# Biomass allocation and multiple resource limitation in tree seedlings

**C.D. Canham, A.R. Berkowitz, V.R. Kelly, G.M. Lovett, S.V. Ollinger, and J. Schnurr**

**Abstract**: We conducted a greenhouse experiment to determine how differences among tree species in allocation of biomass to roots versus shoots affected their responses to different combinations of light, water, and soil nutrients. Across a full range of light levels, we were specifically interested in examining the sensitivity of tree seedlings to additional reductions in aboveground growth due to soil resource limitation, and the relative sensitivity of seedlings to water versus nutrient stress under different light regimes. The four tree species used in our experiment included two species that are the most common initial tree invaders of abandoned agricultural lands (old fields) in the Hudson Valley (red maple (*Acer rubrum* L.) and white pine (*Pinus strobus* L.)) and two species that are less frequently found in old fields, but that are dominant forest species, and are noted for their tolerance of either light stress or water stress (sugar maple (*Acer saccharum* Marsh.) and red oak (*Quercus rubra* L.), respectively). At the lowest light levels (2% of full sun), there was no effect of variation in soil resource availability on shoot growth of any of the four species. At the 9% full sun light level, red maple seedlings showed clear evidence of simultaneous limitation by light, water, and nitrogen. At higher light levels (20–100% of full sun), all four species responded to variation in at least one of the two soil resources. The four species showed two contrasting patterns of allocation of biomass to roots. Red maple and white pine responded to an increase in soil resource availability by reducing relative allocation to roots and increasing aboveground growth. Sugar maple and red oak had much more conservative root allocation patterns: root allocation was high (58–75% of added biomass allocated to roots) and did not vary in response to soil resource availability. Allocation to roots was affected more strongly by variation in soil nitrogen availability than it was by soil moisture availability.

**Résumé** : Les auteurs ont mené une étude en serre afin de déterminer comment des différences interspécifiques d'allocation de biomasse aux racines par rapport à la partie aérienne affectaient leur réaction à différentes combinaisons de lumière, eau et éléments nutritifs du sol. Sur une gamme complète d'intensités lumineuses, ils étaient intéressés particulièrement à la sensibilité des semis à des réductions additionnelles de croissance de la partie aérienne causées par une limitation des ressources du sol, ainsi qu'à la sensibilité relative des semis à un stress hydrique ou nutritif sous différents régimes d'éclairement. Les quatre espèces étudiées incluaient les deux espèces pionnières les plus communes sur des sols agricoles abandonnés dans la vallée de l'Hudson (l'érable rouge (*Acer rubrum* L.) et le pin blanc (*Pinus strobus* L.)) et deux espèces moins fréquentes sur les terres agricoles abandonnées mais qui sont des espèces forestières dominantes et reconnues pour leur tolérance à des stress lumineux ou hydriques (l'érable à sucre (*Acer saccharum* Marsh.) et le chêne rouge (*Quercus rubra* L.) respectivement). Au plus faible niveau d'éclairement (2% du plein ensoleillement), aucun effet sur la croissance aérienne dû à la variation de la disponibilité des ressources du sol n'a été noté pour les quatre espèces. À 9% du plein ensoleillement, la limitation simultanée par la lumière, l'eau et l'azote était nettement évidente chez les semis d'érable rouge. À des niveaux supérieurs d'éclairement (20–100% du plein ensoleillement), les quatre espèces ont réagi aux variations d'au moins une des deux des ressources du sol. Les quatre espèces présentaient deux patrons opposés d'allocation de biomasse aux racines. L'érable rouge et le pin blanc réagissaient à une augmentation des ressources du sol en réduisant l'allocation relative de biomasse aux racines et en augmentant la croissance aérienne. L'érable à sucre et le chêne rouge avaient des patrons d'allocation aux racines beaucoup plus conservateurs : l'allocation aux racines était élevée (58–75% de la biomasse ajoutée était allouée aux racines) et ne variait pas selon la disponibilité des ressources du sol. L'allocation aux racines était plus fortement affectée par des variations en disponibilité de l'azote du sol qu'elle ne l'était par la disponibilité en humidité.

[Traduit par la Rédaction]

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# Introduction

One of the earliest principles attributed to the field of ecology was the "Law of the Minimum," that the performance of organisms is limited by the single resource that is in the most limiting supply (Chapin et al. 1987). While this concept still pervades textbooks and much of the literature on competition between plants (e.g., Tilman 1982), it is clear in principle that plant growth can be simultaneously limited by the availability of a number of different resources (Farmer 1975, 1980; Bloom et al. 1985; Gottschalk 1985, 1987; Conroy et al. 1986; Chapin et al. 1987; Kolb et al. 1990). For example, while light is frequently assumed to be the primary determinant of growth of tree seedlings in shaded microsites, the rate of photosynthesis may be simultaneously limited by the supply of $CO_2$ (Bazzaz et al. 1990; Bazzaz and Miao 1993). Thus, a reduction in soil water availability that causes stomata to close and reduce $CO_2$ uptake can act simultaneously with shading to limit tree seedling growth (Bunce et al. 1977).

As Goldberg (1990) points out, the net competitive effects of a community on tree seedling performance involve two discrete processes: (1) effects of the communities on resource availability and (2) responses of the seedlings to reduced resource levels. There has been a great deal of interest in the degree to which different species and communities can deplete the availability of the resources that are essential for growth and survival of competitors (e.g., Tilman 1989; Wedin and Tilman 1990). In addition, differences in the physical nature of the resources themselves affect the degree to which old-field and forest communities can deplete the availability of light versus water versus soil N (Canham and Kelly 1993). Moreover, even in intact, visually homogeneous old-field vegetation, resources are patchily distributed on very small spatial scales (Kelly and Canham 1992). Thus, tree seedlings in both forests and old-fields are exposed to an extremely wide range of combinations in the availability of light, water, and soil N.

Field experiments demonstrate that the growth of tree seedlings in both forests and old fields can be simultaneously limited by both light and soil resources (e.g., Farmer 1975, 1980; Latham 1992), but that the balance of the effects of aboveground and belowground competition depends on the effects of site quality on the overall availability of soil resources (Putz and Canham 1992). In an old field on a moist, fertile soil, red maple (Acer rubrum L.) seedlings responded only to changes in the availability of light, while on a dry, infertile site, seedlings responded only to changes in soil resources. In an old field with intermediate fertility and moisture, seedlings responded to changes in the intensity of both aboveground and belowground competition, and the effects were additive (Putz and Canham 1992).

Thus the net competitive effects of old-field or forest vegetation on tree seedling establishment and growth will reflect the combined effects of (1) physical site quality, (2) characteristics of the community and the resources themselves that determine the degree of depletion of resource availability, and (3) the physiological and morphological traits of individual tree species that determine their responses to particular combinations of resource availability. In this study, we focus on traits of individual tree species that help determine the effects of depletion of essential resources on tree seedling growth. The general objective of our research was to determine how differences among tree species in one key trait (the allocation of biomass to roots versus shoots) affected their response to different combinations of light, water, and nutrient stress. Across a full range of light levels, we were specifically interested in examining the sensitivity of tree seedlings to additional reductions in growth due to soil resource limitation, and the relative sensitivity of seedlings to water versus nutrient stress under different light regimes.

# Methods

The four tree species used in our experiment included two species that are frequent invaders of old fields in the Hudson Valley (red maple and white pine (Pinus strobus L.)) and two species that are less frequently found in old fields, but that are dominant species of local forests, and are noted for their tolerance of either light or water stress (sugar maple (Acer saccharum Marsh.) and northern red oak (Quercus rubra L.)). Seeds of red maple, white pine, and red oak were obtained commercially from regional seed sources in the fall of 1989 and stratified or stored over winter. In early spring of 1990, seeds of these three species were germinated on misting benches in the greenhouse. Newly germinated sugar maple seedlings were collected from a local forest because of poor germination of the commercially obtained seeds. Of the four species, seeds of three (sugar maple, red oak, and white pine) are dispersed in the fall and most germinate in the following spring. Seeds of the remaining species (red maple) are dispersed in late spring to early summer. In our region, many of the seeds then germinate immediately (i.e., late May to mid-June). However, a portion of the seeds overwinter and germinate the following spring. The seedlings that germinate in early summer presumably experience different conditions for establishment than the seedlings that overwinter and germinate early the next spring. Our particular results may therefore be more representative of spring-germinating seedlings than of the early summer germinating seedlings.

After germination, seedlings were transplanted into PVC tubes (approx. $20 \times 4$ cm top diameter) containing approximately $110 \text{ cm}^3$ of a mix of fine and coarse sand with a small amount of silt. The soil was rinsed several times with deionized water to reduce the initial N content. The sandy medium was selected to provide a relatively infertile medium (to which nutrients could be added experimentally), and to facilitate sampling of roots at the end of the experiment, while the silt was added to improve water-holding capacity and cation exchange capacity. Seedlings of the first three species were placed in the experimental treatments on April 13, 1990; the sugar maple seedlings were placed in the treatments on May 16, 1990. All seedlings were harvested between August 13 and 16, 1990.

## Experimental treatments and design

We used a blocked, split-plot experimental design, in which five light levels were applied (as main plots, using $1.5 \times 1.5$ m shade tents) in four replicate blocks, with a $2 \times 2$ factorial combination of high or low water supply and N concentration applied (as four subplot treatments) to individual seedlings within each light treatment. Each of the four blocks represented a separate row of greenhouse benches. Three seedlings of each species were exposed to each of the four water–nutrient treatment combinations in each light treatment. The multiple seedlings were used to reduce imbalance in the design due to

seedling mortality. Response variables were computed as the mean of the response of the three seedlings unless specifically noted below.

The five light treatments ranged from 2% to 100% of ambient light in the greenhouse (ambient greenhouse light levels were >90% of open sky light levels). Light levels less than 100% ambient were created by constructing 1.5 × 1.5 m shade tents. Levels of 45% and 20% ambient light were obtained using a single layer of spectrally neutral shade cloth (using 55% and 80% shade cloth, respectively). Light levels of 9% and 2% of ambient were obtained by combining layers: i.e., a layer of both 55% and 80% shade cloth for the 9% ambient light level treatment, and 2 layers of 80% shade cloth and 1 layer of 55% shade cloth for an effective light level of 1.8% (rounded to 2% for simplicity in presentation). The layers of shade cloth were separated by 5–10 cm to ensure that they acted as neutral density filters. Light levels in each shade tent were tested for both average level and spatial uniformity using quantum sensors (LICOR, Inc.). Experimental units (groups of three seedlings) were randomly assigned to positions within each shade tent; however, light levels within each shade tent were uniform enough that the positions of the units were not rotated during the experiment. An unavoidable consequence of altering incoming radiation is that ambient temperatures experienced by seedlings varied among the light treatments. Maximum and minimum weekly air temperature was monitored inside one randomly chosen main plot for each light level.

The water and N treatments consisted of contrasting levels of (1) the supply of water and (2) the concentration of N in the water. For the high-water treatment, seedlings were watered to excess (field capacity) twice a week. Our goal for the low-water treatments was to bring the soils back to 50% of field capacity in each of the twice-weekly waterings. At the beginning of the experiment, average field capacity of the soil was determined for a random subsample of the tubes. This figure was used to determine an average initial wet weight for the "low-water" soil in each tube at the start of the experiment. From that point on, a random sample of white pine and red maple seedlings from each light level was weighed before each watering (twice weekly) to calculate average daily water loss during the preceding period. That average daily water loss was then multiplied by the number of days in the upcoming watering period (either 3 or 4 days) to determine the total amount of water needed to bring the soil back to 50% of field capacity. That amount of water was then added to all low-water seedlings of all four species in that light level. This procedure was necessary because water-use was expected (and did, in fact) vary substantially among light treatments (presumably because of effects of light levels on leaf temperature and transpiration rates). Thus, a treatment in which an equal amount of water was added to all low-water seedlings would confound the effects of light and water, and result in highly unequal levels of water stress across different light levels.

Nutrients were added in the irrigation water during the twice-weekly waterings. Nitrogen was added as $NH_4NO_3$ at a concentration of 100 mg N/L in the high-N treatments, and 5 mg N/L in the low-N treatments. Concentrations of other nutrients were as follows (in mg/L) for both the high- and low-N treatments: P, 15; K, 57; Ca, 6; Mg, 6; and S, 11. In the high-N treatments these concentrations represent approximately the optimal nutrient ratios for the growth of trees, as determined by Ingestad (1981). In the low-N treatments, all nutrients are in excess relative to N. Sufficient micronutrients were also added to both solutions. The small amount of N available from the sand–silt mix was not enough to interfere with the treatment effects, as shown by the mean N concentrations in plant tissue from the two treatments at the end of the experiment (see Results, below).

Because the N treatments used different concentrations of N, the total amount of N added to the high-water treatments was greater than the amount added to the low-water treatments. We reasoned that it was better to vary N concentrations rather than N amounts because the seedlings may not have been able to exploit the entire soil volume of the tubes; thus, the actual amount of N available to the plants would vary with the size of the root systems and would be nearly impossible to determine. The inevitable result of varying N concentrations is that the effect of water will be somewhat confounded by N if the plants respond to the total amount of N as well as the concentration. However, the difference in the amount of N between the two water treatments was only about 2-fold, compared with the 20-fold difference in N concentration between the N treatments.

The seedlings were harvested immediately after the water-use measurements. Each seedling was cut at the root collar (omitting any remnants of the acorns of red oaks), and roots were extracted from the soil by washing with deionized water. Stem length was recorded, and total leaf area was measured with a leaf-area meter (LICOR, Inc.). Roots, stems, and leaves were weighed after drying at 70°C for 2 weeks. To test relationships between root allocation and plant N status, whole-plant tissue N concentrations (combining roots, stem, and leaves) for the most vigorous seedling in each treatment combination (species × block × light × water × N; $n = 320$) were determined using a semi-micro Kjeldahl digestion and distillation (Tecator, Inc). We used analysis of covariance (ANCOVA) of the split-plot experimental design to test for effects of tissue N (as a covariate) on root allocation. For that analysis, light and water were treated as fixed effects, and the main effects of light were tested against the block × light interaction term because of the split-plot design. Interactions between the covariate and the main effects were used to test the homogeneity of slopes assumption required for analysis of covariance. The assumption was met (i.e., nonsignificant interaction terms) for all of the species except white pine. Therefore, ANCOVA results are not presented for white pine (see Table 3).

## Results

### Effects of variation in resource availability on aboveground growth

At the lowest light level (2% ambient) there were no significant effects of soil resource availability on shoot weight in any of the species (Fig. 1). Thus, aboveground growth of these four species was limited solely by light in the treatment that imposed shade levels comparable to light levels beneath closed forest canopies of late successional species (Canham et al. 1990, 1994) and the densest closed canopies of old-field communities (Canham and Kelly 1993). Using a functional definition of stress as a reduction in growth, the supply of resources in our low-water and low-N treatments was apparently not low enough to induce additional stress, because light-limited growth rates were so low that the supply of soil resources exceeded demand. Given the extremely low absolute growth rates of red maple and white pine seedlings in 2% light, we would expect significant mortality of seedlings if the supply of water or N was reduced enough to further reduce seedling growth.

At moderately low light levels (9% ambient), red maple seedlings showed clear evidence of simultaneous limitation

**Fig. 1.** Means and standard errors of seedling shoot biomass for each of the four species in each treatment combination. N, nitrogen; W, water.
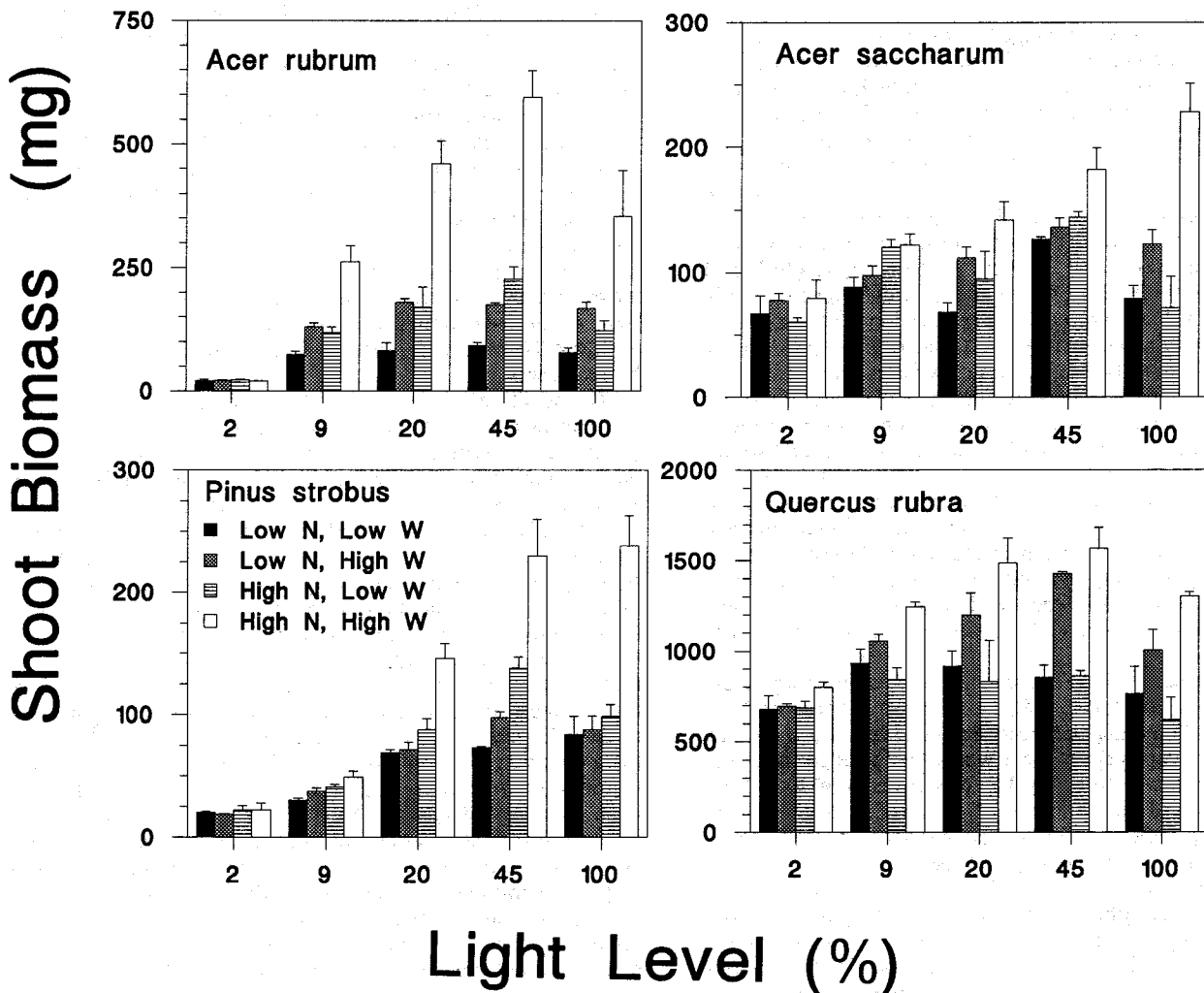


by all three resources (light, water, and N) (Fig. 1 and Table 1). An increase in the supply of either water or N caused increased growth, and the effects of increases in both resources were additive. At moderate to high light levels (20–100% ambient), aboveground growth in all four species responded to variation in at least one of the two soil resources (Fig. 1 and Table 1). All four species at all three light levels (20, 45, and 100%) responded to variation in the supply of water, while only red maple and white pine showed consistent responses to N. Red oak seedlings were insensitive to variation in N supply at any light level, even though leaves in the low-N treatments often appeared chlorotic.

**Sensitivity to soil resource availability**

We have used the ratio of shoot biomass under high soil resource availability (high N, high water) to growth under low soil resource availability (low N, low water) as an index of the sensitivity of aboveground growth to variation in soil resource availability. Using the 9% light treatment as a benchmark, the ranking of the sensitivities of the four species to limitation by soil resources is as follows: red

maple (3.50) >> white pine (1.63) > sugar maple (1.38) ≅ red oak (1.33). This index is obviously unique to the levels of soil resource supply used in this experiment and reflects responses to the combination of low water and low N supply. Given those provisos, shoot growth in red maple is clearly far more sensitive to a reduction in soil resource availability than in the other three species.

Using total plant biomass as the basis for the index, red maple remains the most sensitive (3.08). In contrast, white pine becomes the least sensitive (1.25), while sugar maple (1.38) and red oak (1.73) are intermediate. Thus, the apparent sensitivity of aboveground growth in white pine to variation in soil resource supply was largely a result of shifts in biomass allocation within the plant (see results on root–shoot allocation, below), rather than a result of significant reduction in total plant biomass at low soil resource supply.

As light levels increased, all of the species generally became more sensitive to soil resource availability, although peak sensitivities usually occurred at 45% rather than 100% ambient light. For example, under low soil resource availability in the 20% light treatment, shoot growth in even

**Table 1.** Treatment combinations in which an increase in soil resource availability (either water (W) or nitrogen (N) alone, or additive effects of water and nitrogen (W+N) combined) was accompanied by a significant increase in seedling shoot biomass.

| Species[a] | Light level (%) | | | | |
|---|---|---|---|---|---|
| | 2 | 9 | 20 | 45 | 100 |
| ACRU | — | W, N, W+N | W+N | W, N, W+N | W, N, W+N |
| PIST | — | — | W+N | W, N, W+N | W+N |
| ACSA | — | — | W | W+N | W |
| QURU | — | — | W | W | W |

[a]ACRU, red maple (*Acer rubrum*); PIST, white pine (*Pinus strobus*); ACSA, sugar maple (*Acer saccharum*); QURU, red oak (*Quercus rubra*).

sugar maple and red oak was only one-half to two-thirds of what it was under the high water plus N treatment (Fig. 1). Red oak was consistently the least sensitive to variation in soil resource availability at all light levels. This may be due, in part, to the carbon and nutrient subsidy received by these first-year seedlings from reserves in the acorns.

In general, our results suggest that the two most opportunistic species (in successional terms), red maple and white pine, will be more sensitive to variation in soil resource availability (whether that variation is due to competition or the physical quality of the site) than sugar maple and red oak, particularly in moderately deep shade. From the opposite perspective, at all but the lowest light level, red maple and white pine show much larger relative increases in growth in response to an increase in soil resource availability than either sugar maple or red oak (Table 2).

### Effects of soil resources on the response of growth to light

Our experiment can be used to examine the effects of soil resource availability on changes in the relationship between growth and light availability. The experiment was not designed to test for effects of soil resources on the minimum light levels required by seedlings for positive growth rates (light compensation). An experiment appropriate for that question would require much finer resolution of seedling performance at low light levels. However, our experiment can provide evidence for the effects of soil resource availability on both the maximum potential aboveground growth rate ($G_{max}$) (at any light level) and the approximate light level ($L_{opt}$) at which $G_{max}$ occurs. Interspecific differences in $G_{max}$ and $L_{opt}$ have been assumed to be a major cause of differences in competitive hierarchies across gradients of resource availability in both intact communities (e.g., Shugart 1984; Latham 1992) and disturbances (e.g., Canham and Marks 1985), although there is recent evidence that interspecific differences in the relationship between growth and light availability are not as pronounced as previously thought (Pacala et al. 1994).

In all four species, both $G_{max}$ and $L_{opt}$ varied with soil resource availability (Fig. 1). Red maple shows the most direct relationships: under the low N – low water treatment, aboveground growth reaches an asymptote at a very low growth rate and a light level of only 9% of ambient. Adding water alone increases $G_{max}$ and shifts $L_{opt}$ to 20%

**Table 2.** Changes in sensitivity of aboveground growth to water ($S_W$) versus nitrogen ($S_N$) limitation, as a function of ambient light levels.
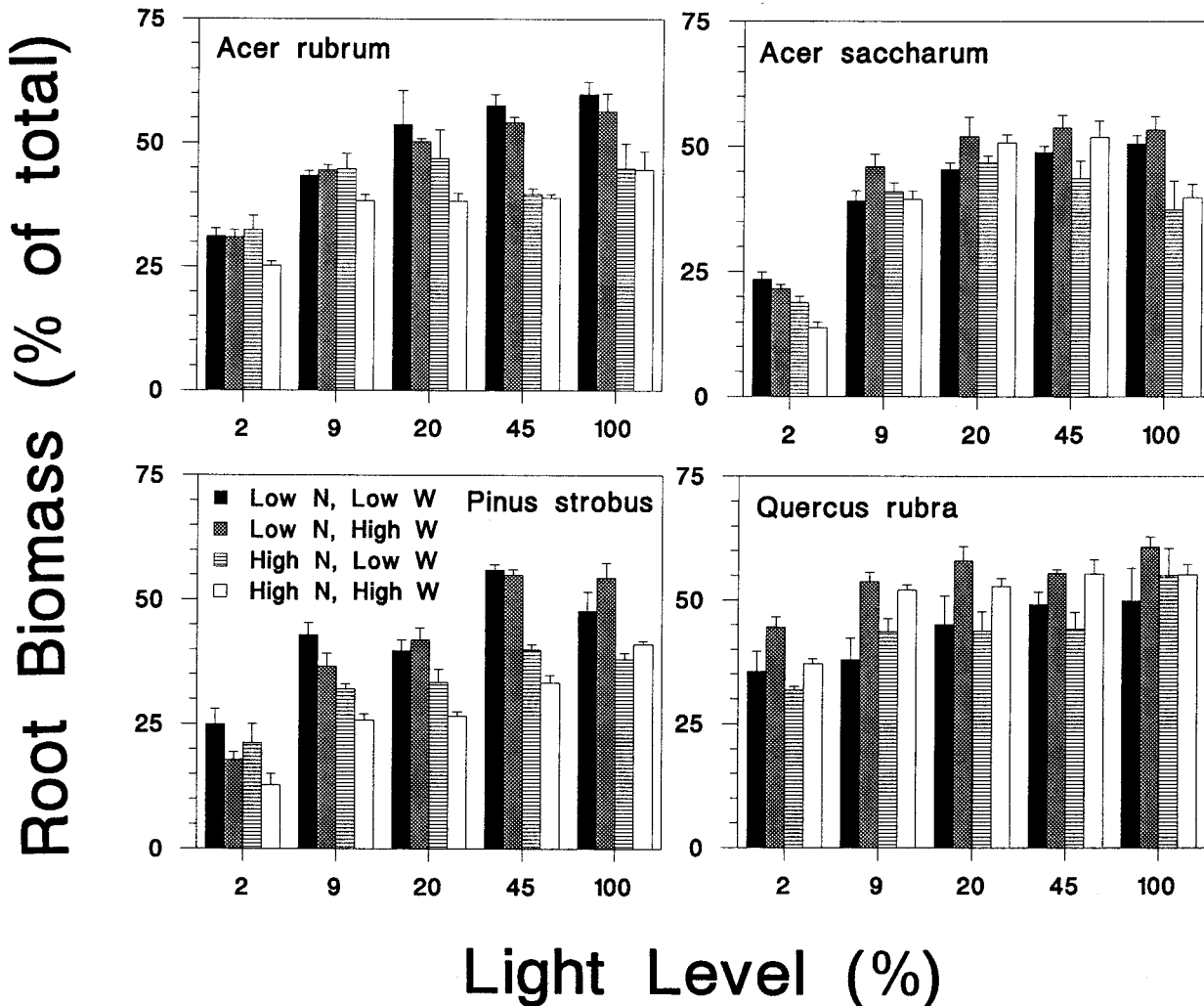
| Species[a] | | Light level (%) | | | |
|---|---|---|---|---|---|
| | | 9 | 20 | 45 | 100 |
| ACRU | $S_W$ | 2.22 | 2.70 | 2.62 | 2.87 |
| | $S_N$ | 2.01 | 2.56 | 3.39 | 2.12 |
| PIST | $S_W$ | 1.20 | 1.66 | 1.67 | 2.42 |
| | $S_N$ | 1.31 | 2.04 | 2.37 | 2.71 |
| QURU | $S_W$ | 1.48 | 1.79 | 1.82 | 2.11 |
| | $S_N$ | 1.18 | 1.24 | 1.10 | 1.30 |
| ACSA | $S_W$ | 1.02 | 1.50 | 1.26 | 3.19 |
| | $S_N$ | 1.25 | 1.27 | 1.34 | 1.86 |

**Note:** Sensitivity was calculated as the ratio of shoot growth under high supply of a particular resource to shoot growth under low supply (using only the two treatments in which the other resource was present in high supply).

[a]See Table 1.

light. Adding N alone has an even greater effect on both $G_{max}$ and $L_{opt}$, while adding both soil resources together causes an even greater increase in $G_{max}$ and $L_{opt}$ (Fig. 1). While the other three species all showed variations on this theme, they differed in the magnitude of the response of $G_{max}$ and $L_{opt}$ to soil resource availability. Since seedling growth rates have such a strong effect on the net rates of tree invasion in old fields (Hill et al. 1995), these results provide a mechanistic link between studies of variation in the availability of different resources among old field communities (e.g., Canham and Kelly 1993) and field studies that have quantified variation in the ability of trees to invade old-field communities (Hill et al. 1995). Our results also suggest that competitive hierarchies among tree seedlings in the moderate to high light levels of forest gaps and clearings will vary with site quality (Latham 1992).

**Fig. 2.** Means and standard errors of root biomass as a percentage of total seedling biomass. N, nitrogen; W, water.



## Allocation to roots

The observed patterns of allocation of biomass to roots suggest two fundamentally different responses of seedlings to variation in soil resource availability (Fig. 2). Red maple and white pine consistently responded to low soil resource availability with high relative allocation to roots (Fig. 2). At low to moderate light levels, root allocation by red maple declined only in response to an increase in supply of both water and N, and then gradually shifted to respond only to N addition at high light (Fig. 2). Root allocation in white pine responded primarily to availability of water at very low light levels and gradually shifted to respond only to N availability in high light. In effect, these two species increase shoot growth relative to root growth when soil resources are plentiful and favor root growth when soil resources are low. However, the soil resource that elicits this response varies as a function of ambient light level. In contrast, sugar maple and red oak showed only minor variation in allocation to roots in response to soil resource availability. In fact, at all light levels, red oak responded to an increase in water with an increase in relative allocation to roots (Fig. 2).

Our results can be used to test recent models (e.g., Reynolds and Thornley 1982; Agren and Ingestad 1987; Levin et al. 1989; Hilbert 1990) that predict relationships between the tissue N concentrations and allocation to roots versus shoots. In general, our results confirm predictions that the fraction of total biomass in roots (%ROOT) declines as tissue N concentration (%N) increases (Fig. 3). Within the range of 1–4 % N, the decline is approximately linear. At higher N concentrations (primarily in white pine), there is evidence that allocation to roots levels off, (as it must, eventually). ANCOVA reveals that the relationship between %ROOT and %N was affected by light level in sugar maple and red oak, but not in red maple (white pine did not meet the homogeneity of variance assumptions for ANCOVA) (Table 3, Fig. 4). The availability of water also had minor but statistically significant effects on the relationship between %N and %ROOT in all of the species except white pine (Table 3, Fig. 3). In effect, variation in light and water can be thought of as producing variation in the demand for N. Given a fixed concentration of N (high N vs. low N), this variation in demand resulted in a gradient in relative N availability (i.e., relative availability = supply

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In general, our results suggest that the two most opportunistic species (in successional terms), red maple and white pine, will be more sensitive to variation in soil resource availability (whether that variation is due to competition or the physical quality of the site) than sugar maple and red oak, particularly in moderately deep shade. From the opposite perspective, at all but the lowest light level, red maple and white pine show much larger relative increases in growth in response to an increase in soil resource availability than either sugar maple or red oak (Table 2).

### Effects of soil resources on the response of growth to light

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In all four species, both $G_{max}$ and $L_{opt}$ varied with soil resource availability (Fig. 1). Red maple shows the most direct relationships: under the low N – low water treatment, aboveground growth reaches an asymptote at a very low growth rate and a light level of only 9% of ambient. Adding water alone increases $G_{max}$ and shifts $L_{opt}$ to 20%

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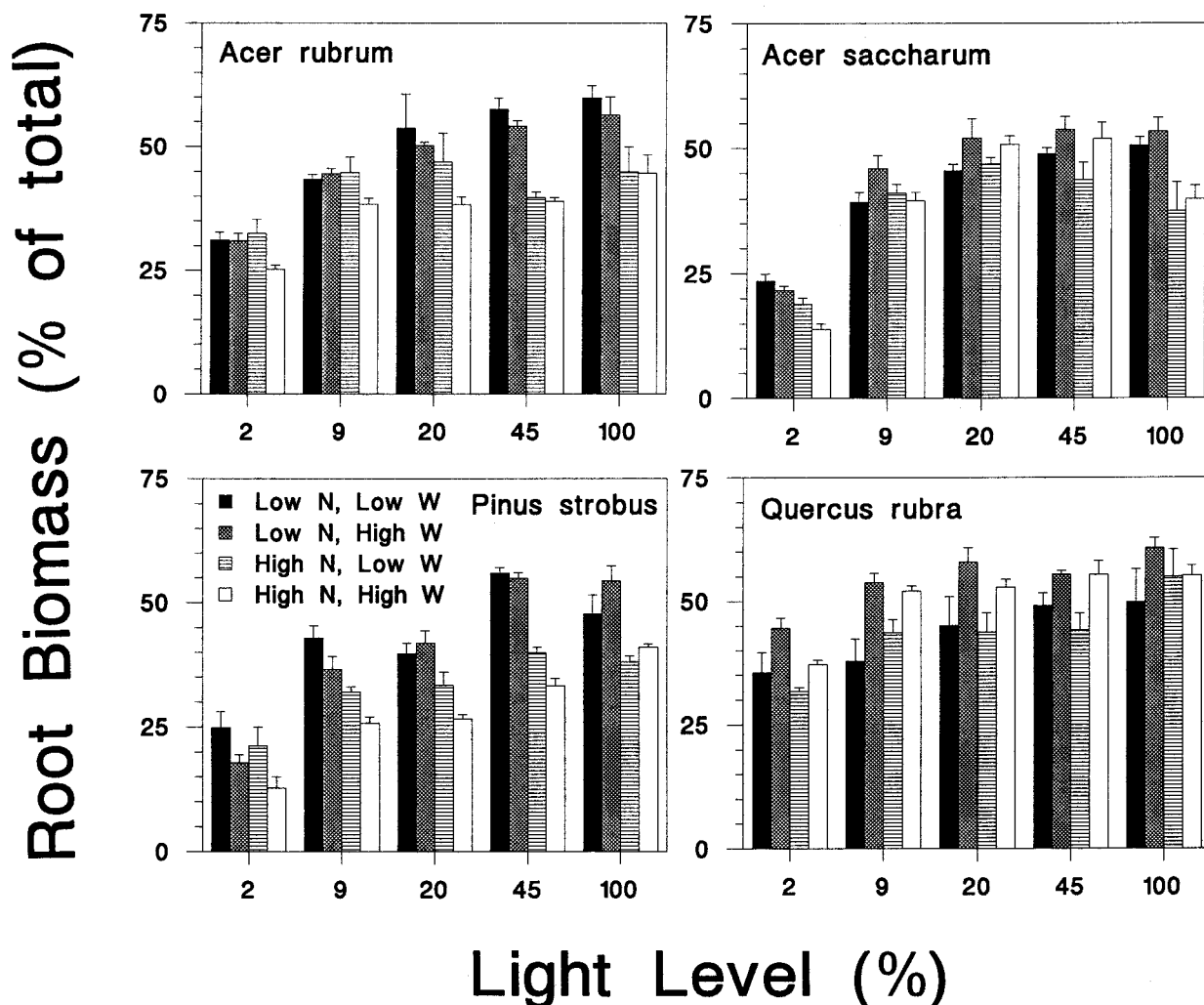
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**Note:** Sensitivity was calculated as the ratio of shoot growth under high supply of a particular resource to shoot growth under low supply (using only the two treatments in which the other resource was present in high supply).

[a]See Table 1.

light. Adding N alone has an even greater effect on both $G_{max}$ and $L_{opt}$, while adding both soil resources together causes an even greater increase in $G_{max}$ and $L_{opt}$ (Fig. 1). While the other three species all showed variations on this theme, they differed in the magnitude of the response of $G_{max}$ and $L_{opt}$ to soil resource availability. Since seedling growth rates have such a strong effect on the net rates of tree invasion in old fields (Hill et al. 1995), these results provide a mechanistic link between studies of variation in the availability of different resources among old field communities (e.g., Canham and Kelly 1993) and field studies that have quantified variation in the ability of trees to invade old-field communities (Hill et al. 1995). Our results also suggest that competitive hierarchies among tree seedlings in the moderate to high light levels of forest gaps and clearings will vary with site quality (Latham 1992).

**Fig. 2.** Means and standard errors of root biomass as a percentage of total seedling biomass. N, nitrogen; W, water.
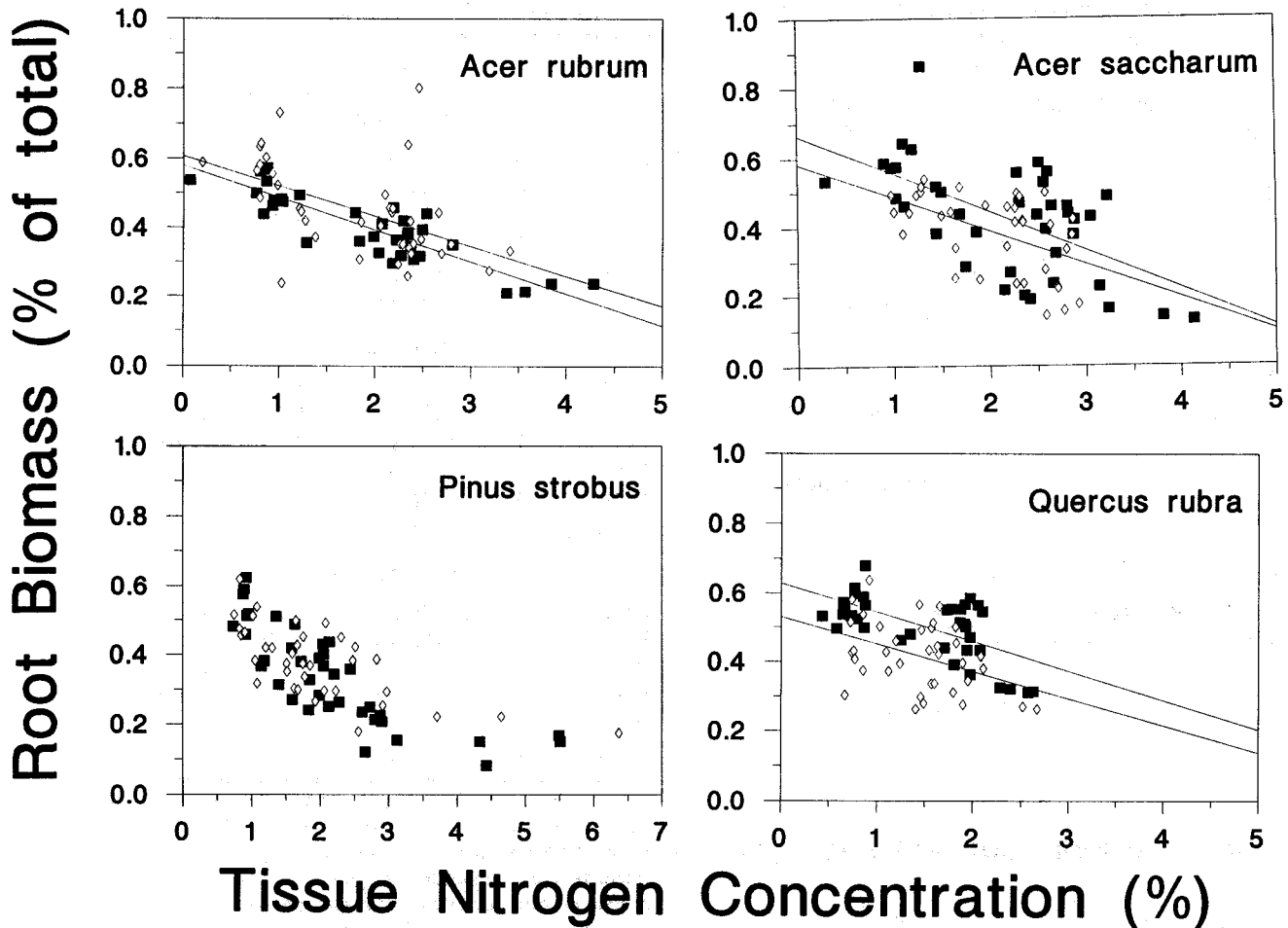


## Allocation to roots

The observed patterns of allocation of biomass to roots suggest two fundamentally different responses of seedlings to variation in soil resource availability (Fig. 2). Red maple and white pine consistently responded to low soil resource availability with high relative allocation to roots (Fig. 2). At low to moderate light levels, root allocation by red maple declined only in response to an increase in supply of both water and N, and then gradually shifted to respond only to N addition at high light (Fig. 2). Root allocation in white pine responded primarily to availability of water at very low light levels and gradually shifted to respond only to N availability in high light. In effect, these two species increase shoot growth relative to root growth when soil resources are plentiful and favor root growth when soil resources are low. However, the soil resource that elicits this response varies as a function of ambient light level. In contrast, sugar maple and red oak showed only minor variation in allocation to roots in response to soil resource availability. In fact, at all light levels, red oak responded to an increase in water with an increase in relative allocation to roots (Fig. 2).

Our results can be used to test recent models (e.g., Reynolds and Thornley 1982; Agren and Ingestad 1987; Levin et al. 1989; Hilbert 1990) that predict relationships between the tissue N concentrations and allocation to roots versus shoots. In general, our results confirm predictions that the fraction of total biomass in roots (%ROOT) declines as tissue N concentration (%N) increases (Fig. 3). Within the range of 1–4 % N, the decline is approximately linear. At higher N concentrations (primarily in white pine), there is evidence that allocation to roots levels off, (as it must, eventually). ANCOVA reveals that the relationship between %ROOT and %N was affected by light level in sugar maple and red oak, but not in red maple (white pine did not meet the homogeneity of variance assumptions for ANCOVA) (Table 3, Fig. 4). The availability of water also had minor but statistically significant effects on the relationship between %N and %ROOT in all of the species except white pine (Table 3, Fig. 3). In effect, variation in light and water can be thought of as producing variation in the demand for N. Given a fixed concentration of N (high N vs. low N), this variation in demand resulted in a gradient in relative N availability (i.e., relative availability = supply

**Fig. 3.** Root biomass (as a percentage of total seedling weight) versus tissue nitrogen concentration for the high-water (■) and low-water (◇) treatments. The data were computed by combining both high N and low N treatments. For three of the species, linear regressions are also shown. Regression lines are not shown for white pine because of the obvious nonlinearity at high N.
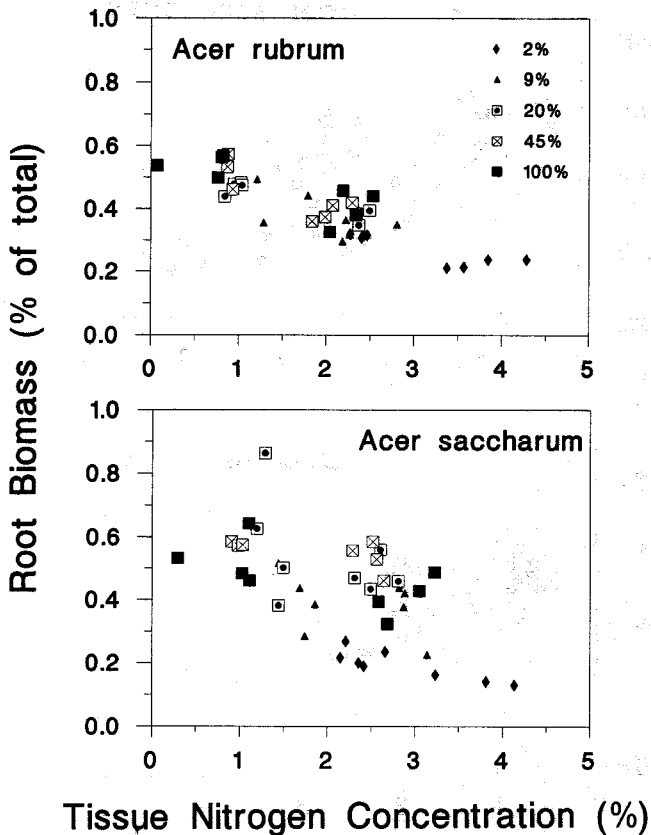


relative to demand). As a result, the underlying relationship between tissue N concentrations and the fraction of biomass allocated to roots was remarkably stable across a broad range of water and light levels (Figs. 3 and 4).

Descriptions of root allocation patterns in small seedlings using either ratios of root/shoot biomass or root mass as a percentage of total mass (%ROOT) can be highly sensitive to very early, transient inequalities in the mass of roots and shoots generated during initial seedling establishment. For this reason, root partitioning coefficients (the proportion of an incremental gain in biomass that is allocated to roots) provide more meaningful, quantitative measures of root allocation than root/shoot ratios. Our data show that root biomass is a linear function of total plant biomass in almost all combinations of species and soil resource treatments (white pine in high resource treatments being the exception). Thus, the root partitioning coefficients can be estimated from the slopes of regressions of root biomass on total plant biomass (Table 4).

The calculated root partitioning coefficients reveal that all four species have high levels of allocation to roots when soil resources are low (55–62% of any increment in biomass is allocated to roots) (Table 4). The root partitioning coefficients for both sugar maple and red oak are relatively insensitive to changes in not only light but also the availability of water or N. In effect, first-year seedlings of both sugar maple and red oak appear to have extremely conservative patterns of relatively high, fixed allocation of biomass to roots. The only exception to this pattern was an extremely high allocation to roots (83%) by sugar maple seedlings in the low N – high water treatment (Table 4). These seedlings were more than 60% larger (in total plant mass) than the seedlings in the low N – low water treatment, but allocated the vast majority of the additional biomass to roots. In contrast with sugar maple and red oak, both red maple and white pine showed clear, consistent variation in root partitioning coefficients in response to soil resource availability (Table 4). In both of these species, addition of N alone caused a larger drop in allocation to roots than addition of water alone, and the lowest relative allocation to roots occurred when both soil resources were increased simultaneously (Table 4).

**Fig. 4.** Root biomass of seedlings in the high-water treatments (with both high-N and low-N treatments included) versus tissue nitrogen concentration. The different light treatments are shown with different symbols. Analysis of covariance (Table 3) reveals that light had a significant effect on root biomass in sugar maple, but not in red maple.



**Table 3.** Analysis of covariance, by species, for the effects of block (B), light (L), and water (W) on the fraction of total biomass in roots (%ROOT), with tissue nitrogen concentration (%N) as a covariate.
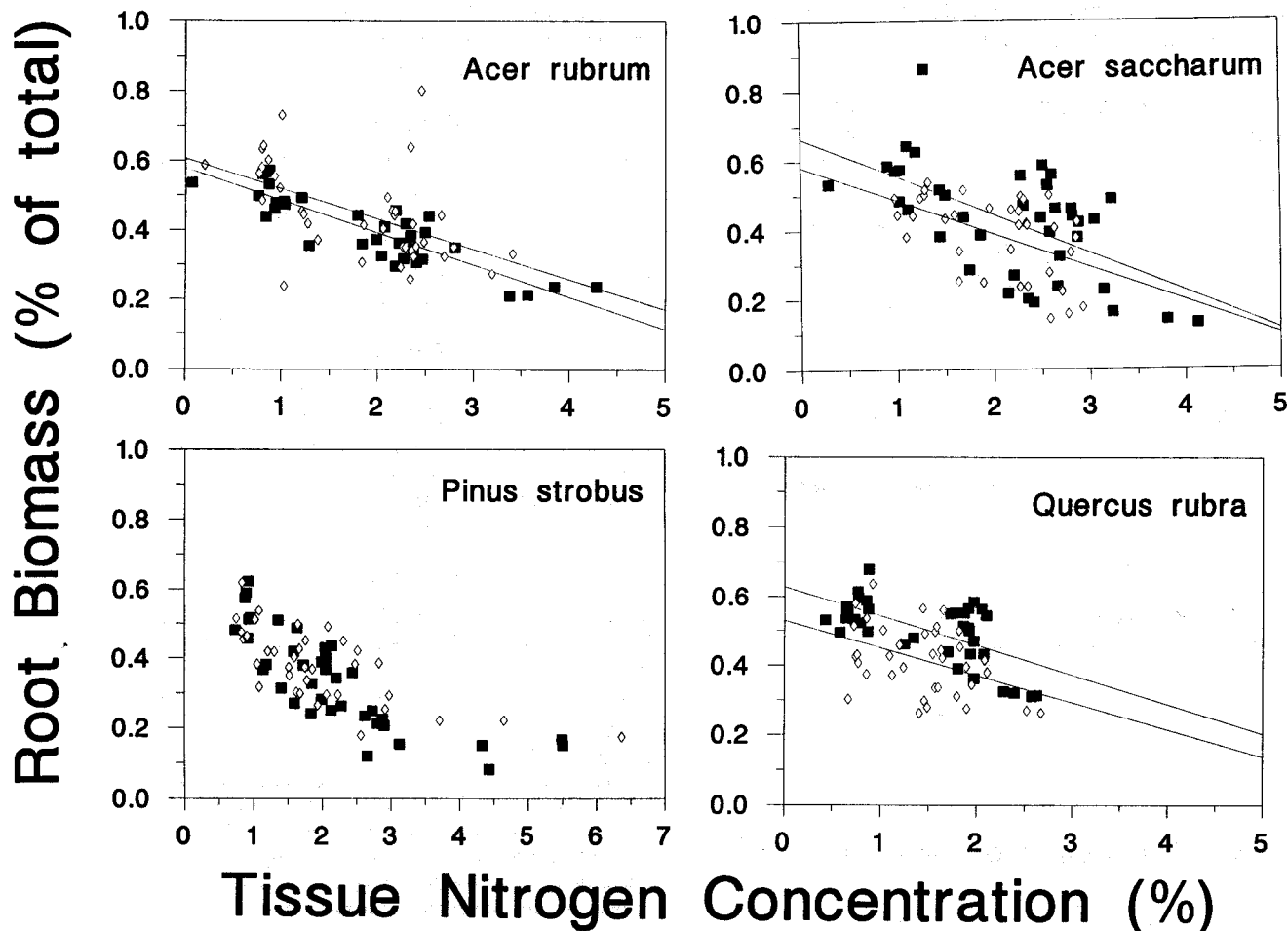
| Source | df | Mean square | F | p |
|---|---|---|---|---|
| **Red maple** | | | | |
| Block | 3 | 41.99 | 0.68 | 0.5704 |
| L | 4 | 249.16 | 2.30 | 0.1183 |
| W | 1 | 304.25 | 4.90 | 0.0311 |
| %N | 1 | 1574.22 | 25.35 | 0.0001 |
| B×L | 12 | 108.23 | | |
| Error | 54 | 62.11 | | |
| **Red oak** | | | | |
| Block | 3 | 90.25 | 1.93 | 0.1354 |
| L | 4 | 422.27 | 15.94 | 0.0001 |
| W | 1 | 1498.92 | 32.13 | 0.0001 |
| %N | 1 | 260.60 | 5.59 | 0.0219 |
| B×L | 12 | 26.49 | | |
| Error | 52 | 46.65 | | |
| **Sugar maple** | | | | |
| Block | 3 | 36.54 | 0.62 | 0.6052 |
| L | 4 | 1448.83 | 26.09 | 0.0001 |
| W | 1 | 388.33 | 6.59 | 0.0131 |
| %N | 1 | 890.70 | 15.11 | 0.0003 |
| B×L | 12 | 55.53 | | |
| Error | 54 | 58.94 | | |

**Note:** Because of the split-plot design, the effect of light (a main plot factor) was tested using the light × block interaction term as the error mean square. Interaction terms indicate homogeneity of slopes with respect to main effects for red maple, red oak, and sugar maple, but not for white pine. Therefore, results for white pine are not presented.

## Discussion

Our results demonstrate that multiple resource limitation occurs over at least some range of resource availability for all four of the species tested here. However, in the lowest light treatment (2%), none of the species showed variation in aboveground growth in response to variation in soil resource availability. There are both forest and old-field communities within the region that are capable of casting comparable levels of shade (Canham and Kelly 1993; Canham et al. 1994). It is worth noting that such dense canopies are generally restricted to soils with at least moderate levels of moisture and fertility. Thus, the results of this greenhouse experiment are in agreement with field experiments that indicate that belowground competition has relatively little effect on seedling performance of these tree species on relatively productive soils beneath intact canopies of either old fields (Putz and Canham 1992) or forests (Pacala et al. 1994).

As ambient light levels increase, soil resource availability has a larger effect on seedling growth (Table 2) in all four species, and the relative importance of belowground competition should increase (Putz and Canham 1992). While greenhouse data must be used with caution in extrapolating to the performance of seedlings in field conditions, our results suggest that belowground competition will predominate at light levels even as low as 9% of full sun. For example, growth of red maple seedlings in the low-N treatments shows very little increase at light levels above 9% (Fig. 1) However, the sensitivity of seedlings of different tree species to variation in soil resource availability is strongly influenced by root allocation patterns: the two tree species with the most conservative patterns of root allocation show the most modest responses to an increase in light or soil resources (Fig. 1). It is noteworthy that this conservative allocation pattern occurs in two species with such different physiologies: a shade-tolerant but drought-intolerant species (sugar maple), and a less shade-tolerant but more drought-tolerant species (red oak) (Wuenscher and Kozlowski 1970, 1971). In sugar maple seedlings, a large root system may serve as a drought-avoidance mechanism, although the relative drought intolerance of the species may still limit it to relatively moist environments. In red oak seedlings, a large root system combined with a more drought-adapted physiology may be necessary for successful exploitation of drier sites.

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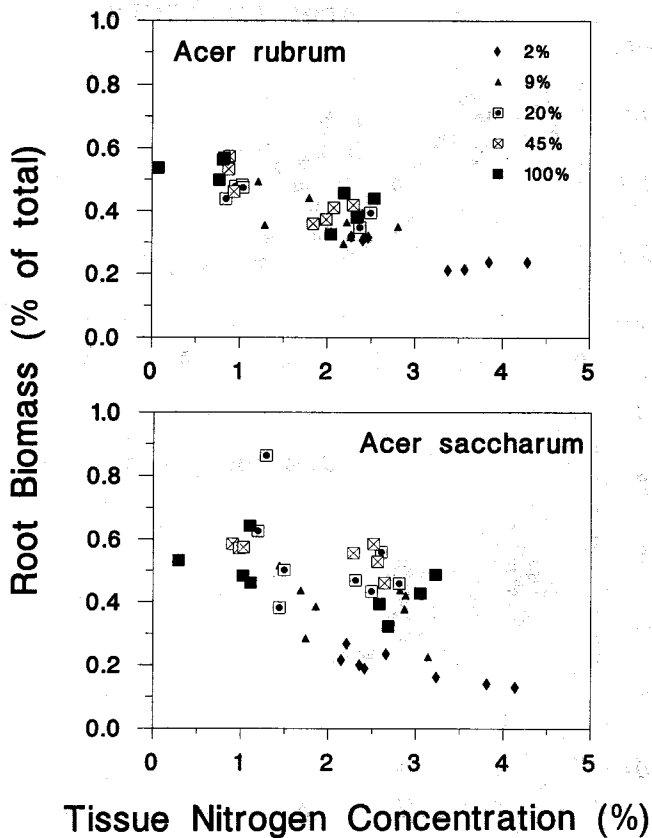


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**Table 4.** Root partitioning coefficients for the four species in each of the four soil resource treatments.

| Treatment[b] | Species[a] | | | |
| --- | --- | --- | --- | --- |
| | ACRU | PIST | ACSA | QURU |
| High N – high W | 0.387 (0.360–0.415) | 0.418 (0.392–0.443) | 0.568 (0.527–0.610) | 0.655 (0.596–0.717) |
| High N – low W | 0.399 (0.369–0.430) | 0.427 (0.392–0.463) | 0.546 (0.503–0.591) | 0.523 (0.435–0.619) |
| Low N – high W | 0.574 (0.539–0.609) | 0.573 (0.538–0.608) | 0.829 (0.779–0.882) | 0.609 (0.562–0.659) |
| Low N – low W | 0.621 (0.584–0.660) | 0.551 (0.491–0.614) | 0.553 (0.505–0.603) | 0.551 (0.435–0.682) |

Note: The partitioning coefficients are the slopes of principal axis regressions (Sokal and Rohlf 1969) of root biomass on total plant biomass, using individual seedling measurements as data points ($n = 47–60$). The 95% confidence intervals on the estimate of the slope are given in parentheses. Species codes are given in the legend for Table 1.
[a]See Table 1.
[b]N, nitrogen; W, water.

There has been a great deal of theoretical interest in the effects of the supply of nutrients (particularly N) on the patterns and significance of partitioning of plant growth into roots versus shoots (e.g., Thornley 1972; Reynolds and Thornley 1982; Agren and Ingestad 1987; Levin et al. 1989; Hilbert 1990). Although the models differ in their exact assumptions and specific predictions, they all predict that in order to optimize relative growth rate, allocation to roots should be a declining function of internal tissue N concentration (Hilbert 1990). Our results do, in fact, show that the relative sizes of the root systems (i.e., root mass/total plant mass) in all four species decline linearly over most of the range of possible tissue N concentrations (Fig. 4). The relationship is remarkably robust across the full range of light levels and is only slightly affected by soil moisture availability (Figs. 3 and 4). However, the species clearly differ in their plasticity in root allocation. It seems unlikely that the root allocation patterns of either sugar maple or red oak are optimal for aboveground growth, at least in the short term. As discussed above, we suspect that root allocation in both of these species reflects compromises between maximizing aboveground growth and minimizing the risk of mortality during periods of drought.

Fortuitously, the levels of resource supply chosen for our low-water and low-N treatments had roughly similar effects on overall shoot growth (Table 2). Thus, in a functional sense, we imposed relatively similar levels of water and nutrient stress (with stress defined operationally by the magnitude of reduction in aboveground growth). However, the low-N treatments had much greater effects on root allocation than the low-water treatments (Table 4). Thus, our results suggest that allocation to roots is affected more strongly by variation in soil N availability than it is by soil moisture availability. The physiological mechanisms responsible for changes in root allocation are still largely unknown, and there has been very little research on the sensitivity of root allocation to different soil resources (Davidson 1969). Plants face a number of difficulties in optimizing root allocation under varying soil moisture regimes. Soil moisture, particularly in drought-susceptible soils, is highly variable over time. Moreover, periods of active growth (i.e., the periods when differences in biomass partitioning would have the greatest effect) are often concentrated in moist periods, when internal water content is high. In contrast, N supply can be expected to be more predictable within a growing season (barring disturbance), and internal tissue N concentration provides the plant with a means for a more accurate assessment of the effects of a change in root allocation on potential resource uptake. Thus, there may be fewer constraints on optimizing root allocation for N uptake than there are for water uptake. This line of reasoning would also suggest that drought-adapted species will have much less opportunistic patterns of root allocation than species adapted to moist but infertile soils.

## Acknowledgements

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