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CO-OCCURRING TREE SPECIES CHANGE RANK IN SEEDLING PERFORMANCE WITH RESOURCES VARIED EXPERIMENTALLY[1]

ROGER EARL LATHAM[2]
Department of Biology, University of Pennsylvania, Philadelphia, Pennsylvania 19104-6018 USA

Abstract. Parallel hypotheses are advanced: (1) the distribution of resources in mesic upland temperate forests is patchy at a scale that is fine grained for adult trees and coarse grained for seedlings and (2) co-occurring tree species differ in abilities to exploit resources, resulting in differences in species rank order, by absolute growth rates of seedlings, among different resource combinations. Spatial variation in growth rate ranking among species may translate, through competition, into patterns of relative species abundances of seedlings that could persist in the community composition of adult trees. Here I report the results of factorial greenhouse experiments that address the second hypothesis. Seedlings of six co-occurring tree species of temperate eastern North American upland forests showed strong interspecific differences in growth rates and patterns of biomass allocation in response to variation in light and mineral nutrients. The ranks of four species in growth measures associated with competitive ability, absolute rates of change in stem height, total leaf area, and root biomass, varied significantly among nutrient treatments. Seedlings of American chestnut, *Castanea dentata,* ranked highest in traits associated with competitive ability over the broadest range of combinations of resource levels.

Key words: allocation; Carya tomentosa; Castanea dentata; *coexistence;* Fagus grandifolia; *growth; light;* Liriodendron tulipifera; Nyssa sylvatica; Quercus rubra; *root/shoot ratio; seedlings; shade tolerance; soil nutrients; specific leaf mass; temperate eastern North America; trade-offs.*

INTRODUCTION

The coexistence of many plant species in close proximity has proven to be a challenge for ecologists. Coexistence among potentially competing animal species has been partly attributed to differences among species in the use of resources. Hypotheses about the diversity of potentially competing animal species often start with differences in feeding niches (Hutchinson 1957, MacArthur 1958, Root 1967, Vandermeer 1972) based on morphological and biochemical differences among plants and plant parts. Among other factors implicated in maintaining species diversity at small temporal and spatial scales are species-dependent effects of disturbance, predation, parasitism, disease, and mutualism. The differential resource-use approach has seldom been applied to plants (Bradshaw 1969, Grubb 1977) because, in strong contrast to animals, all nonparasitic plants use the same resources: growing space, sunlight, carbon dioxide, water, oxygen, and no more than 18 simple molecules and ions. Together with conditions such as temperature and atmospheric water potential, these fundamental resources and their patterns of variation in time and space are the basic building blocks of complex environmental variables often measured by ecologists, such as canopy gap area or microtopography. Although measures of plant performance often vary in relation to such composite environmental variables, plant performance depends on the underlying patterns of resource availabilities and conditions such as temperature.

Because all plants require the same few resources, if co-occurring species partition resources among themselves they are more likely to differ with respect to combinations of availability of multiple resources than with respect to a single resource (Hutchinson 1957, Tilman 1982, 1986). Scientists long ago identified the irreducible resources most often limiting plant growth in moist-temperate forests as photosynthetically active radiation (PAR: light from 400 to 700 nm wavelength), water, and available nitrogen (e.g., Fricke-Beutnitz 1904, Moore 1929, Mitchell and Chandler 1939). According to Liebig's "law of the minimum," only one resource is limiting to a plant's growth at a given time and place. However, resources vary spatially and temporally and species differ in abilities to tolerate resource scarcity. Thus, more than one resource may be limiting at once among microsites or at different times within the same microsite or for different species growing close together.

Foresters and plant ecologists have written much about species differences in tolerance of resource scarcity in general (e.g., Decker 1952, Grime 1977, 1979). However, few investigators have attempted to tease apart the component tolerances of limitation in particular resources. Nor have many addressed the effects

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[2] Present address: Department of Geology, University of Pennsylvania, Philadelphia, Pennsylvania 19104-6316 USA.

TABLE 1. Characteristics of the tree species used in the study.

Species	Mean seed mass (g)*	Shade tolerance rating†	Low-N tolerance rating‡	Drought tolerance rating§	Wood specific gravity‖	Wood anatomy¶
Carya tomentosa (Poir.) Nutt. mockernut hickory	5.0	4	2	1	0.68	ring-porous
Quercus rubra L. northern red oak	3.6	3	1	2	0.60	ring-porous
Castanea dentata (Marsh.) Borkh. American chestnut	3.5	3	...	...	0.42	ring-porous
Fagus grandifolia Ehrh. American beech	0.28	1	2	3	0.60	diffuse-porous
Nyssa sylvatica L. blackgum	0.14	2	2	1	0.48	diffuse-porous
Liriodendron tulipifera L. tuliptree	0.03	4	3	2	0.41	diffuse-porous

* USFS (1974).

† Baker (1949): 1—very tolerant, 2—tolerant, 3—intermediate, 4—intolerant.

‡ Mitchell and Chandler (1939): 1—tolerant, 2—intermediate, 3—intolerant. Rating for *Carya tomentosa* is by analogy with the ecologically similar *Carya glabra* (Mill.) Sweet (USFS 1974). *Castanea dentata* was not rated.

§ Wilde (1958) and Fowells (1965): 1—tolerant, 2—intermediate, 3—intolerant. *Castanea dentata* was not rated.

‖ Average of ends of range given by U.S. Forest Products Laboratory (1974).

¶ Lechowicz 1984.

of synergisms between different limiting resources, either for a single species (but see Phares 1971, Peace and Grubb 1982) or for co-occurring species (but see Donald 1957, Zeide 1980). A lively controversy has arisen (Thompson 1987, Tilman 1987, Loehle 1988, Thompson and Grime 1988, Grace 1990, Grace and Clark 1990) about whether plants can be classified by degree of tolerance to universal resource scarcity or whether tolerances to scarcity of individual resources, for example, light, nitrogen and moisture, may differ substantially within the same plant. Coexistence of plant species may depend on different tolerances of resource scarcity and a patchy distribution of limiting resources. Moreover, it may depend on negative correlations, or trade-offs, in plants between abilities to tolerate scarcity of different resources (Zeide 1980, Tilman 1982, 1988).

Plant species coexisting as adults within a uniform habitat may express niche differentiation at the seedling stage. Although this idea is not new (Braun-Blanquet 1932:314 [footnote], Ricklefs 1976, Grubb 1977), it remains relatively untested (but see Collins and Good 1987, Streng et al. 1989, Collins 1990). Resources that are fine grained to saplings or adult trees may be experienced as coarse grained by seedlings of the same species in the same environment. Saplings and adults grow branches and roots several metres laterally and vertically, simultaneously occupying many microhabitats representing broad ranges of availability of light and soil resources, while tree seedlings grow only a few centimetres in each direction and therefore encompass narrow ranges of availability of resources (Stout 1956, Lyford and Wilson 1964, Lyford 1980, Robertson et al. 1988, Latham 1990).

I hypothesize the existence, for each tree species in a temperate forest, of a range of combinations of scarce resources in which seedlings of that species can outperform seedlings of other, co-occurring tree species. If the hypothesis is true, then experiments should confirm two important predictions. First, individuals of each species should be constrained in their rates of biomass gain and patterns of carbon allocation in a manner different from other species across a variety of resource conditions. Stated in the context of statistical analysis, the species × resource interaction terms should be significant in analyses of variance of growth and allocation data from experiments in which resources are varied factorially. Second, the performance ranks of species, as estimated by rates of gain in biomass, height, and leaf area of seedlings, should vary among sets of resource conditions.

In this paper I report on greenhouse experiments examining the effects of light and soil nutrient variation on seedling growth rates and biomass allocation among six tree species co-occurring in eastern North American upland deciduous forests.

METHODS

Choice of species and seed sources

The species selected for study were mockernut hickory, northern red oak, American chestnut, American beech, blackgum, and tuliptree. They commonly cooccur in the canopies of old-growth forests throughout the central and southern Appalachians and the plateaus east and west of the mountains. Of Braun's (1950) old-growth forest samples, each representing 50–500 adult trees (usually 75–200), 8 included all 6 of the species used in the experiment, 21 included 5 species, and 11 included either 5 or 6 species with 2+ species lumped within a genus.

American chestnut has lived only in the understory as root sprouts for 50–80 yr, since human introduction of the chestnut blight, the phloem-dwelling fungus *Cryphonectria parasitica* (Murr.) Barr. For the latter half of the Holocene, however, the species dominated or was abundant in the canopies of most upland forest stands in the region (Braun 1950, Davis 1981).

The six species represent broad ranges of seed sizes, reported degrees of shade, low-nitrogen and drought tolerance, and density and anatomy of wood (Table 1). These traits reflect differences in how seedlings of each species acquire carbon, water, and mineral nutrients (e.g., Augspurger 1984, Lechowicz 1984, Guthrie 1989).

Seeds of American chestnut were from two sources: a native stand of trees (infected by chestnut blight) in a remote area in the Allegheny Mountains of south-central Pennsylvania and a blight-free planted stand in Minnesota, outside the Holocene maximum range of the species. Seeds of the other species were gathered from sites in the northern Piedmont of Pennsylvania.

Seed treatment and seedling culture

Seeds were stored and treated to break dormancy as recommended for each species in the *Seeds of Woody Plants* manual (USFS 1974). Northern red oak acorns were immersed in water at ≈49°C for 40 min to kill insect larvae. Mockernut hickory seeds were soaked in room-temperature water for at least 1 d, with several water changes per day, before storage. All seeds were washed in a weak solution of the fungicide captan and stored in slightly damp peat moss in plastic bags at approximately 4°C for several months.

The potting medium consisted of equal volumes of (1) washed number 1 silica sand, (2) heat-expanded vermiculite, and (3) sphagnum peat moss sifted through 5-mm mesh wire screen and moistened with water purified by reverse osmosis. The vermiculite, according to information supplied by the manufacturer (W. R. Grace, Fogelsville, Pennsylvania, USA), contained small extractable concentrations of five nutrients (approximately): phosphorus 0.02 mg/kg, potassium 4 mg/kg, calcium 0.5 mg/kg, magnesium 0.4 mg/kg, and iron 0.1 mg/kg. Also added to the potting medium was powdered slow-release micronutrient mix (trade name Micromax; Sierra Chemical Company, Milpitas, California, USA) at 20 mL/12 L medium. The micronutrient mix contributed (approximately, per unit mass of potting medium): sulfur 200 mg/kg (as sulfates), iron 200 mg/kg (from ferrous sulfate), manganese 42 mg/kg (from manganese sulfate), zinc 17 mg/kg (from zinc sulfate), copper 8 mg/kg (from copper sulfate), boron 2 mg/kg (from sodium borate), and molybdenum 1 mg/kg (from sodium molybdate).

Potting medium filled to 35-cm depth sections of polyvinyl chloride (PVC) pipe 40 cm deep and 10 cm diameter, standing in ordinary 15 cm diameter (6-inch) pots with holes at the bottom for drainage. Seeds were placed approximately at depths recommended for each species in *Seeds of Woody Plants* (USFS 1974). A weak solution of captan (empirical formula $C_9Cl_3H_8N_1O_2S_1$) was poured onto the potting medium once a week for ≈1 mo around the time of germination to inhibit damping-off fungi. A light foliar spray of a dilute solution of chlorothalonil (empirical formula $C_8Cl_4N_2$) was applied several times during the growing season in order to inhibit botrytis and powdery mildew fungi, both of which were problems in pilot experiments.

Manipulating light and macronutrients

Greenhouse seedlings were subjected to three light treatments. Light was adjusted for low and intermediate treatments using black plastic horticultural shade cloth. Unlike foliage, the shade cloth does not affect the spectral quality of transmitted sunlight, for example, by reducing the energy ratio of red : far-red light. Although herbaceous plants native to dense grassland (low canopy) may respond to reduced ratios of red : far-red light by increased stem elongation, the response has not been shown for tree and herb species native to bare soil environments (no canopy) and forests (high canopy; Grime and Jeffrey 1965). In a study using two forest herb species, no significant difference in growth rates or allocation was detected between natural shade with a low red : far-red ratio and artificial shade with a high red : far-red ratio (Frankland and Letendre 1978). Thus, I did not attempt to adjust spectral quality in shade treatments in the present study. I used a quantum (PAR) sensor and datalogger manufactured by LI-COR (Lincoln, Nebraska, USA) and integrating light meters (Friend 1961, Sullivan and Mix 1983) to measure the PAR photon flux density at 11 points within each greenhouse light treatment and, concurrently, at an unshaded outdoor site.

Macronutrients (300 mL of fertilizer solution per pot) were applied once per week at three treatment levels: high—concentrations around those recommended for tree seedling culture (Asher 1978, Tinus and McDonald 1979) with adjustment for the nutrient content of the potting medium, intermediate—$\frac{1}{10}$ the concentrations in high treatments, low—no macronutrients added except as trace amounts present in water purified by reverse osmosis. The high-nutrient fertilizer contained (approximately): N 120 mg/kg in nitrate and 103 mg/kg in ammonium, P 27 mg/kg, K 155 mg/kg, Ca 50 mg/kg, Mg 30 mg/kg, and S 90 mg/kg. Because young seedlings are sensitive to nutrient overdose, nutrient solutions were applied half-strength for the first 2 wk of fertilization. Fertilization of each pot was not begun until at least one green cotyledon or leaf was visible. All seedlings were fertilized until they were harvested. Water purified by reverse osmosis was provided between fertilizer applications in amounts sufficient to percolate through the potting medium and prevent accumulation of fertilizer salts. Mineral nutrient analyses were performed on the soil from six pots at harvest, representing all three nutrient treatments of the two species thought to be most and least nutrient demanding, tuliptree and mockernut hickory, respectively (methods are given in Latham 1990).

Experimental design

Three greenhouse benches were divided in half, and each half-bench was subjected to one light level. There were two blocks within each light level: one on the eastern side of the benches, near a bank of evaporative coolers, and one on the western side. Placement of the three light levels on each side was randomized, subject to the constraint that light levels were not the same on both halves of a bench. Each half-bench was divided into three squares. Each square, containing five rows of pots, received a different nutrient level. Each row contained six pots, one per species. All pots were separated by ≈28 cm center-to-center. Assignment of nutrient levels to squares within half-benches and species to pots within rows was randomized. Nine individuals of each species were subjected to each treatment combination (except for tuliptree, of which there were five per treatment combination due to low seed viability).

In order to compare the differences in measured growth responses among treatments between individuals of the same species but of different parentage, and between individuals of the same maternal parent but with different amounts of maternal provisioning, the American chestnut seedlings were divided into three equal groups based on seed source: from single-seeded ("PA_1") and triple-seeded ("PA_3") fruits of a single tree at the Pennsylvania site (PA_1 seeds were larger than PA_3 seeds) and, unsorted by seed number per fruit, from different trees at the Minnesota site ("MN").

Seed and seedling measurement

All seeds were taken from cool, moist storage and soaked in water before planting on 19 February 1987. Seeds of all species except tuliptree were towel dried and weighed after soaking. The very small size of tuliptree embryos and the irregularly broken and decayed condition of the samara wings after moist storage make seed mass for the species meaningless.

Date of germination (appearance of the shoot at the soil surface) was recorded. Seedlings were measured 4 times during the growing season (26–27 March, 29 April–4 May, 9–11 June, and 1 July) and at harvest. Seedling height (if multistemmed, of the tallest stem) and the length of each green leaf or leaflet were recorded. Seedlings were harvested from 22 June to 6 August approximately in the sequence of germination, in order to minimize variation in age at harvest. Roots were carefully hand-washed in a series of trays of clean water in order to remove adhering potting mix and preserve broken fine roots. Seedling height, the length and area of each leaf or leaflet, root dry mass, stem dry mass and aggregate leaf dry mass were recorded. Leaf areas were measured using a LI-COR area meter. Plants were dried at 60°C until mass measurements stablized (≥7 d). Dry mass was determined to the nearest milligram.

Leaf areas at the times of mid-experiment measurements were estimated from leaf lengths using calibration equations based on measurements of all leaves upon harvest. Measurements were fitted to a power function of the form $A = aL^b$ by least squares regression, where A is area (in square millimetres) and L is length (in millimetres).

Data analysis

Multiway factorial ANOVA was used to examine the effects of species, light, nutrients and, for chestnut, seed source on (1) mean absolute rates of change in height and total leaf area between germination and harvest, (2) mean absolute rates of change in shoot, root, and whole-plant dry mass from germination to harvest, and (3) root/shoot biomass ratio, specific leaf mass (SLM), and stem dry mass/length at harvest. All variables except SLM were log transformed to improve homogeneity of treatment-cell variances. Post hoc tests of significance of differences among individual treatment cells (multiple comparisons) were performed using the Tukey-Kramer procedure within treatment cells among species and within species among treatment cells (Sokal and Rohlf 1981, Day and Quinn 1989). Species were ranked by sensitivity to treatments according to the number of all possible pairwise comparisons (within species) between treatment cells showing significance by the Tukey-Kramer test at the $\alpha = .05$ level. Repeated-measures ANOVA was used to test for differences among species in height and leaf area growth curves between mid-experiment measurements.

RESULTS

Bartlett's test showed marginally significant departures from homogeneity of cell variances owing to a few outlying values in each ANOVA. The P values given below, which were calculated under the assumption that cell variances are homogeneous, underestimate the true probability of Type I error and must be interpreted with caution. However, only random (block) effects are tested over cell variances. Main effects are tested over estimated interaction variances, which are less likely to be heterogeneous. Thus the P values given for main effects are closer to the true probabilities of Type I error than those given for random effects.

Comparison of greenhouse and forest resource environments

PAR photon flux densities in (1) low, (2) intermediate, and (3) high light treatments were approximately (1) 3%, (2) 9–14%, and (3) 53–65% of the PAR in full sunlight. These figures are consistent with growing season light fluxes reported from and modelled at ground level in temperate hardwood forests in (1) densely closed canopy, (2) sparsely closed canopy or small gap, and (3) very large (≥2000 m^2) gap environments (Minckler 1961, Marquis 1965, March and Skeen 1976, Riemenschneider and Gilbert 1977, Canham et al. 1990).

TABLE 2. ANOVA of rate of change in height from germination to harvest. Data were natural-log transformed prior to calculations.

Source of variation	df	Error term	MS	F	P
Species	5	species × block (within light)	26.69	235.0	<.0001****
Light	2	block (within light)	3.80	14.0	.034
Nutrients	2	nutrients × block (within light)	20.21	64.2	.0003***
Species × light	10	species × block (within light)	0.52	4.6	.005**
Species × nutrients	10	species × nutrients × block (within light)	2.17	18.8	<.0001****
Light × nutrients	4	nutrients × block (within light)	2.20	7.0	.020
Species × light × nutrients	20	species × nutrients × block (within light)	0.21	1.8	.062
Block (within light)	3	residual	0.27	3.0	.030
Species × block (within light)	15	residual	0.11	1.2	.234
Nutrients × block (within light)	6	residual	0.31	3.5	.003**
Species × nutrients × block (within light)	30	residual	0.12	1.3	.162
Residual	342				

** $P < .01$, *** $P < .001$, **** $P < .0001$.

Samples of potting medium ($n = 6$; see *Methods*) and forest soils ($n = 110$; Latham 1990) were assayed for pH, cation exchange capacity, ammonium N, nitrate N, phosphorus, potassium, calcium, and magnesium. Calcium and magnesium were significantly different between greenhouse and forest samples (Kolmogorov-Smirnov two-sample test, $P < .05$ and .01, respectively). The use of vermiculite as the clay component in the potting medium contributed to high calcium and magnesium levels (mean ± 1 SD: Ca 2.05 ± 0.56 mg/kg; Mg 1.35 ± 0.50 mg/kg) relative to forest soils (Ca 0.66 ± 0.49 mg/kg; Mg 0.37 ± 0.08 mg/kg). In all other assays, the potting medium and forest soils did not differ significantly (Kolmogorov-Smirnov two-sample test, $P > .05$).

Effects of light and nutrients on growth rates

The effects of species, light, and nutrients on rates of change of height, total leaf area, root dry mass, and whole-plant dry mass are given for the period from germination to harvest in Tables 2 and 3. ANOVA of shoot dry mass had the same significance levels for all variables as ANOVA of whole-plant dry mass.

The age at harvest was 121 ± 11 d (mean ± 1 SD). In ANOVA of age at harvest with respect to species and treatments, species was a significant effect ($P <$ .01). Tuliptrees were significantly younger at harvest (mean 111 d) than all other species (Tukey-Kramer unplanned comparisons test, $P < .01$). The germination rate of tuliptree seeds had been unexpectedly low and many individuals of the species were from a second planting (mean germination date for the species was 29 d later than for all others). Also, chestnuts were significantly younger at harvest than hickories and beeches ($P < .05$). Chestnuts grew rapidly to large size, and many were harvested early in an attempt to minimize possible effects of root confinement.

Mean daily change in height.—Species' height growth rates were most dissimilar in high light–low and intermediate nutrient treatments, where chestnut > oak = beech > hickory = blackgum > tuliptree (Fig. 1A). Chestnut ranked highest and significantly exceeded all other species in nearly all treatments. Oak ranked second highest in all treatments and significantly exceeded lower ranking species mainly under low and intermediate nutrient treatments. In the high light–high nutrient treatment, tuliptree was not significantly different from chestnut, with highest rank, but tuliptree ranked lowest or tied for lowest rank in seven of the remaining eight treatment cells.

Hickory showed no significant effect of either light or nutrients (Table 4). Tuliptree was most sensitive to treatments. Tuliptree's response to treatments was driven more strongly by nutrient availability than light availability within the experimental ranges (Table 5). Blackgum, red oak and chestnut showed similar, but lesser, trends.

Tuliptree and hickory reversed relative rank by rate of height gain (Fig. 1A). Tuliptree exceeded hickory in high and intermediate light–high nutrient treatments while hickory exceeded tuliptree in all low nutrient treatments and in the low light–intermediate nutrient treatment. Tuliptree seedlings remained small (25–70 mm tall at harvest, mean age 111 d) at all but high nutrient treatments. At high light–high nutrients, mean height at harvest was 338 mm (maximum 470 mm). Hickory seedlings' heights at harvest (mean age 124 d) varied only from 50 to 135 mm (mean 88 mm) across all treatments.

Mean daily change in total leaf area.—In leaf area growth rate, chestnut ranked highest, significantly exceeding all other species in nearly all treatments, and red oak ranked second highest in all treatments (Fig. 1B). Tuliptree ranked lowest or tied for lowest rank in all treatments except intermediate light–high nutrients and high light–high nutrients, where it tied for highest rank.

Species' sensitivities to the treatments varied from tuliptree, with the highest rank, to hickory, with no detectable response. All species except hickory showed

TABLE 3. ANOVA of growth rates from germination to harvest. Error terms and significance levels are as in Table 2. Data were natural-log transformed prior to calculations.

	Rate of change in total leaf area				Rate of change in root dry mass			
Source of variation	df	MS	*F*	*P*	df	MS	*F*	*P*
Species	5	85.13	332.8	<.0001****	5	106.55	260.8	<.0001****
Light	2	3.52	9.2	.056	2	40.57	87.8	.005**
Nutrients	2	91.13	115.3	.0001***	2	12.21	23.2	.002**
Species × light	10	0.48	1.9	.129	10	0.77	1.9	.128
Species × nutrients	10	9.66	30.1	<.0001****	10	4.55	16.7	<.0001****
Light × nutrients	4	8.28	10.5	.008**	4	3.45	6.6	.023
Species × light × nutrients	20	0.74	2.3	.018	20	0.91	3.4	.002**
Block (within light)	3	0.38	1.5	.221	3	0.46	2.2	.087
Species × block (within light)	15	0.26	1.0	.477	15	0.41	1.9	.019
Nutrients × block (within light)	6	0.79	3.0	.007**	6	0.52	2.5	.022
Species × nutrients × block (within light)	30	0.32	1.2	.194	30	0.27	1.3	.141
Residual	340				342			

a stronger response to the experimental range in nutrients than to the experimental range in light. This was particularly apparent in tuliptree and blackgum in which, for example, seedlings subjected to low light–high nutrients significantly exceeded those exposed to high light–intermediate nutrients.

Hickory and tuliptree, hickory and blackgum, beech and tuliptree, and beech and blackgum reversed relative rank by rate of total leaf area gain (Fig. 1B). Hickory and beech generally exceeded tuliptree and blackgum at all low and intermediate nutrient treatments and in the low light–high nutrient treatment. At high and intermediate light–high nutrient treatments the reverse was generally true.

Mean daily change in shoot dry mass.—Species' shoot dry mass responses were closely similar to their whole-plant dry mass responses (Fig. 1C) except beech = hickory in all treatments but high light–high nutrients. Tuliptree and chestnut were most sensitive to treatments. Hickory showed no significant response. Tuliptree and hickory reversed relative rank from high and intermediate light–high nutrient treatments where tuliptree exceeded hickory to low and intermediate nutrient treatments where hickory exceeded tuliptree.

Mean daily change in root dry mass.—Species' root dry mass responses were closely similar to their whole-plant dry mass responses (Fig. 1C) except chestnut = beech in all treatments but high and intermediate light–high nutrients. Species differed most in the three lowest resource treatments, where chestnut = oak = hickory > beech > blackgum > tuliptree. Chestnut and red oak tied for highest rank in all treatments. Red oak and hickory tied at highest or second-highest rank in all treatments except intermediate light–low nutrients, where red oak significantly exceeded hickory.

Beech was most sensitive to treatments. All species except tuliptree and blackgum showed a stronger response to the experimental range in light than to the experimental range in nutrients. In beech, red oak, and chestnut, for example, seedlings subjected to intermediate light–low nutrients significantly exceeded those exposed to low light–high nutrients. Tuliptree showed a tendency to respond more strongly to the experimental range in nutrients than to the experimental range in light. Hickory, while least sensitive of the six species to treatments in rate of root biomass gain, did show significant response to light levels.

One species pair significantly reversed relative rank among treatments: beech exceeded or tied with blackgum in all treatments except low light–low nutrients, where blackgum exceeded beech.

Mean daily change in whole-plant dry mass.—Species' overall growth rates were most dissimilar in low and intermediate light–low nutrient treatments, where chestnut = oak > hickory > beech > blackgum > tuliptree (Fig. 1C). At high nutrients and with increasing light fewer species pairs were significantly different. At high light–high nutrients tuliptree tied with chestnut and oak. Sensitivities to treatments (Table 4) ranged from 0.31 to 0.39 for all species except hickory, which was about half as sensitive as the other species. No species pairs reversed in relative rank among treatment combinations.

Species differences in height and leaf area growth rate phenology.—Repeated-measures ANOVA showed species, time, and species × time to be highly significant effects on rates of change of height and total leaf area between germination and the three preharvest measurements (seedling mean ages 18, 54, and 90 d). Fig. 2 illustrates the variety of patterns in yearling growth rate phenology represented by the six species. The variation was related, in part, to differences in seed size (Table 1). Tuliptree, with the smallest seeds, had the lowest initial height growth rate but matched or surpassed other species by the 2nd or 3rd mo. The three members of the large-seeded Fagaceae, chestnut, beech, and oak, had high initial height growth rates, but they diverged from one another considerably in height growth rates later in the season. Hickory, with the largest seeds, had only moderately high initial height growth rates, but it had massive allocation to root growth.

TABLE 3. Continued.

Rate of change in whole-plant dry mass			
df	MS	*F*	*P*
5	101.59	325.1	<.0001****
2	32.19	127.1	.004**
2	38.50	86.7	.0002***
10	0.44	1.4	.268
10	5.94	22.1	<.0001****
4	4.47	10.1	.009**
20	0.62	2.3	.018
3	0.25	1.4	.230
15	0.31	1.8	.037
6	0.44	2.5	.021
30	0.27	1.5	.042
342			

Effects of light and nutrients on biomass allocation

In ANOVA of root/shoot ratio and SLM, species, nutrients, and species × nutrients generally were significant effects (Table 6). ANOVA of stem dry mass/length had the same significance levels for all variables as ANOVA of whole-plant dry mass. Unlike growth rates, some allocation variables showed negative as well as positive effects of increasing resource availability.

Root/shoot dry mass ratio.—Species' root/shoot allocation was most dissimilar in the low light–high nutrient treatment, where hickory > oak = beech > blackgum > chestnut > tuliptree. Hickory ranked highest and significantly exceeded all other species in all treatments (Fig. 3A). Chestnut ranked lowest or tied for lowest rank in all treatments; all other species except blackgum significantly exceeded chestnut at high light–high nutrients. All species except chestnut significantly exceeded tuliptree at high light–low nutrients.

Blackgum showed greatest sensitivity to treatments (Table 4). It responded more strongly to the experimental range in nutrients than to the experimental range in light, but the data indicated both a negative effect of nutrients and a positive effect of light (Table 5). Chestnut also showed high sensitivity to treatments, responding negatively to high nutrient levels. Other species responded to treatments in a similar manner to, but more weakly than, chestnut except for hickory, which had no detectable response.

Specific leaf mass.—Chestnut, hickory and red oak ranked highest or tied for highest rank in all treatments (Fig. 3B). Tuliptree ranked lowest or tied for lowest rank with blackgum in all treatments. SLM increased with increasing light in all species. Chestnut, the second most sensitive species (after blackgum), showed evidence of a negative effect of nutrients as well as a strong positive effect of light. Tuliptree responded the least. SLM was the only measured variable to which hickory showed a strong response.

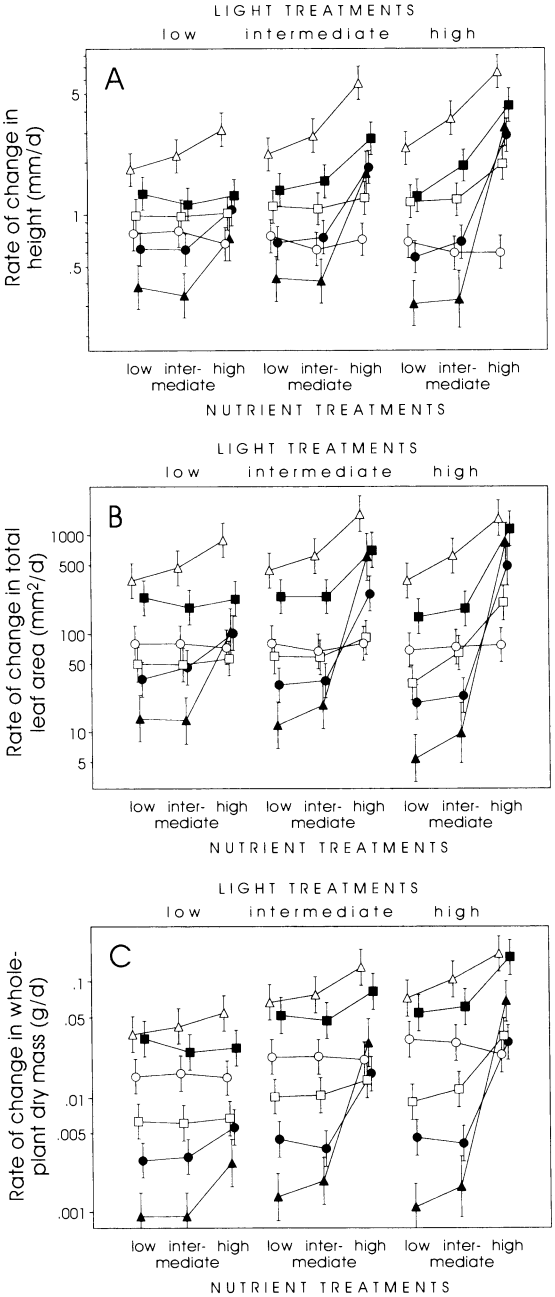

FIG. 1. Treatment effects on growth rates, showing rank reversals between species among treatments as crossed lines connecting data points. Species are, in descending order of seed mass, mockernut hickory (○), northern red oak (■), American chestnut (△), American beech (□), blackgum (●), and tuliptree (▲). Error bars represent 95% confidence intervals for the treatment cell means computed by the GT2 method (Gabriel 1978, Sokal and Rohlf 1981:249–250), a multiple-comparisons test similar to, but somewhat more conservative than, the Tukey-Kramer test (Dunnett 1980).

TABLE 4. Species' relative sensitivity to treatments. Data are the percentage of all 36 possible pairwise comparisons between treatment cells (within species) showing significance by Tukey-Kramer test at $P < .05$.

Response variable	*Carya tomentosa*	*Quercus rubra*	*Castanea dentata*	*Fagus grandifolia*	*Nyssa sylvatica*	*Liriodendron tulipifera*
Rate of Δ height (mm/d)	0	36	28	17	36	44
Rate of Δ total leaf area (mm^2/d)	0	39	31	22	47	56
Rate of Δ shoot mass (mg/d)	0	38	44	28	36	47
Rate of Δ root mass (mg/d)	17	31	22	53	22	39
Rate of Δ total biomass (mg/d)	17	39	33	31	36	39
Root/shoot biomass ratio	0	33	50	19	53	42
Specific leaf mass (mg/cm^2)	53	33	64	42	67	25
Stem dry mass/length (mg/cm)	22	19	28	39	19	39

Stem dry mass/length.—Red oak and chestnut tied for highest rank across all treatments. Tuliptree and beech responded most sensitively to treatments. These two species showed a stronger response to the experimental range in nutrients than to the experimental range in light whereas chestnut and hickory showed the reverse pattern.

The block effect

Block and block × species were significant effects in ANOVA of SLM (Table 6). Block × nutrients was significant in ANOVA of height and leaf area growth rates and root/shoot biomass ratio (Tables 2, 3, and 6). These results may indicate responses to temperature or humidity, since one block in each light level was near a bank of evaporative coolers. Most species tended to have higher mean SLM in the blocks nearer the coolers, especially beech (mean ± 1 SE = 44.22 ± 1.51 vs. 41.06 ± 0.93 g/cm^2), but tuliptree had lower mean SLM in the blocks nearer the coolers (21.13 ± 2.52 vs. 28.08 ± 1.30 g/cm^2). Height and leaf area growth rates tended to be slower with low nutrients and faster with high nutrients in the blocks nearer the coolers. Root/shoot biomass ratio tended to be higher with low nutrients and lower with high nutrients in the blocks nearer the coolers.

American chestnut

American chestnut seedlings ranked higher (or, in root/shoot ratio, lower) across a broader range of resource combinations than any of the other species. In sensitivity to treatments (Table 4), chestnut ranked second highest, after blackgum, in root/shoot biomass ratio and SLM. Chestnut was the only species showing evidence of a negative effect of nutrients as well as a strong positive effect of light on SLM (Table 5). Northern red oak most often tied in rank with chestnut in growth and allocation responses but the two species' sensitivities to treatments were different. Chestnut showed less sensitivity than red oak in all growth rate variables, but it exceeded red oak in sensitivity in all allocation variables.

Within-species differences attributable to seed parent

The chestnuts from the Pennsylvania seed parent weighed significantly less than those from Minnesota (PA 3.54 ± 0.43 mg, MN 5.28 ± 0.72 [mean ± 1 SD]; Mann-Whitney U test, $P < .0001$). Seed mass was significantly negatively correlated with time elapsed from planting to germination ($R_S = 0.55$; $P < .0005$), but the effects of seed mass and seed parent were confounded, since there was no correlation between seed mass and time from planting to germination within seed lots ($P > .5$).

Nuts from the Pennsylvania seed parent occurring singly in the fruit (PA$_1$) significantly exceeded nuts from triple-seeded fruits (PA$_3$) in size (PA$_1$ 3.70 ± 0.34 mg, PA$_3$ 3.33 ± 0.45 mg [mean ± 1 SD]; Mann-Whitney U test, $P < .001$). Seed number per fruit was not a

TABLE 5. Species' relative sensitivity to experimental variation in light (L) vs. nutrients (N). Data are the percentage of all 36 possible pairwise comparisons between treatment cells (within species) showing significance by Tukey-Kramer test at $P < .05$ where the difference in growth or allocation response can be attributed mainly to light where nutrients were constant or varied inversely with light, or mainly to nutrients where light was constant or varied inversely with nutrients. The response variable was higher (+) or lower (−) with higher light or nutrients.

	Carya tomentosa		*Quercus rubra*		*Castanea dentata*		*Fagus grandifolia*		*Nyssa sylvatica*		*Liriodendron tulipifera*	
Response variable	L	N	L	N	L	N	L	N	L	N	L	N
Rate of Δ height (mm/d)	0	0	+6	+14	+3	+6	+3	+3	+3	+17	+6	+22
Rate of Δ total leaf area (mm^2/d)	0	0	+6	+17	0	+14	+3	+8	+3	+28	+6	+33
Rate of Δ shoot mass (mg/d)	0	0	+11	+14	+8	+14	+6	+6	+3	+17	+6	+25
Rate of Δ root mass (mg/d)	+14	0	+22	0	+19	0	+25	+6	+3	+3	+6	+17
Rate of Δ total biomass (mg/d)	+14	0	+17	+6	+8	+3	+8	+6	+3	+17	+6	+17
Root/shoot biomass ratio	0	0	0	−17	0	−36	0	−14	+6	−33	0	−33
Specific leaf mass (mg/cm^2)	+31	0	+25	0	+44	−6	+31	0	+47	0	+22	0
Stem dry mass/length (mg/cm)	+17	0	+6	+3	+11	+3	+6	+17	+3	+6	+6	+17

TABLE 6. ANOVA of biomass allocation from germination to harvest. Error terms and significance levels are as in Table 2.

Source of variation	Root/shoot biomass ratio df	MS	F	P	Specific leaf mass df	MS	F	P
Species	5	24.14	231.2	<.0001****	5	3853.2	64.9	<.0001****
Light	2	2.17	8.1	.064	2	12710.0	43.7	.0097**
Nutrients	2	23.21	92.0	.0002***	2	107.6	3.2	.114
Species × light	10	0.55	5.3	.002**	10	148.1	2.5	.053
Species × nutrients	10	1.05	11.6	<.0001****	10	120.3	4.7	.0006***
Light × nutrients	4	0.59	2.3	.170	4	21.7	0.6	.655
Species × light × nutrients	20	0.19	2.1	.032	20	28.3	1.1	.384
Block (within light)	3	0.27	3.3	.021	3	290.9	14.0	<.0001****
Species × block (within light)	15	0.10	1.3	.211	15	59.4	2.9	.0005***
Nutrients × block (within light)	6	0.25	3.1	.006**	6	33.8	1.6	.137
Species × nutrients × block (within light)	30	0.09	1.1	.309	30	25.3	1.2	.202
Residual	342				342			

significant effect in ANOVA of *PA* seedling growth responses to treatments ($P > .37$), nor was there any significant interaction between seed number per fruit and light or nutrients ($P > .40$). Similarly, the main effect and interaction terms of seed number per fruit were nonsignificant in ANOVA of root/shoot biomass ratio ($P > .57$), SLM (P > .02) and stem dry mass/length ($P > .08$). (The block effect was omitted from these ANOVAs because including it resulted in $n = 0$ for one or more cells.)

By coincidence harvest date and age at harvest were significantly different between seed sources. PA seedlings were harvested an average of 13 d earlier and 9 d younger than MN seedlings (Mann-Whitney *U* test, $P < .0001$). However, with an overall mean age of harvest for the species of 119 d the difference in mean age between the two groups was <8%. The confounding of harvest date with seed source is therefore judged not to invalidate analyses of differences in mean daily rates of biomass gain among seedlings grouped by parentage (Table 7).

In ANOVA of height growth rate during the second measuring period, seed source × light treatment and seed source × nutrient treatment were significant ($P < .001$). In both cases, the MN seedlings grew disproportionately faster than the PA seedlings at higher resource levels than would be predicted by the two groups' relative growth rates at lower resource levels.

DISCUSSION

The experiment addressed one hypothesis about what maintains tree species diversity in upland moist-temperate forests. The results indicate clear differences in the abilities of six tree species that co-occur as adults in apparently uniform habitat, to exploit resources as seedlings. Individuals of each species were constrained in their rates of biomass gain and patterns of carbon allocation in a manner different from those of other species across a variety of resource conditions. When ranked by seedling growth characteristics associated with competitive ability, the hierarchy of four species changed with variation in resource levels. Differences in performance ranking across small-scale resource gradients may translate into different competitive abilities among species. Resulting patterns in relative species

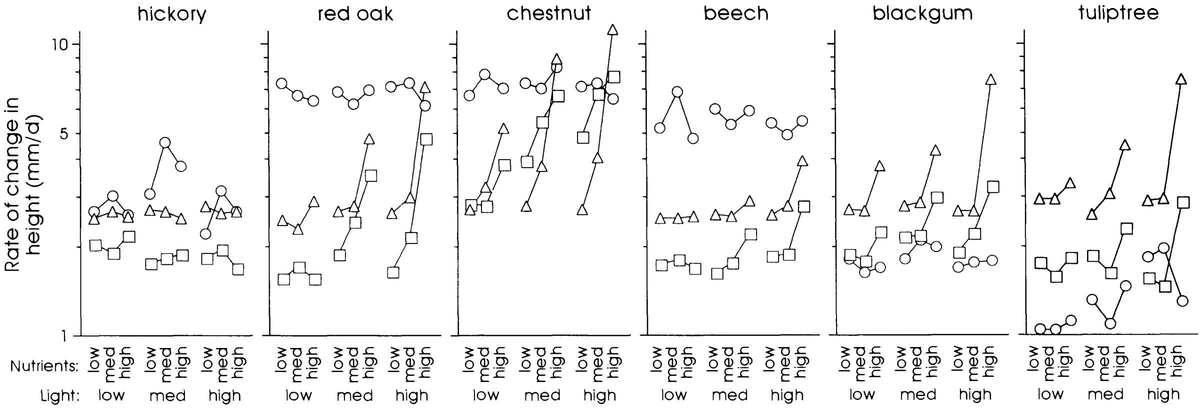

FIG. 2. Species' mean rates of change in height during three time intervals between germination and the three preharvest measurements (mean ages 18, 54, and 90 d): germination to first measurement (○), first to second measurement (□), and second to third measurement (△). Lines connecting treatment-cell means correspond to the lines shown on Fig. 1 (they are not growth curves over time).

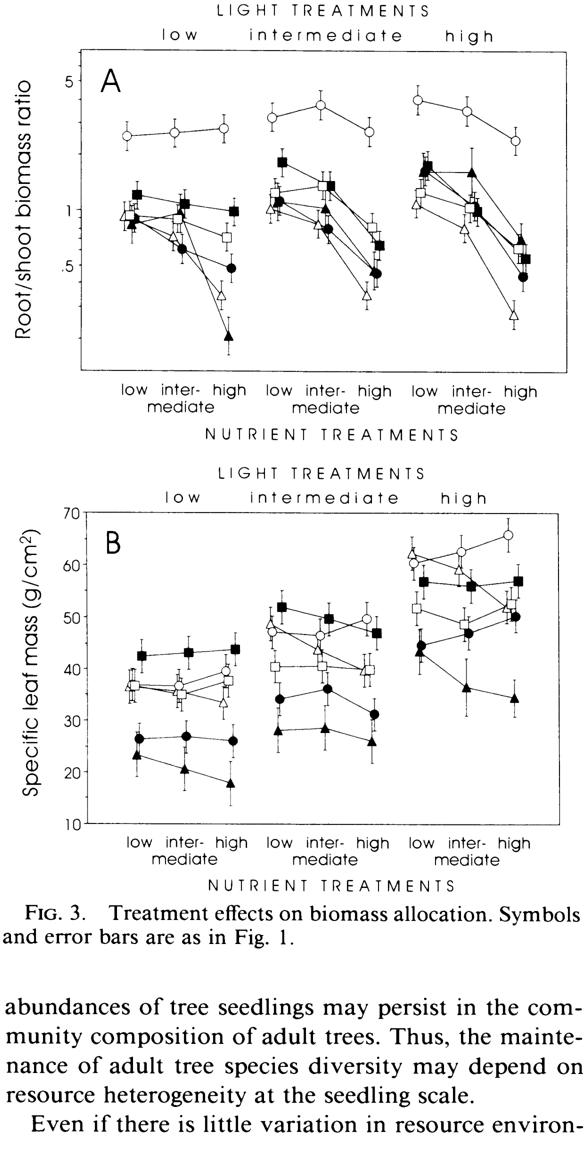

FIG. 3. Treatment effects on biomass allocation. Symbols and error bars are as in Fig. 1.

abundances of tree seedlings may persist in the community composition of adult trees. Thus, the maintenance of adult tree species diversity may depend on resource heterogeneity at the seedling scale.

Even if there is little variation in resource environment between adults of sessile organisms, juveniles in the same community might populate a broad range of habitat conditions owing to their small size and to the spatial scale of resource variation (Grubb 1977). This is especially likely to be true of organisms in which the size disparity between juveniles and adults is very great, for example, trees. This study demonstrates differences among tree species in seedling growth responses across different resource combinations. A companion study (Latham 1990) suggests that the scale of spatial heterogeneity in resources most likely to be limiting across an upland forest floor renders the resource environment much more coarse grained for tree seedlings than for adult trees.

Variation in competitive hierarchies among species with variation in resources at the seedling stage cannot be ruled out as a potentially important factor in determining species composition of adult trees in forests. The regeneration niche idea provides insight into how resource availability and competition may interact to produce the species composition patterns associated with postdisturbance succession. Its predictive power, however, is limited by additional species-specific effects on immigration, mortality, and fecundity from other processes, including dispersal, disturbance, predation, disease, and parasitism. The gap between relative species performance of yearlings and patterns of species composition of long-lived adults is admittedly a wide one.

The work reported in this paper touches on two sets of conceptual models in plant community ecology so far given little experimental attention. Stated as alternative hypotheses, they are: (1) shifting competitive hierarchy vs. fundamental niche differentiation, to explain how different adaptations among species may affect the outcome of competition for the same resources and (2) highest diversity with moderately low nutrients vs. highest diversity with highest biomass, to relate ecosystem productivity and species diversity.

TABLE 7. American chestnut seed-source effect on measured growth variables in ANOVA with seed source (PA = Pennsylvania; MN = Minnesota), light treatment, and nutrient treatment as independent variables ($n_{PA} = 46$; $n_{MN} = 35$).†

Response variable	Mean, PA seedlings	Mean, MN seedlings	*F*	*P*
Rate of Δ height (mm/d), germination–harvest	2.793	4.695	97.8	<.0001****
Rate of Δ total leaf area (mm^2/d), germination–harvest	603.5	1102	84.7	<.0001****
Rate of Δ root dry mass (mg/d), germination–harvest	0.028	0.038	19.4	.0001***
Rate of Δ stem dry mass (mg/d), germination–harvest	0.015	0.027	33.0	<.0001****
Rate of Δ leaf dry mass (mg/d), germination–harvest	0.029	0.048	67.4	<.0001****
Rate of Δ height (mm/d), late March–April	7.62	7.07	2.2	NS
Rate of Δ leaf area (mm^2/d), late March–April	728	1210	52.8	<.0001****
Rate of Δ height (mm/d), May–early June	2.55	6.43	159.7	<.0001****
Rate of Δ leaf area (mm^2/d), May–early June	808	1320	79.9	<.0001****
Rate of Δ height (mm/d), mid- to late June	2.12	3.57	7.3	.009**
Rate of Δ leaf area (mm^2/d), mid- to late June	756	1090	6.5	NS
Root/shoot biomass ratio	0.824	0.623	18.6	.0002***
Specific leaf mass (mg/cm^2)	47.5	43.2	13.9	.0007***
Stem dry mass/length (mg/cm)	43.5	51.6	8.6	.005**

** $P < .01$, *** $P < .001$, **** $P < .0001$.

† The block effect was omitted because including it resulted in $n = 0$ for one or more cells. Analysis of covariance with seed mass as the covariate was performed in each case where seed mass was found to be significantly correlated with the dependent variable.

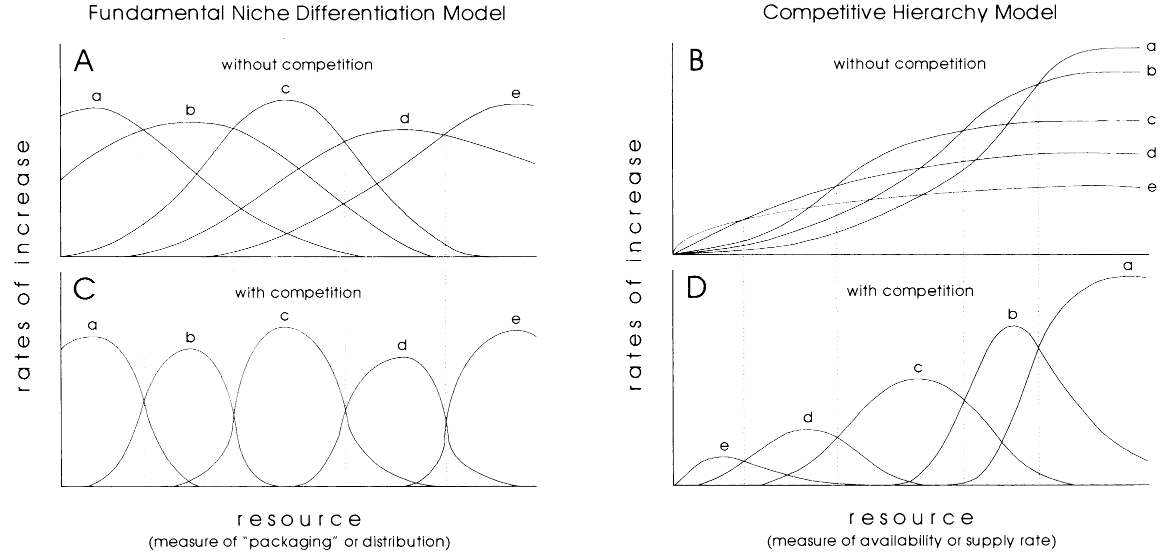

FIG. 4. Comparison of fundamental niche differentiation and competitive hierarchy models of resource partitioning among similar, co-occurring plant species. Competition is assumed to reduce fecundity, survival, and absolute growth rate. The adverse effects of competition are assumed to fall disproportionately upon the smaller of two competing individuals (Thomas and Weiner 1989). Thus, for plants, rates of increase can refer to growth rates of either populations or individuals.

Shifting competitive hierarchy vs. fundamental niche differentiation

Four major hypotheses link species distributions with environmental gradients (Louda 1989): (1) physiological and morphological specialization to different portions of gradients, and changes among species along gradients in (2) relative interspecific competitive abilities, (3) dispersal, and (4) predation pressure. The first two relate directly to gradients in fundamental resources. They have been cast as alternative hypotheses (Keddy 1989): fundamental niche differentiation (Fig. 4A, C) vs. shifting competitive hierarchy across resource gradients (Fig. 4B, D). Results of the experiments described in this paper support a major prediction of both models: with resource variation one should detect variation in performance ranking of species in measures linked with competitive ability. However, the results also support key assumptions of the shifting competitive hierarchy model (Keddy 1989).

The first assumption clearly differentiates the shifting competitive hierarchy model from the fundamental niche differentiation model: the niches of co-occurring species are inclusive, that is, all species perform better at higher levels of limiting resources (Fig. 4B). The idea of inclusive niches conflicts with fundamental niche differentiation in which co-occurring species' performance maxima are separated along resource gradients (Fig. 4A).

The data from this study clearly show better performance in variables associated with competitive ability at higher levels of limiting resources (Fig. 1). All species except mockernut hickory show monotonic increases in rates of gain in total leaf area, height, and shoot mass with increases in light and nutrients. Hickory shows neither an increase nor a decrease across the experimental range of resource variation in these traits but, like the other species, it increases in rate of gain in root mass and whole-plant mass with increasing resources.

Fundamental niche differentiation may apply best to heterotrophs and competitive hierarchy to autotrophs. Fundamental niche differentiation has been applied classically to animals. The resource gradients along which niches are defined have been measures reflecting the vast diversity in how food items are "packaged" and distributed spatially and temporally (Hutchinson 1957, MacArthur 1958, Root 1967, Vandermeer 1972). Because nonparasitic plants are autotrophic and depend on a small number of resource items varying mainly in quantity, all species' fundamental niches virtually coincide with respect to resources alone. The fundamental niche differentiation model might appear to apply successfully to plants when the resource gradient is confounded with a stress gradient. For example, implicit in moisture availability gradients are oxygen deprivation and, in many situations, flood scouring, ice movement, silt deposition, and other effects of inundation unrelated to plants' use of water as an essential resource.

The second assumption presumes an individual's competitive ability and low-resource tolerance (the shape of the resource–response curve, Fig. 4B, D) are largely innate and species specific. Individuals' abilities to adjust in response to environmental cues must be constrained such that a species' competitiveness and tolerance are distinct from those of other species. The assumption is supported by the experimental results in two ways.

First, genetic control of traits associated with competitive ability and tolerance of resource scarcity is shown even within species. Growth and allocation differed significantly among chestnut seedlings grouped by seed source but not among chestnut seedlings grouped by the number of seeds per fruit (thus, by seed size) within the offspring of a single seed parent. The differences thus are more likely due to genetics than maternal provisioning.

Second, ANOVA and post hoc pairwise multiple comparisons demonstrate that between-species differences in growth patterns overshadow within-species differences. The strongly significant effects on growth rates of species, species × nutrients and, in several variables, species × light and species × light × nutrients (Tables 2, 3, and 6) indicate species differences in individuals' growth responses to resource combinations.

Some of the species differences in response to nutrients might have been an artifact of the use of small amounts of fungicide in the greenhouse experiment to prevent damping-off and powdery mildew. Tree seedlings, especially those with coarse roots, may depend to varying degrees upon mycorrhizae for water and nutrient uptake under most natural conditions. The influence of mycorrhizal association upon relative species ranking in growth and allocation variables is an important but neglected area of research. The scant evidence available for trees suggests a general amelioration of competition between hosts, but it also suggests that mycorrhizal effects on tree–tree competition are not simple. The effects may vary widely between different pairs of tree species. Even in a particular tree species pair, effects of mycorrhizae on competitive outcome may vary between different species of fungal associates and in different environments (Perry et al. 1989).

The third assumption (shared with the fundamental niche differentiation model) considers that trade-offs exist between competitive ability on the one hand and tolerance of low resource levels on the other. Due to constraints imposed by ancestry and to the incompatibility of key physiological and morphological traits, members of a species can be good at one or the other but not both. Plants that can thrive in the shade or on infertile soil or in a dry habitat generally grow slowly even if they live where there is no resource shortage (Grime 1977, 1979, Chapin 1980). Inherently slow growth apparently is a side effect of the adaptations enabling plants of some species to grow in difficult environments (Chapin 1980). Plants that can take advantage of resource abundance by growing fast and quickly depriving their competitors of sunlight usually languish or die in situations of low resource availability. This trade-off is thought to be a necessary condition for the maintenance of plant species diversity (Salisbury 1929, Tilman 1988, Petraitis et al. 1989). If there were no such trade-off, then either the brunt of natural disturbance or predation must always fall hardest on competitively superior species or generalist super-competitor species should be expected to dominate all environments.

Certain patterns in the data reported here (Figs. 1 and 3) support the trade-off assumption. Tuliptree is classified as the most resource-demanding, i.e., least tolerant of resource scarcity of the six species (Table 1). Consistent with a trade-off model, it achieved highest rank in height and total leaf area at the highest resource levels (tied with chestnut and red oak) but was significantly smaller in both measures than all other species at the lowest resource levels. Alternatively, it is possible that the effect of having the smallest seeds may have persisted through much of the period from germination to harvest, particularly since tuliptrees were harvested slightly younger than other species.

Mockernut hickory is classified as the most drought tolerant of the six species (Table 1). Consistent with a trade-off model, it grew more slowly in height and total leaf area than all other species at the highest resource levels despite having the largest seeds. Its shoot growth rates at the highest resource levels were not significantly faster than at the lowest resource levels.

The contrasting growth responses of chestnut seedlings from different seed sources also support the idea of trade-offs. PA genotypes were significantly slower growing and had significantly higher root/shoot biomass ratio and SLM than the MN genotypes (Table 7). All three traits are associated with greater tolerance of nutrient-poor environments and relative competitive inferiority in nutrient-rich environments (Chapin 1980).

However, American chestnut's overall performance represents an apparent exception to the assumption of trade-offs and to the prediction of shifting species' performance ranks with resource variation. The ranges of light and nutrients used in the experiment include no resource combination where the species was outranked by any of the other five species in rates of gain in height or total leaf area. In a companion study conducted at a forest site (Latham 1990), chestnut yearlings raised from the same seed lots as those in the greenhouse experiment were outranked in shoot growth rates by yearlings of other tree species only at very low light levels. Chestnut may be, at least in mesic upland temperate forests of eastern North America, both a broad generalist and a strong competitor.

Before the first half of this century when chestnut blight eliminated all mature stems, American chestnut was one of the most abundant tree species over its $>800\,000$ km^2 historic range. Across much of the area chestnut trees comprised $>50\%$ of the forest canopy (Braun 1950). Chestnut's Holocene range expansion from refugia it occupied during the Wisconsinan glacial maximum was the most recent of all the wind-pollinated forest tree species in eastern North America. It reached Pennsylvania $\approx$6000 yr ago and southern New England only 2000 yr ago, some 2000–8000 yr later than eastern hemlock, maples, oaks, American beech, and the heavier seeded hickories (Davis 1981). Thus, chestnut must have seized canopy dominance from many long-established species in a remarkably short period.

The high performance ranking by chestnut seedlings over a broad range of resource conditions may have contributed to the species' rapid Holocene invasion across a major portion of the North American moist-temperate forest biome. The highly competitive mode of American chestnut has been demonstrated in the wild, outside the Holocene maximum range of the species (Paillet and Rutter 1989). It may portend the rapid recovery of chestnut's former prominence if blight-resistant strains emerge (Burnham et al. 1986) or if the viroid-induced decline in the virulence of the blight fungus becomes widespread (Anagnostakis 1987).

Soil moisture was not included as a treatment variable in this study but, like light and nitrogen, it is often cited as a potentially limiting resource in plant communities to which co-occurring species have different responses (e.g., Davies and Kozlowski 1975, Bunce et al. 1977, Federer 1977, Roberts et al. 1979, Ginter-Whitehouse et al. 1983, Pallardy et al. 1983, Bahari et al. 1985, Masarovičová and Elias 1986, Abrams 1988). Although strong root allocation may increase a plant's competitive ability for both nutrients and moisture simultaneously, a plant's competitive ability for nutrients may not predict its competitive ability for moisture. Other morphological and physiological properties are involved in competitiveness for the two resources besides robust root allocation, and they are not the same for nutrients as they are for moisture (compare Chapin 1980 and Pallardy et al. 1983). Root mass allocation and nutrient response data from this study hint at ways in which soil moisture variation might affect competitive hierarchy among the species examined.

Mockernut hickory has a lower maximum rate of gain in height, total leaf area, and shoot mass than the other five species but allocates a much greater proportion of its biomass to root tissue. Neither light nor nutrients had any detectable effect on rates of gain in height, leaf area, or shoot mass. Hickory seedlings appear to invest heavily in roots, including a large taproot, no matter where they establish. Large seeds, rich in stored nutrients, enable them to form a large taproot even in low light–low nutrient environments. Neighboring small plants with smaller roots and larger shoots might outcompete a hickory seedling as long as soil moisture remained high, but they may be incapable of surviving a drought. Hickories, in a sense, may trade the ability to compete for light in the short term for the ability to remain alive in the event of a severe water shortage. The trade-off fits Goldberg's (1990) category of "mechanisms of tolerance that increase survival but not short-term growth rates at low resource levels."

Beech and blackgum have similar, intermediate tolerances of nitrogen scarcity but blackgum is highly tolerant and beech highly intolerant of a lack of moisture (Table 1). Beech exceeded or tied with blackgum, when ranked by rate of root biomass gain, in all treatments except low light–low nutrients, where blackgum exceeded beech. One of the adaptations of beech allowing it to persist in heavy shade (Table 1) may be allocation to leaves and stem at the expense of root production at the lowest light levels. Preferential allocation to the shoot may entail increased risk of mortality in case of drought. One of the characteristics of blackgum enabling it to survive in drought-prone habitats may be allocation to roots at the expense of shoot growth at the lowest light levels as insurance against future drought. Blackgum's drought tolerance differs from that of hickory. It ranked low across all treatments in rate of root biomass gain and had the highest rank of all six species in sensitivity to treatments in root/shoot biomass ratio. It showed both a positive response to nutrients and a negative response to light in root/shoot biomass ratio. Blackgum appears to economize strongly on root investment in response to environmental cues, at least within the experiment's range of high moisture availability. On the other hand, its resistance to drought and rank reversal with beech in root biomass accumulation rate seem to indicate that blackgum is also responsive to environmental cues related to the likelihood of moisture deficit, cues presumably absent in the moisture-abundant conditions of the greenhouse experiment.

Highest diversity with moderately low nutrients vs. highest diversity with highest biomass

One set of theories links greater energy flow through a system and the resulting higher biomass with more individual organisms, greater environmental heterogeneity and, thus, more species (Pianka 1966, Brown 1981, Wright 1983). Others predict the highest species diversity at moderately low nutrient levels and low to intermediate biomass (with environmental heterogeneity held constant). For example, Huston (1979) hypothesizes that low nutrient availability slows a community's approach toward competitive equilibrium. Natural disturbance at a given rate in a low-nutrient system is thus more likely to prevent dominance by strong competitors and elimination of weak competitors than disturbance occurring at the same rate in a more rapidly growing high-nutrient system. Tilman's (1982, 1986) theory of competition for resources in a heterogeneous environment predicts greater niche diversification in plant communities at low nutrient levels where two or more resources may be limiting, each in a different set of microhabitats, than at higher nutrient levels where only light is likely to be limiting. Increasingly, investigators are finding ecosystems with moderately low nutrients to have higher species diversity than similar systems with the highest levels of nutrients and biomass (e.g., Huston 1980, Moore et al. 1989).

Data showing higher levels of diversity in low-nutrient systems have been mainly observational. This study and associated studies in a low-nutrient forest (Latham 1990) experimentally address the crucial question, in relating species diversity and nutrient levels, whether performance hierarchies among species shift with resource variation. The occurrence of performance rank shifts among species across the nutrient gradient is consistent with the idea that competitive hierarchy helps to maintain species diversity in a heterogeneous environment, assuming that meaningful vestiges of the relative abundances and distributions of seedlings persist in adult populations. The rank reversals in shoot growth rate of five species pairs all occurred between nutrient treatments, often within a light treatment. Most previous research showing different growth responses of tree species among resource levels has focused on light (e.g., Loach 1967, 1970, Lorimer 1983, Augspurger 1984, Canham and Marks 1985). This study suggests that tree species, as seedlings, may vary as widely in the morphological and physiological traits associated with nutrient uptake as in traits associated with light utilization.

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