the clearcut. Significantly, red maple showed no change in temperature optimum (~18°C) for photosynthesis in the understory versus the clearcut. Though there was modest physiological acclimation to high light irradiances following switching, especially in maximum assimilation rates, the authors emphasized that most of the acclimation was due to architectural adjustment, including more branches and steeper leaf angles off horizontal. Their conclusion was that red maple was well suited to growth in either understory or gap environments, largely because of this architectural plasticity.

Many more published studies exist for sugar maple than red maple. Logan and Krotkov (1968) studied growth and photosynthesis under four experimental garden irradiances (13, 25, 45, and 100% full sun). They concluded that morphological and physiological patterns showed opposing trends. Sugar maple's unit area photosynthetic rates declined with irradiance increases to 100%, but the production of more leaves and a greater shoot leaf area resulted in the highest shoot assimilation rates in full sun (100%). In fact, end-of-season biomass estimates were

correlated with estimated shoot assimilation, but not leaf area rates, when measured under saturating irradiances. This latter correlation was observed for all species in the present study.

In a series of studies of responses to fluctuating conditions, Wuenschel and Kozlowski (1970, 1971a, 1971b) demonstrated that sugar maple stomatal behavior differed from co-occurring oak species (*Quercus*) in ways that led to the lowest water use efficiencies in nearly all light and temperature levels. This was confirmed by Davies and Kozlowski (1972, 1974, 1977), Kozlowski et al. (1974), and Pereira and Kozlowski (1977), who showed that sugar maple transpired less than three hardwood associates of lesser shade tolerance, in part due to much greater cuticular resistance. Geis et al. (1971) found the same result in measurements of gas-exchange by sugar maple and several oaks in the understory and a medium-sized canopy gap (~400m²) in Illinois. Sugar maple surpassed the other species in diurnal carbon assimilation in the understory, but due to stomatal closure at lower temperatures and PPF levels during gap exposure, its assimilation and consequently its water use efficiency were lower than that of bur oak (*Quercus macrocarpa*) in gaps. Hinckley et al. (1978a) found similar relationships for sugar maple versus several oak species in Missouri, when the water relations and gas-exchange of saplings were studied in the field before and during natural short-term drought.

The consensus from these field and glasshouse studies is that sugar maple is a drought-avoider, closing stomates quickly beyond relatively narrow ranges of optimal irradiance, temperature, and possibly relative humidity. The result of drought avoidance is reduced carbon assimilation, and under certain environments, including forest gaps,

(Geis et al. 1971), lower assimilation and water use efficiencies than competing species. This behavior was observed by sugar maple in both large and small gap north plots during field sampling in this research, where it typically closed stomates sooner than the other species after direct beam irradiance began in the morning and maintained the lowest conductances of the three species throughout clear days.

Saturation rates and irradiances and temperature optima were reported by several authors for sugar maple, and the results are in closer agreement to the population-level light curve characteristics presented in this research than for red maple. In general, sugar maple light saturates anywhere from 150-600 micromol/m²/s at assimilation rates of 2.8-5.0 micromol C/m²/s, while optimal leaf temperature ranges from 20-26°C (Hinckley et al. 1978a; Ledig and Korbobo 1983; Loach 1967; Logan and Krotkov 1968; Weber et al. 1985; Jurik et al. 1985).

Weber et al. (1985) generated one of the most interesting and comprehensive data sets of integrated field and laboratory gas-exchange measurements for any eastern deciduous species, using sugar maple seedlings in the age (10 years) and size range (40cm tall) employed here. Their analysis of seedling response to understory environments in Michigan showed that sugar maple captured enough net carbon on a seasonal basis such that only 30% was needed to maintain the current crop of leaves and store enough carbon for the following year's leaves, leaving 70% for stem and root maintenance, growth, and storage. Their data question the common assumption that suppressed understory seedlings, even those of shade tolerant species, operate near photosynthetic compensation much of the time. In contrast to other studies on the photosynthetic importance of sunflecks, Weber et al.

(1985) calculated that sunflecks only accounted for a maximum of 12% of total seasonal carbon gain. They concluded that 60% of the carbon gain takes place when PPFD levels are below 50 micromol/m²/s.

Finally, Jurik et al. (1985) conducted a large study of photosynthetic behavior in the field by several tree species in the northern hardwoods forests of Michigan. As noted earlier, this is the only study containing data on all three maple species. Differences among the species in understory saturation rates (PEN = 3.07, RUB = 4.43, and SAC = 3.90 micromol/m²/s) were not as great relatively as differences in dark respiration (PEN = -0.10, RUB = -0.22, and SAC = -0.14 micromol/m²/s). The PPFD levels required to reach 90% of saturation, a measure of the steepness of the initial slope of assimilation versus PPFD, differed little (PEN = 100, RUB = 120, and SAC 155 micromol/m²/s), but in a relative pattern that corresponded to maximum assimilation rates. These saturation rates and irradiances are consistent with the understory values reported in this research, except that sugar maple performed relatively better in Michigan. The temperature optima for photosynthesis was the same for red and sugar maple in the understory (20°C).

This summary of photosynthesis in the experiment gap project, and the comparisons to published data for the study species, may now be set in the broader context. The relationships between photosynthetic behavior and ecological performance in response to intact and disturbed forest environments have been explored in many systems over the last decade, though most of the work has occurred in tropical rainforests. Three themes have dominated this work:

- (1) the degree to which apparent successional roles and/or gap

size preferences of species exhibit the classic differences in sun versus shade photosynthetic syndromes (Boardmann 1977; Bazzaz 1979; Bjorkman 1981; Fetcher et al. 1983; Oberbauer and Strain 1984; Read and Hill 1985; Thompson et al. 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) differs among apparent generalists versus large-gap or small-gap specialists (Bazzaz and Carlson 1982; Bazzaz and Pickett 1980; Chazdon and Field 1987; Walters and Field 1987; Pearcy 1987; Langenheim et al. 1984; Field 1988; Osmond and Chow 1988; Thompson et al. 1988; Fetcher et al. 1983; Doley et al. 1988); and

(3) the importance of shoot-level and whole-plant assessments of performance in distinguishing species (Field 1988; Givnish 1988; Mooney and Chiariello 1984).

A fourth, more recently emphasized, theme is the degree to which fluctuating light environments produce theoretical and empirical values of carbon assimilation different from steady-state results, and the role this may play in different forest environments, particularly understories (Gross 1982; Chazdon and Pearcy 1986a,b; Chazdon 1988; Pearcy 1988). These and related studies have produced variable results, particularly on acclimation potential. As a whole, they indicate the turbidity of our understanding of the linkages between physiological behavior and ecological performance among co-occurring tree species in complex forest environments.

With respect to the present research, the authors of these studies concur in the importance of plant response to fluctuating environments

characteristic of closed forests in general and canopy gaps in particular. They also emphasize the importance of whole-plant response, especially the interactions among physiological and architectural flexibility. The three maples in this study exhibited different degrees of both types of acclimation, with architectural behaviors producing the most striking divergences. The effects of leaf number and area on estimated shoot assimilation were particularly important, reversing the rank order of assimilation across sites based on leaf area rates alone.

The degree to which differences in photosynthetic performance were responsible for survival and growth patterns along the gap-understory gradient is difficult to determine, given the many other physiological processes and biotic interactions that influence the fates of trees. Field (1988) has succinctly expressed the situation: "Photosynthetic characteristics are several steps removed from ecological success." Nonetheless, net carbon assimilation at the shoot level provides the energetic input necessary for all plant metabolism, and no doubt contributed greatly to the differences in growth observed among the three maple species in this research.

CHAPTER 6

SYNTHESIS: GAP PARTITIONING IN *ACER*

The discussions in the previous sections answered the first three of the six questions posed at the outset of this study. The microclimatic nature of the gap-understory gradient (Question #1), the patterns of survival, growth and architecture (Question #2), and photosynthetic performance (Question #3) have all been presented and compared to published research. As mentioned in the Introduction (Section 1.5.), the gap partitioning hypothesis involves predictable relationships among these three components if the null hypothesis of no partitioning is to be rejected. Section 6.1. will make those connections (Questions #4). Then Section 6.2. will present the conclusion on gap partitioning (Question #5) and discuss its generalizability. Finally, Section 6.3. will discuss the implications of the presence or absence of partitioning for community diversity and predicting forest regeneration (Question #6).

6.1. CONNECTIONS AMONG MICROMETEOROLOGICAL GRADIENTS, SEEDLING SURVIVAL AND GROWTH, AND PHOTOSYNTHESIS

6.1.1. MICROMETEOROLOGICAL GRADIENTS VERSUS SURVIVAL AND GROWTH

The data presented in Sections 3 and 4 clearly illustrated that a micrometeorological gradient exists across understory and gap sizes created here, and that species differed significantly in survival and growth across the gradient. What remains is the connection between the two patterns. Rather than present the gradient qualitatively (i.e., site/plot ranks for micrometeorological and species response variables),

Figures 6-1 through 6-6 express the gradient quantitatively by plotting several survival and growth variables against the mean PPF and temperature values for all site/plot positions. Species can thus be compared directly across several independent variables specific to site/plot positions.

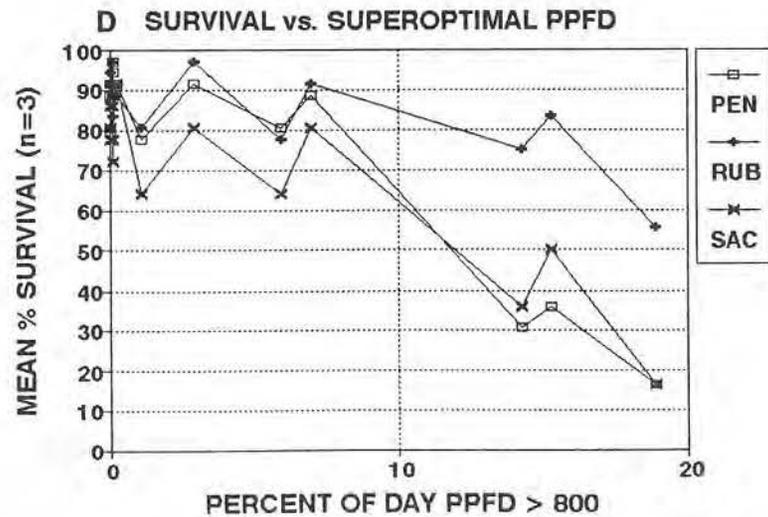
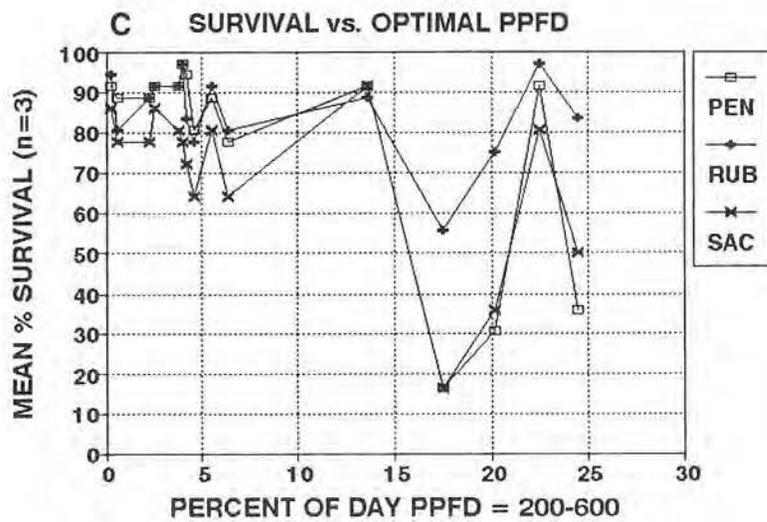
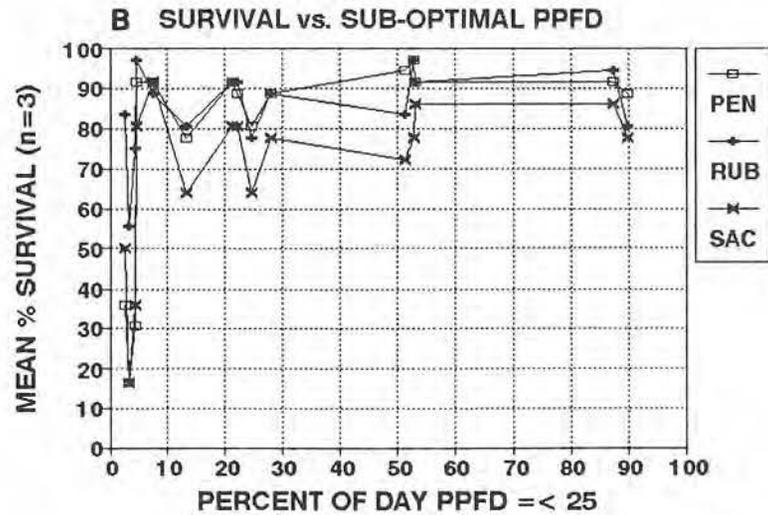
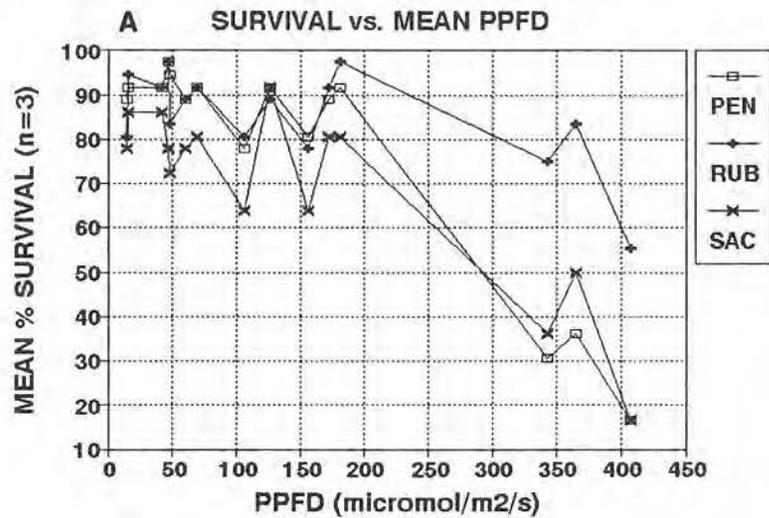
As discussed in Section 3, the gap-understory physical gradient is driven by incoming radiation, and the rank order of sites and plots based on declining mean values and diurnal ranges of irradiance and temperature on combined days across the season was given as:

$$\begin{aligned} \text{LGNW} \sim \text{LGNE} \sim \text{LGC} > \text{SGNW} \sim \text{SGNE} > \text{LGSW} \sim \text{LGSE} > \text{SGC} > \text{SGSW} \sim \\ \text{SGSE} > \text{LUC} \sim \text{LUSE} \sim \text{SUSW} > \text{LUNE} \sim \text{LUNW}. \end{aligned}$$

This pattern was based on the biweekly sampling in the large gap, small gap, and large understory of Block 1. Variations in replicate gap geometry and the canopy structure over understory plots would change this order slightly. For example, small gaps narrower in the N-S dimension would place the north plots lower in the overall ranking, and many understory sites would not show variation as great as that between the north and south plots in the Block 1 large understory. Nonetheless, micrometeorological sampling done in replicates of each gap size and understory site confirmed the broad pattern described in Section 3 and listed here. Site and plot positions are not labeled on the data points in Figures 6-1 through 6-6 to avoid unnecessary clutter. With few exceptions, the order on the abscissas corresponds to the ranking above.

Figure 6-1 plots overall survival by the three species as functions of four combined day PPF variables. Both mean PPF (Figure 6-1a) and superoptimal PPF (Figure 6-1d) show significant declines in survival for the three most exposed plots, the large gap C, NE, and NW. But

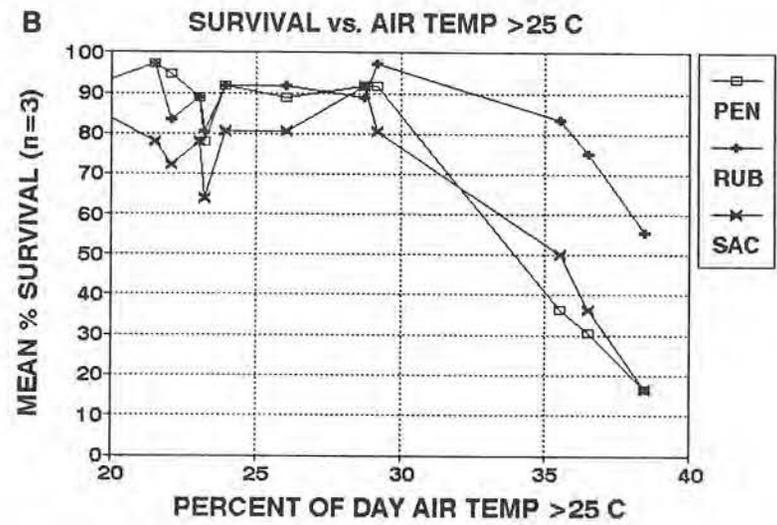
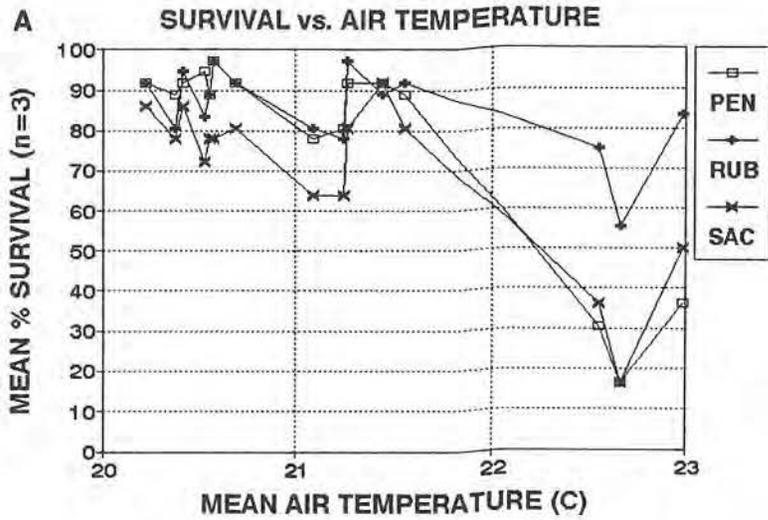
Figure 6-1. Species survival versus PPFD (combined clear plus overcast days) across all large gap, small gap, and large understory plot positions (n=15). (A) Survival versus mean daily PPFD, (B) Survival versus percentage of day with PPFD ≤ 25 micromol/m²/s, (C) Survival versus percentage of day with PPFD = 200-600, (D) Survival versus percentage of day with PPFD > 800 .



survival shows no consistent trend for any species at all PPFD levels below these three plots. Surprisingly, survival by all species is not reduced when suboptimal PPFD frequency rises as high as 90% of the day (Figure 6-1b). In fact, there is no consistent trend across 10-90% of the day, and survival rates drop only when durations of suboptimal PPFD drop below 10%, reflecting the most exposed plots (large gap C, NW, NE). Survival shows the the greatest inconsistency across optimal PPFD durations (Figure 6-1c), suggesting that this PPFD range is least important in distinguishing species. The two major points to be derived from this figure are that (1) survival does not reflect the underlying continuity of the gap-understory gradient, since it is reduced substantially only at the extreme exposure end, and (2) the species show nearly parallel responses and the same rank order (RUB => PEN => SAC) in all site/plot positions.

Survival responses to temperature variables are shown in Figure 6-2. In broad terms, the pattern is analogous to that for PPFD variables, in that only the 3-4 most exposed plots in large gaps with higher mean temperatures or durations of high temperatures elicit markedly lower survival. Survival declines in general, though not monotonically, when mean daily air temperature exceeds 21.5°C (Figure 6-2a). These higher means are correlated with air temperature durations above 25°C, but the trend is even clearer, with a monotonic decline when durations rise above 30% of the day. Surface soil temperatures are not related to survival until they exceed 21°C on average, but the reductions in survival after this point are not consistent (Figure 6-2c). Finally, the threshold above which survival drops is lower in absolute terms for deep soil temperature (17.5°C), since this point in

Figure 6-2. Species survival versus temperature profile (combined clear plus overcast days) across large gap, small gap, and large understory plot positions. (A) Survival versus mean daily air temperature, (B) Survival versus percentage of day air temperature exceeds 25°C, (C) Survival versus mean daily soil surface temperature (1cm), (D) Survival versus mean daily deep soil temperature (15cm).



the profile averages lower values (Figure 6-2d). Due to the tight, though temporally asynchronized, relationship between surface and deep temperatures, the 4 plots in the reduced survival region show parallel trends. But the variations are played out over a greater absolute range for the deep (17.3-20.5° range) as opposed to surface (21.2-22.7° range) temperatures.

The remaining four figures plot 1987-89 total leader extension (Figure 6-3), 1987-89 total shoot extension (Figure 6-4), 1987-89 cumulative height change (Figure 6-5) and 1987-89 cumulative basal diameter change (Figure 6-6) against the four PPF variables used in Figure 6-1. Although there are numerous differences among the patterns for these variables, several common themes emerge. First, the three species are well separated across most of the independent variable ranges in all scatterplots. Second, these differences are maintained with few crossovers, such that relative species trends across entire ranges are obvious. Third, the scales and overall visual separation among data points in both total extension and cumulative basal diameter plots are affected by the presence of an outlying point, which is identifiable as red maple in large gap centers. This contrasts with leader extension and cumulative height change, whose ordinates show narrower ranges and the differences among species across the abscissas are easier to determine.

Finally, the rank order among species is consistently PEN > RUB > SAC for leader extension and cumulative height change. The order applies for cumulative basal diameter change as well, except for large gap centers. Since total extension was highly correlated with branch growth due to dieback, and since red maple exhibited the greatest ability to

Figure 6-3. Leader extension (survivors only, 1987-89) versus PPFD (combined clear plus overcast days) across all large gap, small gap, and large understory plot positions (n=15). (A) Extension versus mean daily PPFD, (B) Extension versus percentage of day with PPFD ≤ 25 micromol/m²/s, (C) Extension versus percentage of day with PPFD = 200-600, (D) Extension versus percentage of day with PPFD > 800 .

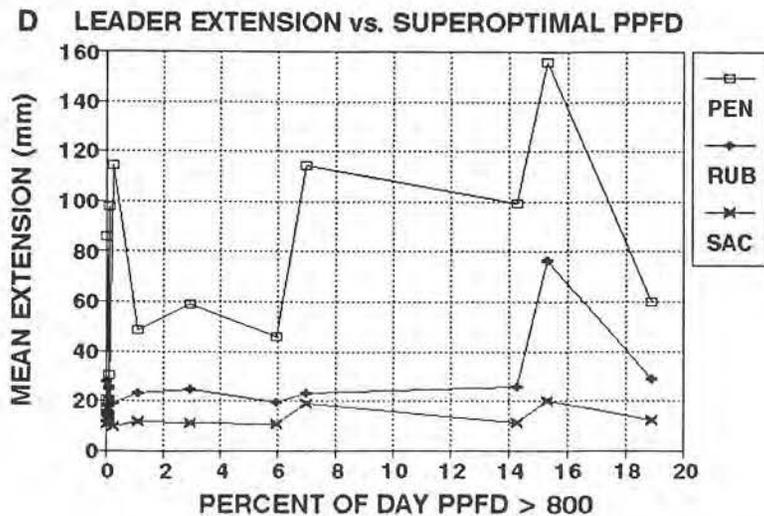
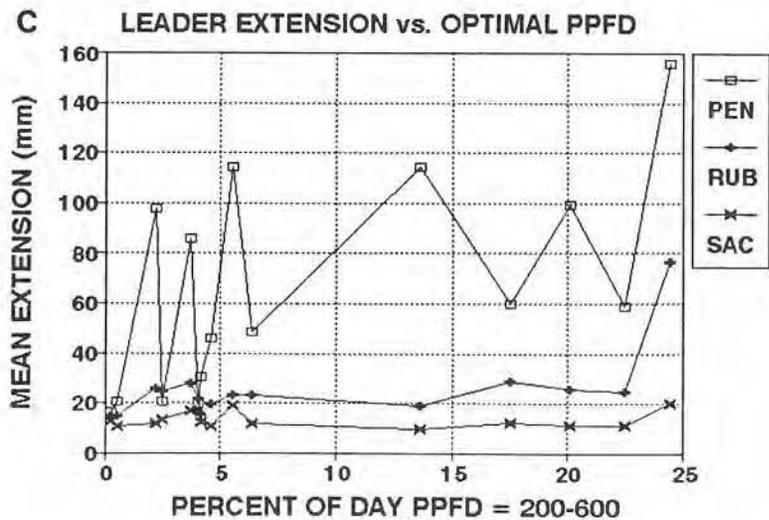
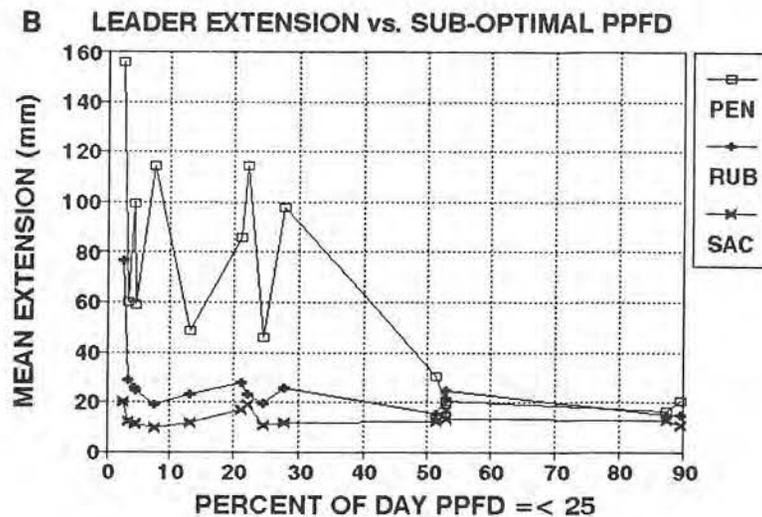
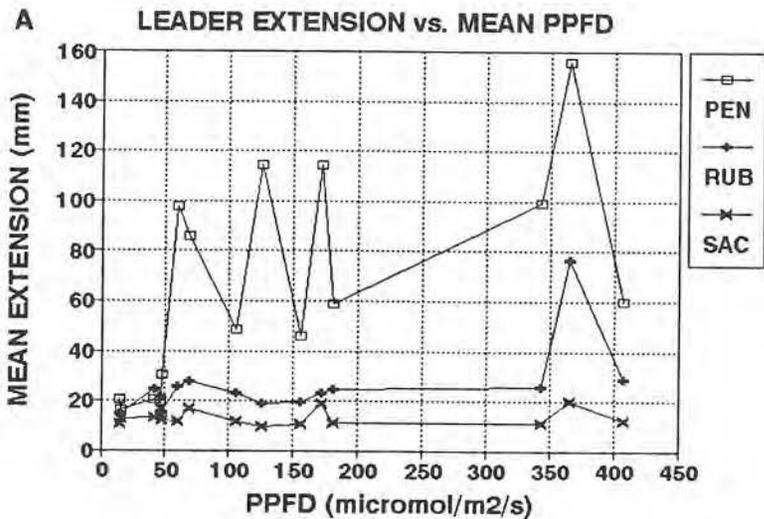


Figure 6-4. Total shoot extension (leader plus branches, survivors only, 1987-89) versus PPFD (combined clear plus overcast days) across all large gap, small gap, and large understory plot positions (n=15). (A) Extension versus mean daily PPFD, (B) Extension versus percentage of day with PPFD ≤ 25 micromol/m²/s, (C) Extension versus percentage of day with PPFD = 200-600, (D) Extension versus percentage of day with PPFD > 800 .

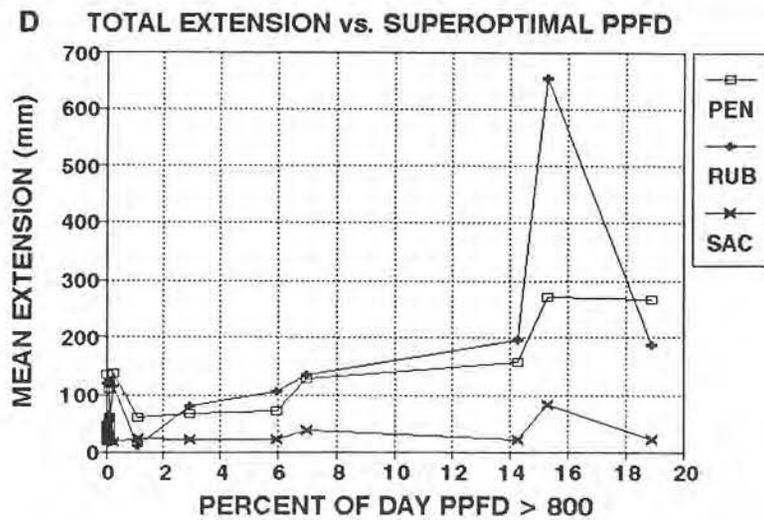
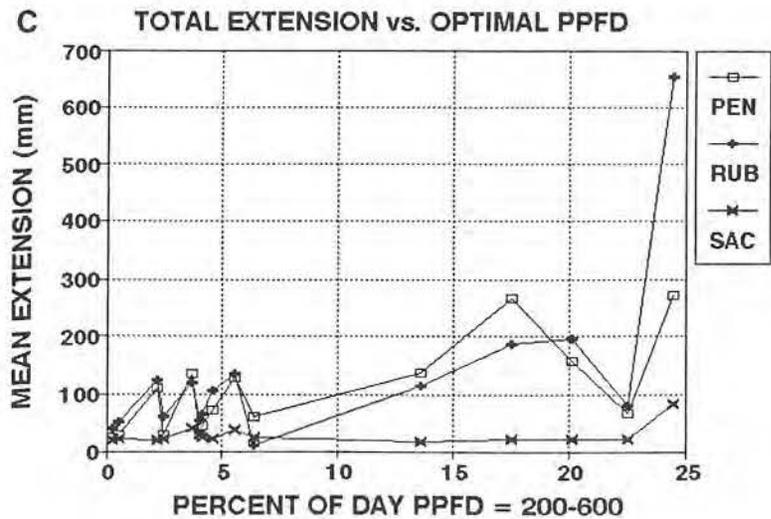
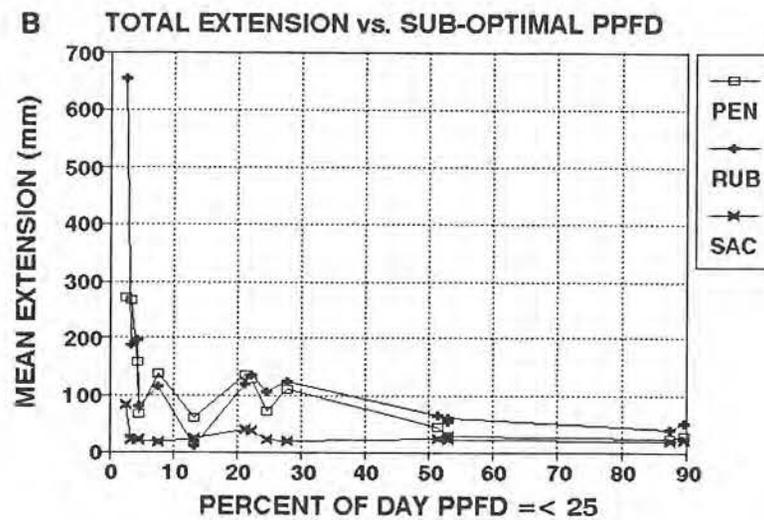
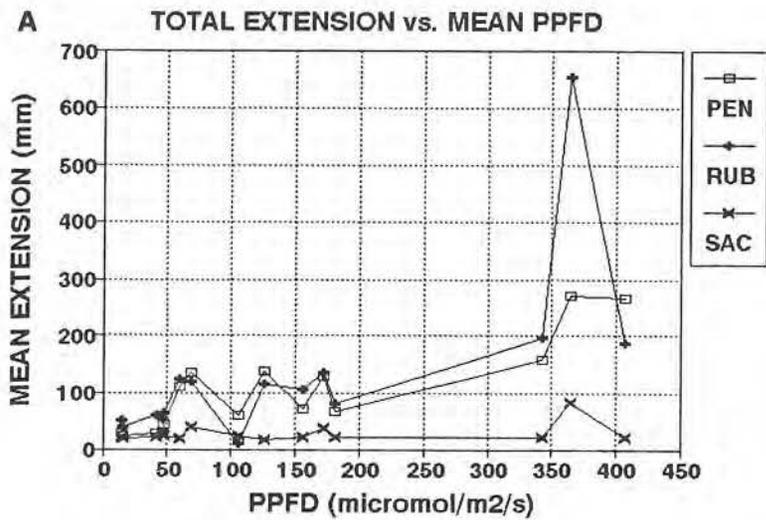


Figure 6-5. Cumulative seedling height change (survivors only, 1987-89) versus PPF_D (combined clear plus overcast days) across all large gap, small gap, and large understory plot positions (n=15). (A) Height change versus mean daily PPF_D, (B) Height change versus percentage of day with PPF_D < 25 micromol/m²/s, (C) Height change versus percentage of day with PPF_D = 200-600, (D) Height change versus percentage of day with PPF_D > 800.

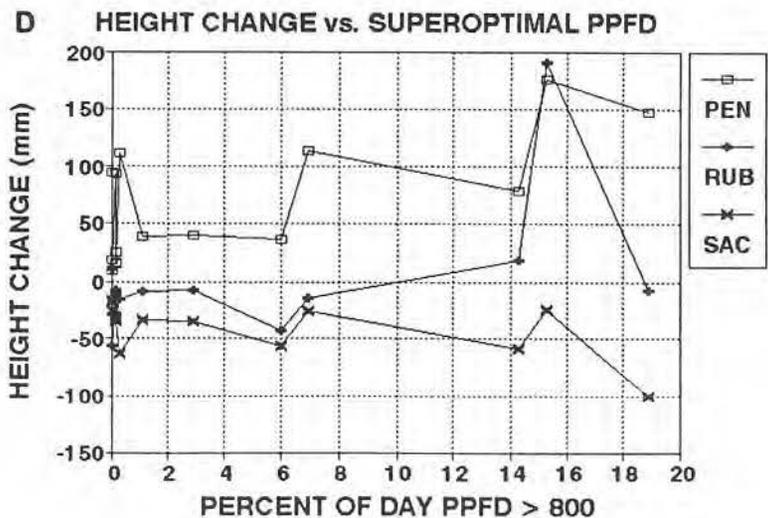
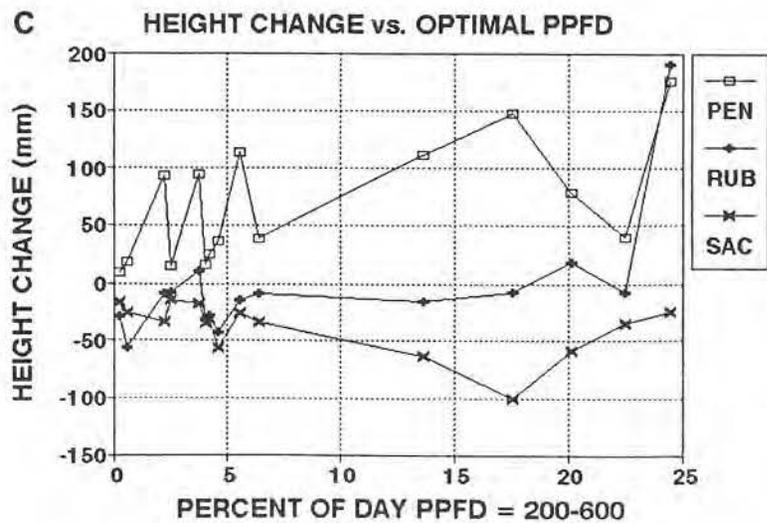
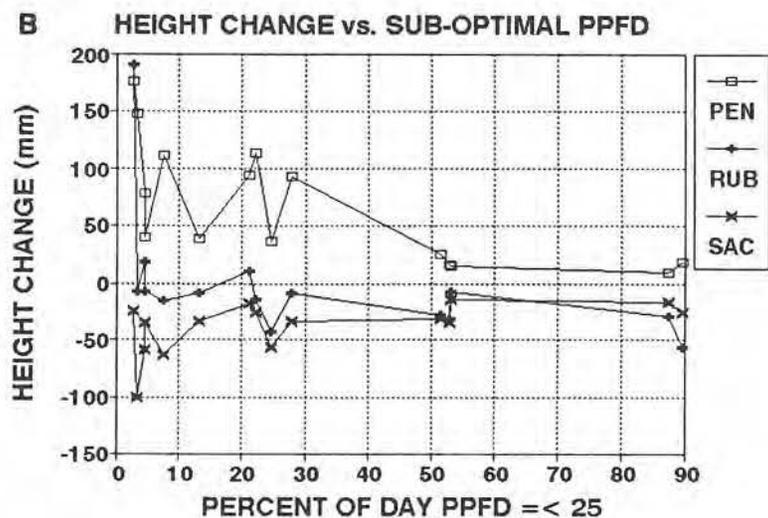
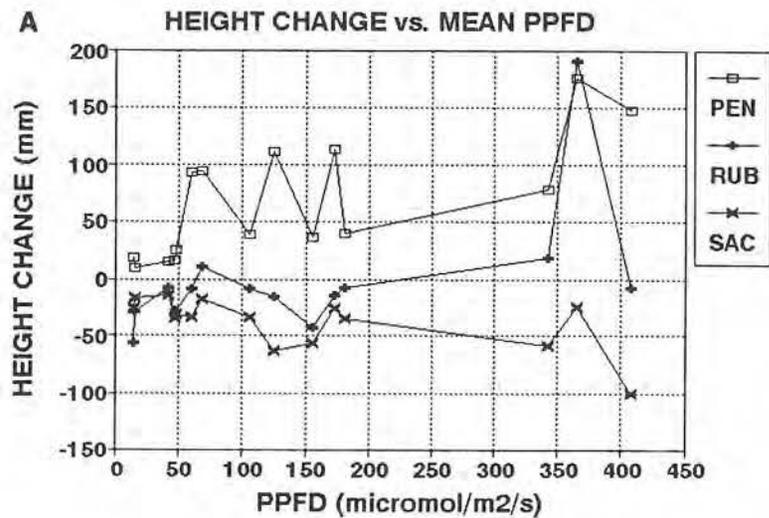
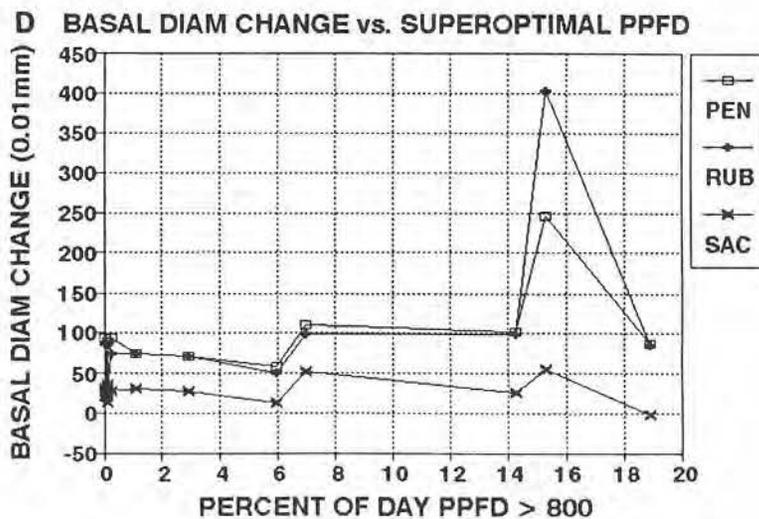
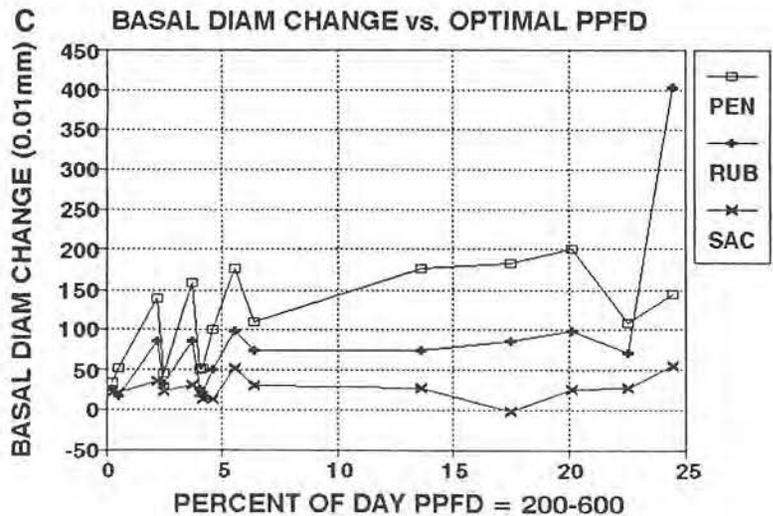
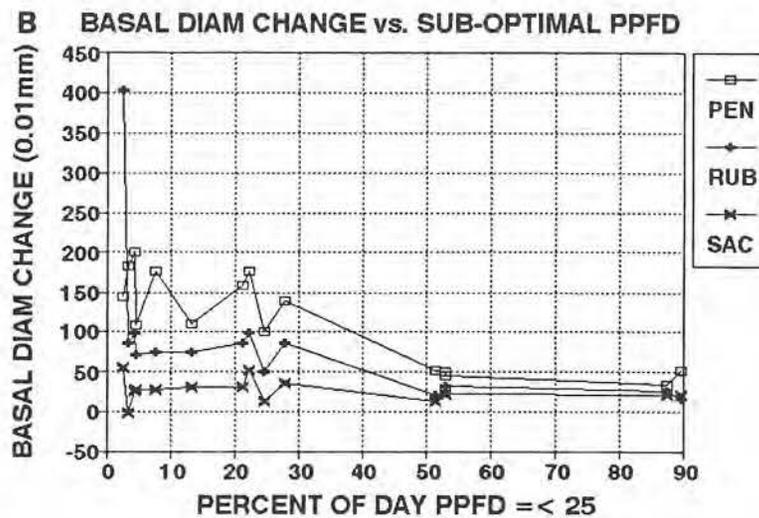
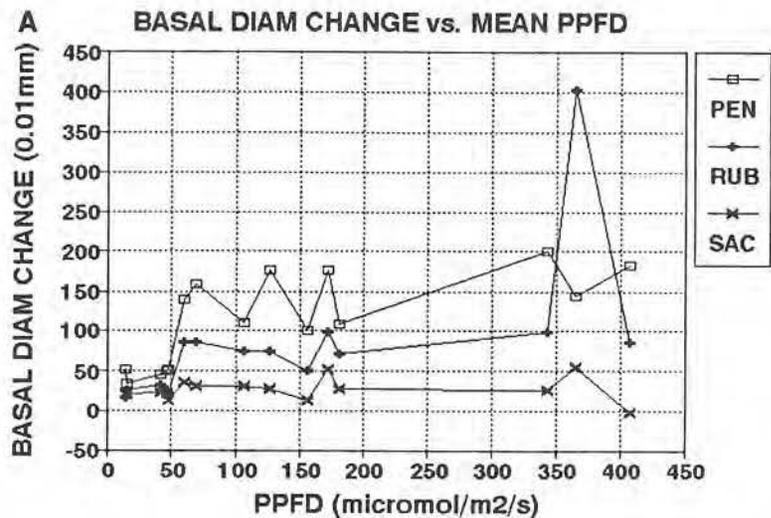


Figure 6-6. Cumulative basal diameter change (survivors only, 1987-89) versus PPFD (combined clear plus overcast days) across all large gap, small gap, and large understory plot positions (n=15). (A) Basal diameter change versus mean daily PPFD, (B) Basal diameter change versus percentage of day with PPFD ≤ 25 micromol/m²/s, (C) Basal diameter change versus percentage of day with PPFD = 200-600, (D) Basal diameter change versus percentage of day with PPFD > 800 .



recover from leader loss (Section 4.5.), the graphs for total extension (Figure 6-4) show that RUB => PEN > SAC across most of the PPF gradient. These statements provide direct evidence that gap partitioning does not occur.

Of the three species, striped maple shows the greatest variability at low to middle PPF ranges (e.g., 50-200 micromol/m²/s in Figure 6-3a). Sugar maple shows the least variation, almost negligible in many cases.

Specific points from each of the graphs are as follows. Leader extension by striped maple shows greater variability in response to PPF levels because of its sensitivity to changes in irradiance (Wilson and Fischer 1977). The small gap plots and the south sides of large gaps apparently trigger the shoot developmental shift described by these authors. Red maple shows no change in leader response except for large gap centers. Figure 6-3 shows that the differences among the species are initiated and maintained at all mean irradiance levels above 50 micromol/m²/s, and that only site/plot positions with durations of suboptimal PPF above 50% of the day cause the species to converge. This represents the north plots of the large understory.

The cumulative height change plots (Figure 6-5) show some interesting features. Red maple and sugar maple show parallel, variable trends up to mean PPF levels of 200 micromol/m²/s. Striped maple is variable and independent of these species to the same point. Above 200 micromol/m²/s, red maple achieves positive growth while sugar maple shows even greater height losses (Figure 6-5a). The species show the most divergent behaviors in the 6-17% range for duration of optimal PPF (Figure 6-5c), where red maple shows little change at about -10mm,

striped maple rises linearly from ~45mm to ~150mm, and sugar maple declines from -30mm to -100mm. But overall, the highest PPF levels elicit the greatest differences among species.

Basal diameter change versus mean PPF (Figure 6-6a) shows three zones of species differences. For 0-50 micromol/m²/s (understory north plots), the species show uniformly low rates. From 50-175 micromol/m²/s, the species exhibit much greater separation and react similarly to changes in PPF. Then above 200 micromol/m²/s, they diverge into separate patterns, with red maple showing its outlying peak at ~365 micromol/m²/s while striped maple shows modest increases and sugar maple shows modest decreases.

In summary, the gap-understory gradient, as represented by PPF and temperature variables, is broad enough to elicit both survival and growth differences among species. However, all species survived well across most of the gradient, diverging only in the exposed plots (NW, NE, C) of large gaps. Growth variations occurred across all site/plot positions except the most shaded understory plots, and the patterns strongly suggest a PEN > RUB > SAC superiority throughout. These results are for all survivors in 1989. The same rank order applied uniformly across all growth variables for plants with intact leaders as opposed to leaderless plants (Section 4.5.), and the relative differences among the species were even greater. Thus the conclusion of no tradeoff among the species is even stronger for undamaged seedlings.

6.1.2. PHOTOSYNTHESIS VERSUS MICROMETEOROLOGICAL GRADIENTS

The photosynthetic patterns presented in Section 5 were limited to the north and south plots of the large gap, small gap, and understory.

The diurnal traces and population-level light response curves supported each other in many ways in explaining species assimilation differences. This section will discuss species comparisons across the six site/plot positions for both diurnal and population light curves.

Although comparison across the NW and SE plots sites is not accurate in absolute terms, since the samples were taken on widely different days (6.25.88 versus 8.8.88), the relative ranks among species can be compared, giving a sense of performance along the gap-understory gradient. In unit area rate terms, red maple showed higher assimilation rates in all sites and plots except the large gap SE, where PEN => RUB. Striped maple finished second in the large gap NW and both small gap plots, while sugar maple was second in both understory plots. This rank order agrees only in part with the predicted order of site preference. The tradeoff between striped and sugar maples in the small gaps versus understory was expected, but red maple's nearly consistent higher rates than either of the other species, even in the understory, runs counter to shade-tolerance predictions.

In contrast, the shoot-level results were more in line with predictions, especially for 1989. Red maple dominated in the most exposed end of the understory gradient (large gap NW) and striped maple dominated in the less exposed large gap SE and small gap plots. Both species did as well or better than sugar maple in the understory plots, which was not predicted. Overall, the 1989 shoot-level assimilation data supported the results for survival and growth (Sections 4.2. and 4.3.) in broad terms, particularly for seedlings with intact leaders.

The population-level light curves showed similar patterns across the gradient. As a combined group, the species achieved their best

overall performance in the following site/plot order:

SGN > LGS > SGS > LUS > LGN > LUN.

It would appear that the three species were suppressed in understories overall, but particularly in the north plot, due to low irradiances. They were inhibited in the north plots of large gaps, probably due to the excessive irradiances that characterize these microsites, and the many physiological problems that such PPF levels induce. The less exposed south side of large gaps was more favorable than the south side of small gaps due to the generally higher diffuse irradiances and greater frequency of direct beam. The small gap south plots do receive slightly higher diffuse irradiances than the understory, and this may have accounted for its rank above the understory plots. Finally, the north sides of small gaps appeared to be the best environment overall, when all species are considered together.

There were differences in species preferences, however:

Striped: LGS > SGN > LUS ~ SGS > LGN > LUN

Red: SGN ~ SGS > LGS > LUS > LGN > LUN

Sugar: SGN > LUS > SGS > LUN > LGS > LGN

The notable species-specific deviations from the combined trend above are (1) the large gap south plot was preferred more by striped maple than the other species, and (2) sugar maple preferred the two understory plots, and did worse in both large gap plots, than red or striped maple.

The microsite preferences based on shoot-level assimilation in 1989 were somewhat different:

Striped: LGS > SGS > SGN > LUS > LUN > LGN

Red: SGS > SGN > LGN > LGS > LUS > LUN

Sugar: SGS > LUN > LGS > LUS > SGN > LGN

The contrasts with microsite preferences based on leaf-level data were that (1) the small gap south and north plots were reversed for all species, (2) the large gap north plot was not as detrimental for both striped and red maple, and (3) sugar maple showed a surprisingly high preference for the most shaded microsite, the large understory north.

It should be emphasized that these rankings are visual judgments based on Figures 5-11 through 5-16. There are no easy ways to compare complex curves objectively. The judgment was based on several factors, including saturation rates and sustained high assimilation, apparent compensation points, and net assimilation declines above inhibitory PPFD levels.

6.1.3. SURVIVAL AND GROWTH VERSUS PHOTOSYNTHESIS

While carbon assimilation is not the only important process affecting seedling success, it certainly showed close correspondences with patterns of survival and growth for these three species across the gap-understory gradient. This correspondence was greater for estimated shoot assimilation (particularly 1989) than unit leaf area rates. And the patterns were essentially the same for diurnal samples as for population-level light response curves.

The greater survival by red maple in the north plots of large gaps paralleled assimilation, in that such plots were the only case where red maple showed the highest shoot photosynthetic rates. No photosynthetic data were available for the large gap centers, but it is the author's opinion that this correspondence for red maple would have held in this plot position as well. In all other sites and plots positions (5), the significant differences among species in shoot assimilation (PEN > RUB >

SAC) did not yield significant differences in survival. Thus all species were able to sustain positive carbon balance at levels necessary to insure survival, regardless of growth success.

With respect to growth, two discussions are necessary due to the prevalence of dieback, branching, and resprouting. First, for all surviving seedlings in 1989 (intact plus leaderless), shoot assimilation differences among species were correlated with all 1987-89 growth variables, with the same rank order of PEN > RUB > SAC in nearly all sites and plots. The only exception was that red maple exhibited a greater cumulative basal diameter change than striped maple in large gap north plots. However striped maple showed greater leader extension and 1989 stem height and basal diameter than red maple, so the higher 1989 shoot assimilation by red maple did not give it the same edge in growth as it did in survival.

When branch growth (and thus total shoot extension) are considered, red maple showed greater values than striped or sugar maple in most sites and plots, running counter to shoot assimilation. However, as emphasized in Section 5, the shoot estimates do not apply to damaged seedlings with complex architectures, precisely those seedlings that gave red maple the branch and total extension superiority over striped and sugar maple. It is highly likely that measurements of leaf area rates and estimates of shoot assimilation on these seedlings would correlate with total growth.

It is in this context that the second discussion applies. The analysis of intact versus leaderless seedlings (Section 4.5) showed that the rank order among species was made more uniform and the relative differences larger for intact seedlings. Since the photosynthetic data

apply more precisely to such seedlings, the conclusion is that the correlation between assimilation and growth is even stronger for intact seedlings.

6.2. CONCLUSIONS ON GAP PARTITIONING

The conclusion on the existence of gap partitioning among maples has been presaged several times already. The clear answer to Question #5 is this: There is no partitioning among striped, red, and sugar maple across the microenvironmental gradient generated by the experimental creation of small- (75m^2) and medium-sized (300m^2) canopy gaps in the mixed deciduous forests of central New England. With the exception of the most exposed end of the gradient (large gap north plots) where red maple exhibited better survival, higher shoot assimilation, and greater basal diameter growth than the other species, the rank order across the entire gradient was STRIPED > RED > SUGAR in both shoot assimilation and all growth variables. Thus among these species striped maple is considered 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.

It is difficult to imagine how the patterns could have been more persuasive, and thus the conclusion on the gap partitioning hypothesis is considered to be solid, *under the conditions of this experiment*.

The italicized phrase in the last sentence is important. There are limits to the extrapolation of the results of this study to natural gap dynamics. Some of these were voiced in the discussions of gap creation, site treatment, and plot preparation in Sections 2.5 and 2.6. The basal cutting of healthy trees does not mimic the selective mortality induce

by natural disturbance agents. Natural gaps of the same actual canopy opening area differ greatly in shape and orientation, and thus the controlled gaps in this study is not completely representative of natural geometric variation in this size range. The removal of all felled biomass eliminated structural and microclimatic heterogeneity and any possibility of nutrient pulses due to the decomposition of increased litter levels. Cutting back regrowth maintained the exposed conditions longer than would occur in regenerating natural gaps, and suppressed the likely occurrence of competition between different size classes of advance regeneration and sprout regrowth. The seedling plot preparations eliminated most, if not all belowground competition, probably increased nutrient mineralization rates, and no doubt altered soil moisture conditions as well. The transplanted seedlings were of a limited age and size range compared to the breadth of advance regenerant status in uneven-aged forests. So the results may be different for other age/size classes. Finally, the data include just two years of gap release, and while the patterns at this stage are clear, it is uncertain whether or not current trends will continue.

For these reasons, the experimental gaps used here demonstrate more the potential for gap partitioning rather than the likely occurrence at precise positions in natural gaps of this size range. The key is to think of plot positions not in geometric and structural terms, but rather as points in the dynamic four-dimensional pattern of physical and chemical fluxes to which plants respond. Then any given plot exhibits a set of fluxes that could occur at many different structural locations according to gap geometry, heterogeneity in downed and regrowing biomass, and substrate variation. Indeed, this is why the gap

partitioning hypothesis is worded as "differential species success in different gap sizes or positions within gaps". This was the logic behind the growth versus micrometeorological gradient plots in Section 6.1.1. and it also underlies the emphasis on a process as opposed to state viewpoint discussed in Section 1.3. and in greater detail by Bazzaz and Sipe (1987) and O'Neill et al. (1986). Had this perspective been used more widely by forest ecologists, it would not have been necessary for Lieberman et al. (1989) to emphasize that forests are not "Swiss cheese" composed of clean canopy holes in a uniform matrix.

Under this perspective, the experimental gaps used here generate misleading interpretations only if the combinations of microenvironmental fluxes studied in the various plot positions do not include sets of fluxes under which the species would show relative performances widely variant from those actually measured. The inclusion of five plot positions in all sites made this unlikely, and while more plot positions on the N-S axis in large gaps would have been useful in refining the spatial patterns, the author's opinion is that the range of microenvironmental conditions was adequate to support the generality of the above conclusion. Furthermore the potted seedling simulated release experiment in natural gaps in Tom Swamp 1 supported the experimental gap conclusions very well (Section 4.6.), suggesting that the cleared gaps adequately captured enough microenvironmental variation to produce stable conclusions on gap partitioning among these species in the Harvard Forest area.

The results of the experimentally cleared gaps apply directly to silvicultural gaps, especially under single-tree and group selection harvest practices. Thus the predictions about the success of these three

maple species should apply to silvicultural management employing small cuts in comparable forests in central New England. And the microclimatic data should provide guidelines for many more species whose responses to light and temperature are known with sufficient accuracy.

The superior success of striped maple will come as no surprise to foresters, who have had to manage for the interference of this "weed" species in order to favor more commercially desirable species in harvest cuts from New England to the Appalachians and the Great Lake States (e.g., Horsley and Bjorkbom 1983). Of even greater concern perhaps will be the lack of sugar maple's response to either gap size. It is known not to respond as well to larger canopy openings, so the question remains as to how to favor its regeneration. Godman and Tubbs (1973) recommended that advance regenerants be at least 1m tall to yield high survival rates under two-step shelterwood cutting, so the smaller size classes used here may have been expected to show greater mortality. However, Marquis (1982) showed very high survival rates for red and sugar maple seedlings smaller than those used here when exposed to large clearcut conditions. It is likely that seedling-scale heterogeneity in downed and regrowing biomass is critical in the survival and growth of small advance-regenerated seedlings. Since this can vary enormously from one silvicultural cut to another, conflicting results are not surprising. In any event, it is probable that sugar maple regeneration will be difficult to achieve on the coarser, less fertile soils similar to those used in this study, particularly when there is heavy competition from other trees, shrubs, and herbs.

6.3. IMPLICATIONS FOR COMMUNITY DIVERSITY AND PREDICTING FOREST REGENERATION

The final question posed at the outset focuses on the significance of the presence or absence of gap partitioning for the maintenance of community diversity and success in predicting forest regeneration. Judging the effects on diversity under natural disturbance regimes is affected by the semi-artificialized nature of the experimental gaps. It appears that all three species are capable of survival under suppressed understory conditions, and that gap release is not critical for early seedling success. Post-release survival is high for all species in all but the most exposed conditions of the large gaps, and thus it is difficult to imagine natural gap conditions that would lead to massive mortality, especially in the most common size range of natural gaps ($<300\text{m}^2$). Thus the importance of understanding differential performance by species during advance regeneration stages is clear (Brokaw and Scheiner 1989; Canham 1989; Connell 1989; Poulson and Platt 1989). The frequency of leader dieback and net height loss after gap formation, particularly by red and sugar maple, implies that adjustment to small and large gap conditions is difficult for these species. Thus the degree to which advance regeneration could confer an advantage for the maple species over other woody (and herbaceous) competitors is not clear.

The likely presence of competitors (tree, shrub, and herb) in natural gaps could modify survival and growth patterns if the three species differ in competitive ability. But it is important to remember that neighboring individuals may benefit tree seedlings as well as interfere with them, particularly through interception of superoptimal radiation in exposed microsites. Indeed, this is the very basis for the

shelterwood harvest/regeneration system. So the balance between positive and negative effects of neighbors in natural gaps is microsite- and species-specific. The effects of neighbors on these three maple species, and consequently their contribution to tree community diversity, cannot be generalized in the absence of careful experimentation.

One variable about which more needs to be known is the degree to which red and striped maple can endure repeated suppression-release episodes like sugar maple (Canham 1985). This may not be as important for striped maple, which as a subcanopy tree can achieve reproductive maturity in smaller gaps (Hibbs 1979; Hibbs et al. 1980), but it may be critical for red maple. The overall conclusion is that the current disturbance regime in unmanaged forests will maintain these species indefinitely. The presettlement disturbance regime would have produced similar results, except that the greater incidence of even smaller fire events would have disfavored all three species during the advance regeneration stage, and thus disadvantaged them in competition with fast-growing pioneer species that colonize burned areas (e.g., *Betula populifolia*, *Betula papyrifera*, *Populus tremuloides*, *Prunus pennsylvanica*).

As for the prediction of forest regeneration, silvicultural cuts should elicit comparable responses among these species due to the similarities between the experimental gaps and small silvicultural openings (selection and small patch harvest). In addition, the natural gap experiment in Tom Swamp 1 suggests that the experimental gap results would hold under natural disturbance regimes on soils comparable to the Gloucester and Charlton series, unless the maple species would be affected differently by competition.

Final conclusions on the wider validity of the patterns found in this work are not possible until (1) sufficient case histories of survival and growth response to natural gap disturbance are completed in forests of different composition, structure, and site characteristics, or (2) our knowledge of microenvironmental patterns and species ecophysiological behaviors under different combinations of physical/chemical fluxes progresses to the point that species success can be predicted on the basis of the mechanisms underlying survival and growth. Such mechanistic knowledge is a worthwhile goal, though it is difficult to achieve, because it promises greater latitude of applicability than site-specific case histories. This approach to predictive capability reinforces the importance of the explanatory connections diagrammed in Figure 1-1, and drives home the point made by Womble (1951; cited in Brown and Curtis 1952) that "dynamic processes must be sought, not in the differentiated, but in the differentiating."

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