RESPONSES OF EARLY SUCCESSIONAL NORTHERN HARDWOOD FORESTS TO CHANGES IN NUTRIENT AVAILABILITY

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Abstract. In many mesic forests the dominant trees are limited concurrently by light and soil resources, and understanding the mechanisms of competition and predicting outcomes of competition are especially difficult when co-limitation exists. We altered soil resource availability during the early stages of stand development after clearcutting of northern hardwood forests to examine the mechanism of competition. Specifically, we sought empirical evidence about the role of various physiological, morphological, allocational, and architectural responses in regulating plant competition. We expected the competitive ability of the extreme pioneer species, *Prunus pensylvanica* (pin cherry), to be enhanced by increased nutrient supply, with consequent effects at the community and ecosystem levels of organization. Nutrient availability was increased by about three-fold by monthly fertilization for 6 yr in nine even-aged northern hardwood stands dominated by pin cherry, three each of three ages (6, 12, and 18 yr at initiation of the experiment). Measurements in the control plots indicated that the interval of stand development from age 6 to 23 yr was marked by a peak in basal area and leaf area of pin cherry at about age 17 yr, followed by a steady decline in *P. pensylvanica* dominance thereafter. Fertilization increased and prolonged the dominance of *P. pensylvanica*, indicating that nutrient limitation accelerates the demise of this species during the second and third decades of stand development.

All species in the plots responded to fertilization with increased foliar nutrient (N, P, and K) concentrations and often higher specific leaf area (area : mass ratio), and these responses were most pronounced for *P. pensylvanica*. Although the light-response curve for photosynthesis of *P. pensylvanica* was altered by fertilization, with higher rates at low light levels, photosynthesis of its principal competitor, *Betula papyrifera*, was not affected. The marked growth response of *P. pensylvanica* was accompanied by changes in its canopy architecture, as the trees had more leaf area per unit stem basal area, and proportionally more of this leaf area was in the upper canopy. In contrast, height and leaf area of *B. papyrifera* were similar in the control and fertilized plots. Seed deposition of *P. pensylvanica* also increased in the fertilized plots during one year of high seed production. Thus, the performance in competition of *P. pensylvanica* was improved by the removal of apparent nutrient limitations on its physiological performance, canopy growth, and ability to compete for light.

Leaf area index of the fertilized plots was only slightly higher than the control plots, and the same was true for stand basal area. The removal of nutrient limitation increased the intensity of one-sided competition for light by concentrating the dominance among the largest trees; consequently, very high mortality of suppressed stems of all species occurred. The increased dominance of the fast-growing *P. pensylvanica* contributed to increases in aboveground net primary productivity (ANPP) in the fertilized plots. Some of this ANPP response was probably associated with reduced C allocation to roots in some of the fertilized plots, but this pattern was not consistent across all the stands. The results indicate that the outcome of interspecific competition in mesic forests, where co-limitation by light and soil resources prevails, depends upon the effect of site quality upon the relative intensity of one-sided competition (for light).

Key words: birch; canopy architecture; co-limitation; competition; leaf area index; northern hardwood forests; photosynthesis; pin cherry; productivity; Prunus pensylvanica; *resorption; specific leaf area.*

INTRODUCTION

Natural vegetation exhibits a complex three-dimensional structure (i.e., spatial distribution of leaves, roots, and stems) that influences its function both in ecosystem energetics and material cycling, and in the regulation of biotic interactions and maintenance of biodiversity. The development of this complex structure through the process of plant succession following large-scale disturbance has been the subject of numerous observational studies (Finnegan 1984) as well as some manipulative experiments. Among the conceptual

models of the plant succession process is the initial floristics model, according to which all the floristic elements of the recovering plant community establish soon after a disturbance event (Egler 1954). The initial floristics model often applies in forests (Hughes and Fahey 1991), so that the eventual structure and composition of the mature plant community is dictated by the initial colonization process followed by intense intra- and interspecific competition, which eliminates most individuals through time. Hence, to predict the course of forest development following large-scale disturbance in many forest ecosystems we must understand both plant colonization and resource competition within and among populations of colonizers. These interactions also will dictate the patterns in nutrient cycling and energy flow during secondary succession. Ecosystem development has been characterized in detail for northern hardwood forest ecosystems in the northeastern United States (Bormann and Likens 1979), and the mechanisms of colonization following disturbance are well known (Marks 1974, Hughes and Fahey 1991); however, a detailed understanding of competitive interactions among colonizers is still lacking. The overall goal of the present study was to better understand competitive interactions in northern hardwood forest ecosystems, and thereby to advance our knowledge of forest ecosystem structure and function.

For monospecific communities, the process of competition during stand development can be described most simply by self-thinning models (Yoda et al. 1963), but these models lack desirable mechanistic attributes. Although Clark (1990) has analyzed the connections among plant growth, mortality, and resource availability during stand development in monospecific forests, the complexities introduced by interspecific variation in plant morphology, allocation, and life history strategies make the analytical treatment of the succession process difficult in mixed natural stands. Tilman (1985) described a theoretical model of interspecific competition for belowground resources and then tested the theory's predictive capacity (e.g., Tilman 1987). However, problems introduced by competition for light or co-limitation by light and soil resources complicated analytical treatment (Tilman 1990). In reviewing the literature on competition for light in forests, Cannell and Grace (1993) concluded that practical, empirical approaches for describing stand development have run far ahead of our mechanistic understanding of species' responses. Systematic information on physiological, morphological, and allocational responses of different species to changes in resource availability are needed to advance our ability to predict competitive outcomes—especially at the level of entire forest ecosystems.

In the conceptual framework described by Goldberg (1990), the outcome of interspecific competition depends upon a suite of species traits related to effects upon and responses to changing availability of resource

intermediaries (light, water, nutrients, space). Such traits include plant carbon and nutrient allocation to resource-acquiring organs; the architecture and physiological activity of these organs; and resource retention, conversion efficiency, and a variety of indirect effects on resource availability. Although the role of competition in structuring plant communities might be understood in these terms, there is little empirical information on the effects of resource availability on the plant traits that mediate these interactions (Goldberg 1990). Undoubtedly, these interactions also play an important role in regulating patterns of primary productivity and nutrient cycling in forests. For example, age-related declines in the productivity of even-aged forest stands have been clearly established (Assman 1970) and the syndrome has been associated with structural and physiological features of the forest stands (Ryan et al. 1997). In natural, mixed-species stands, the scramble for canopy dominance mediated by the species traits will also play a crucial role in the ecosystem-level pattern of energy flow. We hoped to improve our understanding of the mechanisms of plant competition in early successional forests, and their implications for ecosystem processes, by examining stand development in natural, mixed-species stands that arise following clearcutting. By altering soil resource availability in forests consisting of a mixture of a few species with contrasting life history traits, we hoped to provide empirical evidence for (1) the role of various physiological, morphological and allocational responses in determining competitive interactions among trees; (2) the outcome of changes in competitive interactions for population structure and community composition; (3) ecosystem-level feedbacks to resource availability and energy flow, including resource retention, conversion efficiency, and recycling rates; and (4) the implications of these mechanisms for secondary plant succession and temporal patterns of forest production.

Mature northern hardwood forests, composed of sugar maple (*Acer saccharum* Marsh.), American beech (*Fagus grandifolia* Ehrh.), and yellow birch (*Betula alleghaniensis* Brit.) dominate the lower montane zone of the White Mountains of New Hampshire, and similar forest types are common throughout the northeastern and north-central United States (Eyre 1980). The pattern and process of ecosystem development of these forests following large-scale disturbances like logging or catastrophic windstorms has been described and interpreted in detail (Bormann and Likens 1979). Secondary succession follows the initial floristics model. In the early stages, vegetation is often dominated by the fast-growing pioneer tree species, pin cherry (*Prunus pensylvanica* L.), which arises in high densities from dormant seeds in the soil seed bank (Marks 1974). This species serves to hasten the return of the ecosystem to conservative nutrient cycles (Marks and Bormann 1972). During the second and third decades of recovery, dominance shifts to the longer lived, mature forest species as pin

TABLE 1. Forest and site characteristics of nine stands in White Mountain National Forest, New Hampshire.

| Stand no. | Year of clearcut | Slope | | Pre-cut forest dominants† | Soil pH | | % SOM‡ | Basal area (m²/ha) | |
		Aspect	Angle		Organic	Mineral		Total	Pin cherry
Y-1	1984	N	gentle	RM–RO	4.3	4.8	9.9	4.4	3.3
Y-2	1984	NNE	moderate	B–SM	5.1	5.4	8.6	13.6	5.7
Y-3	1985	SE	moderate	B–YB–SM	4.5	4.9	11.2	10.1	8.1
M-1	1978	SW	gentle	YB–SM	4.6	4.9	11.2	16.9	12.0
M-2	1978	W	gentle	YB-SM	4.7	5.1	7.8	18.2	14.0
M-3	1978	N	moderate	SM–B–YB	4.7	5.0	10.2	16.4	10.2
O-1	1971	SW	moderate	B–YB	4.7	5.1	11.2	28.2	14.5
O-2	1971	NE	gentle	YB–fir	5.3	5.5	11.3	27.8	15.6
O-3	1971	N	gentle	B–PB–YB	4.8	5.2	8.7	25.8	12.0

† RM = red maple, RO = red oak, B = beech, SM = sugar maple, YB = yellow birch, PB = paper birch.
‡ SOM = soil organic matter of the upper 10 cm of mineral soil, based upon loss-on-ignition.

cherry abundance progressively declines. The life history strategy of pin cherry is an extreme case of an ''exploitive species,'' described by Bormann and Likens (1979) as ''getting while the getting is good.'' It attains dominance on cutover sites by a combination of attributes that allows it to grow very rapidly when resources are abundant (e.g., low root : shoot [R:S] ratio, high maximum photosynthesis rate). Bormann and Likens (1979) suggested that as resource competition becomes acute after canopy closure, pin cherry loses out to the dominant species of the mature forest whose attributes confer advantages under conditions of low resource availability (e.g., high R:S ratio, shade tolerance, high nutrient-use efficiency). By stand age 35 yr, nearly all pin cherry trees have died. From the point of view of interspecific competition, it is unclear whether mortality of the pin cherry overstory allows the mature forest species to gain the canopy, or whether these competitors succeed in growing up to and through the pin cherry canopy and then outcompete it for light.

We hypothesized that increased soil resource availability would prolong the interval of pin cherry dominance in successional northern hardwood stands by conferring upon it a competitive advantage over the mature forest species. Conversely, we expected reduced soil resource supply to hasten the demise of pin cherry. More mechanistically, we expected that changes in physiological and morphological attributes of foliage, and shifts in allocation to roots, would be the principal responses accounting for species responses to soil resource manipulations. Further, we anticipated that the responses of pin cherry populations to soil resource manipulation would be accompanied by consequent responses in competing species, particularly the marginally tolerant birches—that is, delays in the decline of pin cherry would suppress their growth.

METHODS

Study sites

Nine stands were selected for detailed study within the White Mountain National Forest. The stands were chosen to meet the following criteria: (1) pre-cut forests were dominated by mature northern hardwood forests growing on well-drained soils of gentle to moderate slopes in the elevation range from 300 to 400 m; (2) all had been recently clearcut, with three stands harvested in each of the time periods 1971, 1978, and 1984–1985; (3) the naturally regenerating forests were dominated by northern hardwoods, with a high proportion of total basal area (>40%) composed of pin cherry; and (4) road access was available to within a few hundred meters of each stand. After screening many sites using USDA Forest Service timber sale maps, the nine stands described in Table 1 were selected. The stands generally fulfilled our criteria. Except for stand Y-1, all the pre-cut forests were classified in the maple–beech–birch cover type (Eyre 1980) and were dominated by a combination of American beech, yellow birch, or sugar maple. The pre-cut forest of stand Y-1 was dominated by red maple (*Acer rubrum* L.) and northern red oak (*Quercus borealis* Michx.) The soils of all the sites were moderately to strongly acid, and soil organic matter concentration in the upper mineral soil was comparable across sites (range = 8–11% loss-on-ignition).

Treatments

In each stand, three 20 × 20 m quadrats were located with the aim of providing treatment plots that were as similar and uniform as possible in terms of vegetation, given the high inherent variability that occurs at this scale within regenerating clearcuts (Mou et al. 1993). The quadrats were assigned to one of three treatments: soil resource augmentation, nutrient depletion, and control. To facilitate access, the resource-augmentation plot was usually assigned as the plot closest to road access, while the other two treatments were assigned randomly to the remaining quadrats. All quadrats were separated by at least 30 m.

All treatments were applied in a 17 × 17 m plot in the center of the main plot, and all measurements of responses were made on a central 15 × 15 m plot. It should be acknowledged that this 2-m buffer would not completely eliminate artifacts, owing to the extension

of tree roots between treated and untreated areas; the magnitude of these possible artifacts is unknown.

The aim of the soil-resource-augmentation treatment was to eliminate any limitation of soil resources (water and nutrients). A balanced fertilizer including micronutrients was added to the soil surface in six applications at 4-wk intervals during the growing season (May–October) each year (1989–1994). The annual macronutrient additions were (in grams per square meter): N = 16.7, P = 5.8, K = 25.4, Ca = 31.0, and Mg = 3.7. The N additions consisted of the inorganic forms, NH_4 and NO_3, in equal proportions by mass of N, and the fertilizer dosage was chosen to roughly triple N availability in early successional northern hardwoods (Mou et al. 1993). During the first year of the study (1988), two of these fertilizer applications were made at the end of the growing season (September–October).

During the first four years of treatment, we also attempted to eliminate any soil water limitation in the resource-augmentation plots by irrigating when soil moisture was at a minimum. A gravity-fed irrigation system was installed on the treated plots in seven of the stands, and streamwater from nearby streams was added to achieve ~2.3 cm of rainfall equivalent per application. Two applications were made in 1989 and 1990 and one in 1991 and 1992. Severe droughts are uncommon in the study area (Federer et al. 1990). These water additions may have alleviated moderate drought conditions experienced when monthly precipitation in July of 1990 and June of 1991 and 1992 at nearby Hubbard Brook Experimental Forest fell within the bottom 25th quartile of growing-season precipitation based on 30 yr of records (Federer et al. 1990). Two stands were not irrigated because of difficulty of access (stands Y-1 and O-2; Table 1). Hereafter, the resource-augmentation plots are referred to simply as the fertilized plots.

The nutrient-depletion treatment was designed to reduce nutrient availability and consisted of two separate approaches in each stand: hardwood sawdust and granular sucrose were added to immobilize N and P (Waring and Pitman 1985), and the Oi litter layer was removed to reduce nutrient recycling from aboveground litterfall. In 1989, ~1 kg/m² of sawdust (containing ~1.8 g N/m²) was added to each plot. We measured N immobilization in the sawdust using mesh bags in six stands, and observed a doubling of N content of the sawdust over 2 yr with no consistent differences among stands. Hence, nitrogen was immobilized in the sawdust at ~2 g/m². In 1990 and 1992 we added an additional 0.7 kg/m² of sawdust in each stand, which increased total immobilization to ~5 g N/m² over 5 yr of treatment. Removal of the Oi litter layer (which also removed most of the added sawdust) was carried out in fall 1989, 1991, and 1993; measurement of litter removal indicated that total removal of N ranged from ~10 to 16 g/m² over the 6 yr of treatment. Thus, the magnitude of nutrient removal was only ~20% as great

as nutrient addition; however, on an annual basis, nitrogen removal was similar in magnitude to atmospheric deposition in this region (Lovett and Lindberg 1993).

Response measurements

Tagged trees.—To provide detailed information on population and community responses, trees in each plot were tagged and numbered in summer 1988 prior to initiation of treatments. In general, 45 individuals of each of the dominant species (pin cherry, beech, sugar maple, striped maple [*Acer pensylvanicum* L.], paper birch [*Betula papyrifera* Marsh.], and yellow birch) in each plot were chosen randomly after stratifying each population into three size classes. If <45 individuals of a particular species were present in a plot, all individuals were tagged.

The diameter of each tagged tree was measured in October or early November each year from 1988 to 1994. Caliper micrometers were used to measure diameter to ±1 mm precision at a marked location at breast height (1.37 m) on each tree.

Foliage chemistry and morphology.—Twigs were clipped from mid-canopy of four to five healthy trees of each species in each plot for analysis of foliar chemistry and morphology of the six dominant species. Collections for chemical analysis were made in early summer 1990 and in late summer 1990, 1991, 1992, and 1993. Foliage from trees within plots was pooled by species, dried at 55°C, and ground to pass through a screen of mesh size 0.6 mm. Nitrogen was determined following micro-Kjeldahl digestion. All other element determinations were made by argon plasma spectroscopy (Mou et al. 1993). Samples were dry-ashed in quartz crucibles at 450°C, and the ash was dissolved in concentrated HNO_3 plus 30% H_2O_2 and heated to dryness. The ash was then dissolved in a 10% HCl plus 10% HNO_3 solution, centrifuged, and run on the plasma analyzer.

In 1992 and 1993, the areas of 12–15 individual leaves of each species (three leaves from mid-canopy twigs of four or five trees) from each plot were measured with a LI-COR leaf area analyzer (LI-COR, Lincoln, Nebraska). Each leaf was then dried to constant mass at 55°C and weighed to ±0.1 mg on an analytical balance. Specific leaf area (SLA, calculated as area/mass) was calculated for each individual leaf. To allow accurate characterization of nutrient resorption, fresh leaf-litter samples were collected from six stands (two of each age) during the middle of the peak leaf-fall period in October 1991 and 1992. These samples were obtained by spreading plastic sheeting over the ground in each plot and collecting the accumulated leaves after several rain-free days. Samples were sorted by species and dried at 55°C before being ground and chemically analyzed by the same procedures as for live foliage. In addition, in 1993 fresh leaf-litter samples were collected from control and fertilized plots at six stands (two of each age), and SLA was measured for 12–15

leaves of each species in each plot. Based upon comparison with live foliage, the differences in SLA were used to correct resorption estimates to a per-leaf basis.

Ground vegetation.—Lesser vegetation (herbs, shrubs, and tree seedlings) was measured with 20 permanent quadrats (each 1.0 m^2) positioned randomly in each plot. Vegetation plots were surveyed in midsummer (late July to mid-August) in 1989, 1990, 1991, 1994, and 1995. Stem counts were made for all species except multi-stemmed shrubs such as *Rubus* spp., for which the percentage canopy coverage was estimated visually.

Litter and seed fall.—A network of seven randomly placed traps was used to collect litterfall and seedfall in each plot in 1989–1991. Unfortunately, because of technical problems, leaf-fall data were not available for these first three years of treatment. For 1992–1994, 11 litter traps, consisting of plastic clothes baskets (0.18 m^2 each) with a mesh liner, were positioned randomly in each plot. Traps were collected in May, August, and November of each year. Each litter sample was sorted into four components: leaves, fruits, other nonwoody litter, and woody litter. Leaves and fruits were further sorted by species, and the number of each was counted for each litter sample. In 1994, a random subsample of 12–18 leaves of each species from each plot was selected for determination of leaf area using a LI-COR leaf area analyzer. Together with leaf counts from litter traps, these provided an unbiased estimate of leaf area index (projected one-sided leaf surface area per unit ground surface area) by species in each plot.

Fine roots.—To evaluate the initial responses of fine root growth to the treatments, we employed in situ root screens as an index of relative root growth (Fahey and Hughes 1994). In fall 1988, 25 screens (5 cm wide) were inserted to the depth of obstruction in each plot at three stands, one of each age (stands Y-3, M-3, and O-3; Table 1). On each of four dates (22 August and 12 October 1989, and 22 June and 1 October 1990) the number of fine roots (<1 mm) intersecting five randomly chosen screens was counted.

Soil cores for fine root biomass determination were collected in late summer 1991 and 1994 using the following procedure. In each plot four soil cores (1.9 cm diameter) were taken to the depth of obstruction at randomly chosen locations within each of four plot quadrants. The four cores from each quadrant were separated into organic and mineral horizons, pooled, and thoroughly mixed, and all roots were removed by hand-sorting from a 25% subsample. Living roots were recognized by standard criteria (Fahey and Hughes 1994). After corrections for subsample dry mass and for soil mineral contamination (from loss-on-ignition measurements), fine root biomass was calculated per unit ground area for organic and mineral horizons.

In 1994 all fine root handling was done with gloves to avoid contamination, and fine root subsamples were retained for mineral nutrient determinations. These samples were ground to pass a screen of mesh size 0.6 mm. Nutrient analyses were performed as described for foliage, and corrections were made for soil mineral contamination by expressing results on an ash-free dry mass basis.

Soil respiration, microbial biomass, and nitrogen availability.—In summer 1993, soil respiration was estimated in the control and fertilized plots at seven of the stands (excluding stands Y-1 and O-2) using a soda-lime trap method (Edwards 1982). Measurements were made for 48-hr intervals in late June, mid-July, mid-August, and mid-September in each stand. In each plot 13 rectangular plastic chambers (each 425 cm^2 in area) were positioned randomly on the soil surface, and emitted CO$_2$ was trapped with 25 g of fresh soda-lime held in 35-cm^2 paper containers to meet the specifications for efficient CO$_2$ capture (Raich and Nadelhoffer 1989). Although the accuracy of the soda-lime method has been questioned (Nay et al. 1994), comparisons between plots should not be compromised because any artifacts due to effects on headspace CO$_2$ would be consistent across treatments.

Treatment effects on soil microbial biomass were evaluated in 1995. Two 5-cm diameter soil cores were collected randomly from each plot in mid-July, separated into organic and mineral horizons based upon our standard visual criteria, and stored at 2°C. Microbial biomass carbon was estimated from the mass of CO$_2$ produced in a 10-d room-temperature incubation of a chloroform-fumigated and reinoculated sample (Jenkinson and Powlson 1976). Similarly, microbial biomass N was estimated from the inorganic N produced in 10-d incubations of fumigated/reinoculated samples. Readily mineralizable C and N were estimated as the CO$_2$ and extractable NH$_4$ + NO$_3$ produced in a 10-d room-temperature incubation of unamended soil at field moisture content.

Stand structure and canopy architecture.—After >5 yr of treatment, an intensive effort was made to characterize the response of stand structure and canopy architecture to the altered competitive interactions within the successional forests. In fall 1993, the diameters of all trees ≥2 cm dbh were measured in each of the 15 × 15 m plots. In summer 1994, the architecture of the canopy was quantified in each plot by an integrated set of procedures.

In the fall of 1994, canopy height in the control and fertilized plots was estimated by dividing the plot into four quadrants and measuring the height of the four tallest trees in each quadrant using a height pole. In addition, the dbh and height of the four tallest individuals of each tree species present in the plot were measured. Mean canopy height was calculated from the quadrant data, and species-specific mean canopy height was calculated from individual data.

Leaf area index (LAI) of each tree species in the plots was determined for 1994 from counts of leaves in 11 litter traps in each plot. This ''litterfall'' measure

of LAI was assumed to be the most accurate, least biased estimate of total stand LAI. To estimate the vertical distribution of LAI in each plot, we mounted a LI-COR LAI-2000 plant canopy analyzer (Gower and Norman 1991) on a pruning pole. Beginning near the top of the canopy and ending at ground level, we took a vertical sequence of 10–13 LAI readings at eight points along the perimeter of the 15×15 m plot. At the four plot corners, a 25% hemisphere view was taken facing toward plot center; at the mid-point between corners a 50% hemisphere view was taken at each height. The average LAI at each height was computed using open sky readings from a paired sensor placed in a nearby clearing. All LAI measurements were made at times approximating isotropic skylight distribution (i.e., either during uniformly overcast days, or most commonly, at dawn and dusk).

To estimate the vertical distribution of LAI by species, an intersect method was used. The center 10×10 m of the 225-m^2 study plot was divided into a 2×2 m grid. At each of the 36 grid intersections, a 10 cm diameter cylinder (a height pole with a 10 cm long cross attached to the tip) was lifted through the canopy. A vertical profile of foliage was obtained by recording the height and species of any leaf that intersected the plane of the cylinder. A level attached to the height pole was used to maintain a vertical orientation. When the cylinder was in dense parts of the crown (>1 leaf per meter) with leaves from more than one tree species present, care was taken to accurately identify the species and heights of all intersections. When the cylinder was in dense parts of the crown where leaves from only one tree species were present, only the first and last intersections were recorded. If this last intersection was the top of the canopy, the species-specific mean canopy height was used as the last intersection height. Points and heights above which no canopy was present were also recorded. In practice, three people were often necessary to make these measurements in dense canopies—one person to work the pole and two people situated at different viewpoints to spot leaf intersections and to identify the species.

Leaf area profiles were constructed for each plot by first averaging the eight LAI estimates at each height. We calculated the best fit linear equation to interpolate the LAI at 1-m increments in the canopy. In all but one case, the corrected R^2 of the interpolation was >0.99. For the exception, R^2 was >0.98. Because both leafy and woody parts were included in these profiles, we corrected for the woody components by measuring "leaf-off" LAI profiles. After leaf fall in November 1995, we made LI-COR LAI-2000 measurements in the control and fertilized plots at a young site (Y-3), a mid-age site (M-2), and an older site (O-3). Measurements were made at two heights: 4.5 m and 0 m (ground level). A 50% hemisphere view was taken at the midpoint between corners (four points). For each height these four LAI estimates were averaged. Interpolated

leaf-off profiles were constructed for each plot. LAI was assumed to equal 0 at the top of the canopy (top estimated as the mean of 16 tallest trees, 4 trees/quadrant). For all the leaf-off LAI interpolations, R^2 exceeded 0.99. To calculate the final corrected LAI profile, the leaf-off LAI values were subtracted from the total LAI values. The leaf-off profile for stand Y-3 was applied for stand Y-1 and Y-2, and the analogous procedure was followed for the mid-age and older stands.

We used the results from the plane intersections to partition the corrected leaf area profile by tree species. From the height data, we estimated the canopy top for each species present in the plot. We divided the canopy into 1-m increments. For each of the 36 vertical planes lifted through the canopy, we calculated the number of times a species had at least one leaf intersecting the plane in the 2-m interval. In parts of the canopy where only one species was contributing to the leaf area, we assumed that there was at least one leaf intersection per meter. Earlier trials in which we recorded every leaf intersection support this assumption: the average number of intersections per meter was 1.4 (J. J. Battles and T. J. Fahey, *unpublished data*). The proportion of the total number of intersections that a species accounted for in each 1-m segment of the canopy was the metric used to partition leaf area by species.

We summarized the total leaf area profiles by calculating the half-way height—the height at which there was an equal amount of leaf area above and below. Half-way heights were expressed as a proportion of the total canopy height to allow comparisons between stands of different heights. To describe the species-specific area distributions, we divided the species-specific leaf area above the half-way height by the total leaf area above the half-way height. This variable, termed the leaf area dominance, measures the proportion of leaf area for each species in each stand that is not overtopped by the majority of the canopy.

Aboveground biomass and net production.—Aboveground biomass was estimated for each plot in 1993 on the basis of allometric relationships between tree diameter and biomass components. Allometric equations were available for most of the species from studies at nearby Hubbard Brook Experimental Forest (Whittaker et al. 1974, Reiners 1992, Mou et al. 1993). We extended the information for three of the dominant species (pin cherry, paper birch, and yellow birch) by harvesting representative trees from unfertilized forests at two of the stands (M-1, O-3). Eighteen pin cherry, 10 yellow birch, and 10 paper birch trees were harvested and dissected for standard allometric analysis. These samples were used to extend the available allometric equations into the size ranges encountered in our sites.

Aboveground net primary production (ANPP) for each plot was estimated for the interval 1991–1993. Growth-rate data for tagged stems were used to estimate the dbh in 1991 of all trees measured in 1993.

Biomass increment between 1991 and 1993 of perennial tissues was calculated for each plot on the basis of the allometric equations, and the production of non-woody tissues, and turnover of woody tissues was estimated from litterfall collections (average values for 1992–1994).

Photosynthesis and leaf respiration.—Foliage gas exchange measurements were made using a LI-COR 6200 photosynthesis system. A cut-branch method for examining photosynthesis of canopy foliage was evaluated in summer 1990 on two clearcut sites, 2 and 6 yr old, at Hubbard Brook Experimental Forest. Photosynthesis rates of pin cherry were compared between leaves on detached twigs and intact twigs under full sun conditions between 0900 and 1600 in June, July, and August. Twigs were cut with a pole pruner and the cut end immediately submerged in water; photosynthesis was measured over the ensuing 0.5 h. No significant differences were observed for a total of 26 paired measurements in these trials.

In 1993 and 1994, photosynthesis measurements were made on cut branches placed either in full sun or under a combination of neutral-density shade cloths providing a range of 30–90% shade. This procedure allowed us to manipulate light levels in order to quantify light-response curves. Pin cherry photosynthesis was measured in 1993 in stands Y-2 and M-1, while paper birch was measured in 1994 at stand Y-2 (Table 1). Sunlit leaves were cut from mid-canopy (8–12 m) with pole pruners. The cut ends of the branches were immediately submerged in water and positioned under shade cloths or in full sun. After 10 minutes, to allow adjustment of gas exchange rates, photosynthesis was measured with the LI-COR 6200. Shade-cloth densities were then changed and an additional 10 min elapsed before further photosynthesis measurements. Branches from fertilized and unfertilized plots were always measured side by side to ensure that samples from both treatments were exposed to similar environmental conditions. All measurements were made on days with uniform light conditions, and in particular, no measurements were made on days with patchy cloudiness, so that light levels at the interval of measurement would be comparable to those immediately preceding sampling.

One leaf was measured from each twig at each light level, and cuttings were measured for up to 1.5 h before discarding. Trials were conducted on cut branches to demonstrate that photosynthetic rates did not change significantly during this period of time. The portion of leaf in the gas exchange chamber was marked, pressed, and dried so that both area and mass could be quantified.

Dark respiration of pin cherry and paper birch leaves was measured. Branches were sampled in the same way as for photosynthesis, and the twigs were positioned under a box to exclude light. Cuvette measurements of CO_2 emission were made ~0.5 h later to allow full stomatal closure. Three leaves from each branch of each species were placed in the cuvette, which was covered with aluminum foil to exclude light during measurements.

Litter decomposition and mineralization.—The effect of fertilization on the rate of decomposition and nutrient mineralization of leaf litter was evaluated with a litterbag experiment conducted in the mid-age stands. In fall 1993, fresh litter was collected from fertilized and control plots in these stands. Leaf litter was air-dried, sorted by species, and pooled across stands. The six species chosen for study were paper birch, yellow birch, pin cherry, sugar maple, striped maple, and American beech. Samples of ~1 g were placed into nylon-coated, fiberglass mesh bags (mesh size = 2 mm), and each sample was weighed to ±0.1 mg on an analytical balance. Three samples of each species and treatment were selected randomly for determination of initial moisture and chemical concentrations.

Although the experimental design was the same for all species, the number of replicates and blocks was different for the most intensively studied species, paper birch, than for the others. For each species the factorial experiment included two litter chemistry treatments (control [C] and fertilized [F]) and two plot chemistry treatments (again, C and F). For paper birch there were three blocks (each of the three mid-age stands), and five replicate litterbags were collected on each of three collection dates. For the other species there were two blocks (stands M-1 and M-2) and usually three replicate bags per date; however, animal disturbance reduced the sample size for pin cherry and yellow birch on the last two collection dates.

Litterbags were placed in the field in late May 1994. They were anchored with aluminum stakes to assure contact with the underlying forest floor. Randomly chosen samples were retrieved from the field in late October 1994 and early June and early November 1995. Samples were cleaned of adhering debris and oven-dried to constant mass at 80°C before being weighed. Replicates were pooled and then ground to pass through a fine-mesh sieve before being chemically analyzed by the same procedures as for foliage. In addition to mineral nutrients, the initial samples were analyzed gravimetrically for lignin by extracting ground tissues with 13.6 mol/L H_2SO_4, autoclaved at 250° for 1 h (Weider and Yavitt 1994).

Analysis

This experiment was a 3 × 3 factorial design with stand age (5, 11, 16 yr in the beginning) and treatment (soil resource addition, nutrient depletion, and control) as main effects. For most analyses of average plot-wide responses a two-way analysis of variance was used to detect significance ($P = 0.05$) of age and treatment effects. When significant effects were observed, post hoc analysis was done using Tukey's hsd. This approach applied to the following response measure-

ments: cumulative tree mortality by species for each year of treatment, foliage and fine root chemistry, foliage morphology (specific leaf area, leaf size), nutrient resorption, canopy height, leaf area index, tree height, half-way height, leaf area dominance (as defined in *Results: Canopy architecture response*), the ratio of leaf area to basal area, seed deposition, fine root biomass, mineralizable C and N, soil CO_2 evolution, microbial biomass, basal area, and aboveground production and growth efficiency. The response of relative growth rates (percentage increase in individual tree basal area) for each species was analyzed by repeated-measures ANOVA. Treatment effects on mass loss and nutrient release from decaying litter were detected using a fully factorial ANOVA. Where informative, we also analyzed between-plot differences within stands, recognizing the limits of interpretation of such patterns.

To characterize the effects of treatment and age on the relationship between individual tree growth and the likelihood of survival, a case-control study approach was used. A maximum likelihood estimator of the growth–survivorship relationship was constructed on pooled data for each species across ages and treatments. A logistic model predictor of survivorship was employed (C. McCulloch, personal communication) in the following form:

$$\text{Survivorship} = \frac{e^{b_0 + b_1(\text{growth})}}{1 + e^{b_0 + b_1(\text{growth})}}. \tag{1}$$

The parameters were estimated by nonlinear regression using the simplex algorithm (Wilkinson et al. 1992).

Because complete plot surveys were conducted only at the end of the treatment interval (1993), initial stand structure was back calculated on the basis of the tree growth and mortality information for the tagged trees in each plot. The basal area at the start of the experiment of each stem that survived through 5 yr of treatment was estimated from the average growth rate of tagged stems of each species within the three size-class categories in each plot. The initial density by species and size-class was estimated from mortality of tagged stems for each plot. These estimates of initial basal area and density by species were used only to provide a general picture of the pattern of change in relative basal area of pin cherry across stand ages and treatments.

Photosynthetic light-response curves for pin cherry and paper birch for each stand and treatment were constructed using a hyperbolic function. We followed the approach of Teskey et al. (1994) in comparing the photosynthetic light-response curves between the control and fertilized plots. Although the response curves must be viewed with caution because of coincident variations in other factors that influence photosynthesis (e.g., temperature, vapor pressure deficit), the comparison of treatment effects should be valid since control and treated foliage were measured together. A hyperbolic function was constructed:

$$A = \frac{a(\text{PAR})A_{\max}}{a(\text{PAR}) + A_{\max}} \tag{2}$$

where a is the slope of the light-limited part of the light-response curve, PAR is photosynthetically active radiation, and $A_{\max}$ is the light-saturated photosynthetic rate in micromoles per square meter per second (Teskey et al. 1994). Statistical comparisons of the estimated parameter values of a and $A_{\max}$ between fertilized and unfertilized trees were carried out using Student's t distribution to estimate 95% confidence intervals for the regression parameters. These comparisons were made on both a unit leaf area and leaf mass basis for pin cherry at each of two stands (Y-2 and M-1) and for paper birch (in one stand, Y-2). For paper birch we also constructed the light-response curves separately for each individual twig in an attempt to account for between-tree variation in a and $A_{\max}$. In this case, the mean parameter values were compared between treatments using Student's t statistic.

RESULTS

Stand development and soil resource availability

The control plots provided a chronosequence of pin cherry-dominated, successional northern hardwoods that illustrates the trends in stand development expected in the absence of treatments. The interval of stand development from age 10 to 23 yr (as measured in 1993) was marked by a decline in stem density and an increase in stand basal area, canopy height, and LAI. Average density (of stems ≥ 2 cm dbh) decreased from 4.60 stems/m^2 at age 10 yr to 2.78 stems/m^2 at 16 yr and 1.26 stems/m^2 at 22 yr (Table 2). Average basal area increased from 20.3 m^2/ha at age 10 yr to 23.0 m^2/ha at 16 yr and 27.8 m^2/ha at 22 yr. Canopy height increased from 8.3 to 10.1 to 13.2 m along the age sequence, while LAI (in 1994) increased from 4.38 to 5.71 (Table 2). All these changes were statistically significant. Although slight increases in fine root biomass were calculated, high within-age-class differences among stands masked any significant trend with stand age.

Pin cherry was a dominant species in all the stands in terms of basal area, but pin cherry basal area appeared to peak in the mid-age stands and to decline in the older stands. Moreover, the proportion of stand LAI comprised of pin cherry was much lower in the older stands (18%) than in the young and mid-age stands (33%), illustrating the initiation of the progressive decline in pin cherry abundance that appears to occur during the third decade of stand development (Bormann and Likens 1979). To further illustrate this pattern, we calculated changes in the basal area of pin cherry on the basis of measurements of the growth and survivorship of 45–50 tagged stems per plot. In the reference plots, pin cherry basal area increased markedly from age 6 to 17 yr before sharply declining to age 23 yr (Fig. 1). These dynamic results strongly reinforce the

TABLE 2. Stem density and basal area (for all stems >2 cm dbh), leaf area index (LAI), and fine root biomass in 1993; aboveground net primary production (ANPP), 1992–1993; and canopy height and leaf area index in 1994 for control and treated plots in each of the nine study sites.

Stand	Stand age	Treatment	Stem density (no./ha)	Stem basal area (m²/ha)	Canopy height (m)	LAI Total	LAI PC†	ANPP (g·m⁻²·yr⁻¹)	Fine root biomass (g/m²)
Y-1	10	control	5.27	12.3	6.4	3.30	1.12	782	400
		fertilized	2.18	22.1	9.5	3.24	2.76	2201	635
		depleted	5.03	12.9	NA‡	2.21	1.01	801	647
Y-2	10	control	3.44	28.0	12.1	4.64	0.64	1478	304
		fertilized	2.74	25.8	12.1	5.48	2.01	1902	213
		depleted	5.15	20.7	9.6	4.74	1.24	1164	295
Y-3	9	control	5.10	20.6	9.0	5.21	1.20	950	436
		fertilized	2.08	18.7	10.8	5.56	2.77	1484	438
		depleted	4.24	17.8	NA	4.40	0.79	1008	452
M-1	15	control	1.39	21.4	10.6	4.96	1.32	1122	453
		fertilized	1.21	22.5	12.4	5.76	1.37	1389	487
		depleted	1.98	23.8	NA	4.35	1.58	1087	355
M-2	15	control	2.54	23.4	9.2	3.76	2.13	690	367
		fertilized	1.39	24.8	12.0	5.69	2.82	1351	217
		depleted	3.10	19.1	NA	4.57	1.62	916	315
M-3	15	control	4.42	24.1	10.6	4.29	1.78	1011	466
		fertilized	2.53	24.4	12.5	4.70	3.08	1455	417
		depleted	4.83	22.4	NA	5.18	1.61	1029	492
O-1	22	control	1.29	23.0	14.1	6.07	1.08	974	453
		fertilized	0.73	25.7	15.6	7.11	1.82	1778	396
		depleted	1.08	25.2	NA	4.32	0.68	962	359
O-2	22	control	1.10	29.1	13.7	5.20	0.85	1077	665§
		fertilized	0.65	31.1	13.7	5.34	0.72	1270	330§
		depleted	0.69	27.9	NA	6.13	1.93	1164	NA
O-3	22	control	1.38	31.2	11.9	5.87	1.26	1938	252
		fertilized	0.88	26.2	14.0	6.63	2.76	1990	235
		depleted	1.26	29.2	NA	5.67	1.40	1385	303

† PC = pin cherry.
‡ NA = data not available.
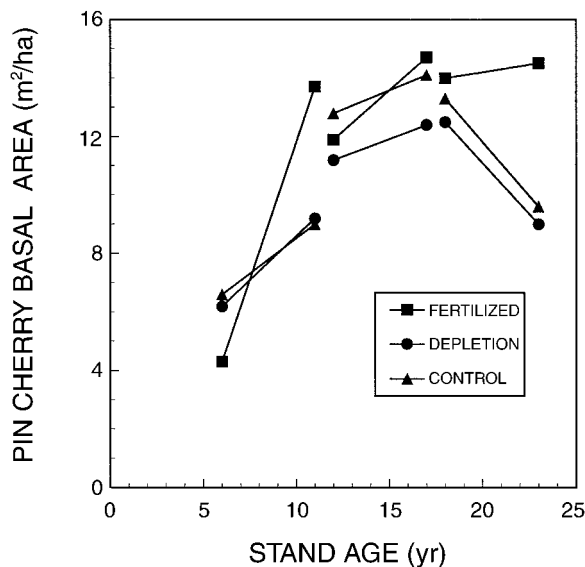§ Values are for 1991.

FIG. 1. Changes in the basal area of pin cherry (*Prunus pensylvanica*) over 5 yr of treatment in control, fertilized, and nutrient-depletion plots along a successional chronosequence in the White Mountains, New Hampshire.

pattern inferred from the static measures available from the chronosequence.

Changes in soil resource availability altered the stand development process in several ways; however, only the soil resource additions caused significant responses. The nutrient-depletion plots exhibited patterns of stand development that were very similar to the reference plots.

The most dramatic and consistent effects of fertilization on stand structure and composition were statistically significant reductions in stem density and increases in the dominance of pin cherry. Across all stands, stem density in the control plots was nearly twice as high as in the fertilized plots, and pin cherry LAI was nearly twice as high in the fertilized as the control plots (Table 2). Although the magnitude of the response of pin cherry LAI to fertilization tended to decrease with stand age, this trend was not statistically significant ($P = 0.132$).

Surprisingly, fertilization did not result in significantly higher tree basal area. Moreover, although there was a trend toward higher total LAI in the fertilized plots (true for 7 of 9 stands, Table 2), this pattern was not statistically significant ($P = 0.12$). Canopy height increased significantly in the fertilized plots by an average of ~2 m, and most of the increase was associated with the height growth response of pin cherry, which

TABLE 3. Macronutrient concentrations in foliage and fine roots in control (C), fertilized (F), and nutrient-depleted (D) plots.

Species	Treatment	Nutrient concentration (% dry mass)				
		N	P	K	Ca	Mg
Pin cherry	F	3.34 (0.43)	0.297 (0.067)	2.15 (0.27)	0.84 (0.32)	0.240 (0.047)
	D	2.28 (0.32)	0.172 (0.036)	1.48 (0.28)	1.00 (0.26)	0.275 (0.042)
	C	2.28 (0.22)	0.195 (0.057)	1.53 (0.24)	1.09 (0.30)	0.284 (0.048)
Beech	F	2.51 (0.22)	0.159 (0.027)	0.99 (0.17)	0.55 (0.13)	0.170 (0.029)
	D	2.08 (0.25)	0.125 (0.030)	0.86 (0.15)	0.57 (0.09)	0.252 (0.035)
	C	2.13 (0.19)	0.125 (0.030)	0.88 (0.16)	0.55 (0.10)	0.154 (0.040)
Striped maple	F	2.45 (0.28)	0.228 (0.031)	1.96 (0.24)	1.09 (0.22)	0.264 (0.043)
	D	1.85 (0.24)	0.174 (0.036)	1.48 (0.21)	1.13 (0.18)	0.270 (0.043)
	C	1.92 (0.17)	0.167 (0.036)	1.42 (0.18)	1.21 (0.20)	0.275 (0.051)
Yellow birch	F	2.77 (0.26)	0.269 (0.065)	1.75 (0.25)	0.85 (0.15)	0.297 (0.065)
	D	2.12 (0.37)	0.150 (0.035)	1.09 (0.23)	0.92 (0.15)	0.293 (0.063)
	C	2.26 (0.29)	0.160 (0.039)	1.12 (0.19)	0.97 (0.16)	0.318 (0.057)
Paper birch†	F	2.51 (0.32)	0.234 (0.050)	1.63 (0.46)	0.74 (0.14)	0.182 (0.039)
	D	2.08 (0.13)	0.141 (0.030)	0.99 (0.22)	0.74 (0.17)	0.179 (0.053)
	C	2.09 (0.17)	0.124 (0.024)	0.94 (0.13)	0.78 (0.19)	0.166 (0.040)
Fine roots (organic horizon)	F	1.89 (0.18)	0.141 (0.024)	0.135 (0.029)	0.68 (0.06)	0.073 (0.012)
	C	1.70 (0.17)	0.113 (0.014)	0.091 (0.011)	0.53 (0.10)	0.051 (0.009)
Fine roots (mineral horizon)	F	1.47 (0.15)	0.133 (0.021)	0.105 (0.025)	0.36 (0.09)	0.043 (0.016)
	C	1.36 (0.21)	0.098 (0.024)	0.073 (0.028)	0.30 (0.10)	0.036 (0.011)

Notes: For foliage values, means are for nine stands over four years of sampling, with overall standard deviations in parentheses ($n = 36$). For fine roots, values are for collections from nine stands in 1993.

† Data are for 1993 only.

was the only common species showing a significant height response to fertilization.

In sum, the overall effect on stand development of the fertilization treatment was to greatly stimulate the early rates of increase in pin cherry basal area (age 6–11 yr) and height, and to delay the onset of the decline in pin cherry dominance (Fig. 1). The aims of our additional measurements of treatment responses were to identify the mechanisms explaining these stand development responses at the individual and population levels and to examine the implications and feedbacks at the ecosystem and broader community levels.

Physiological and morphological responses

Foliage chemistry, morphology, and resorption.—Foliar concentrations of N, P, and K for five dominant tree species responded significantly to soil resource treatments in the successional northern hardwood forests (Table 3). In all cases the response was attributed to increased concentrations in the fertilized plots, as no significant differences were observed between the control and nutrient-depletion plots. In 1992, the fourth year of treatment, a weak signal of a nutrient-depletion effect on foliar K concentration was observed for pin cherry ($P < 0.15$). No stand age effects were observed. Moreover, no prominent temporal trends in foliar chemistry, or its response to fertilization, were observed through the four years of collection. Foliar concentrations of Ca and Mg did not respond to treatment in the same way as for N, P, and K; and in fact in some years and species the concentrations of these macronutrients were significantly lower in the fertilized plots. This was

particularly prominent during the first 2 yr of treatment, after which treatment effects on foliar Ca and Mg were not significant.

Foliar N:P ratios were generally lower in fertilized than unfertilized plots, but this pattern was significant only for the two birch species. For example, in 1993 foliar N:P of paper birch was much lower for fertilized (10.7) than control (16.9) plots, and observations for yellow birch were comparable. The magnitude of nutrient enrichment of foliage in the fertilized plots was compared across species using a one-way ANOVA of percentage differences in N and P concentrations between control and fertilized plots for 1992 and 1993 (Fig. 2). This analysis showed clearly that N enrichment of foliage in response to 4–5 yr of fertilization was much greater for pin cherry (55% higher in fertilized than control) than the other species (average = 27%; no other significant differences between species). In contrast, the significant differences observed across species for P enrichment of foliage were associated with two groups: high enrichment for pin cherry and the two birches (~80% higher in fertilized than control) and lower enrichment for beech and striped maple (~40% higher, Fig. 2). These patterns became more prominent as the treatments continued, as no significant between-species differences were observed in 1990 and 1991.

Several significant age and treatment effects on leaf morphology (leaf size and specific leaf area [SLA]) were observed. Most prominent were highly significant ($P < 0.01$) treatment effects on SLA of pin cherry and striped maple and marginally significant ($P < 0.10$)
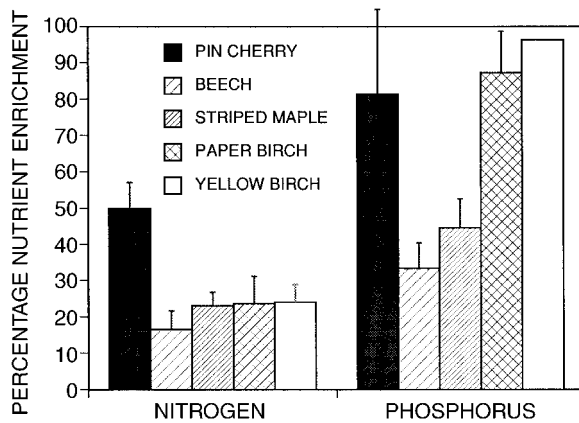
FIG. 2. Percentage increase in nitrogen and phosphorus concentrations of foliage of five species in fertilized plots compared with control plots. Values are averages for five years (1989–1993) across nine sites, except for paper birch (sampled in 1993 only). Standard errors for between-stand variation are indicated.

treatment effects on SLA of yellow birch and paper birch. In all cases, these responses were associated with higher SLA (hence, thinner leaves) in the fertilized treatment (Fig. 3). Similarly, leaf size responded to the fertilizer treatment, with significantly ($P = 0.01$) larger leaves of pin cherry, yellow birch, paper birch, and beech in the nutrient-amended plots. Several significant stand age effects on leaf morphology were observed as well, but interpretation of these effects is not straightforward. For example, SLA of pin cherry, beech, and striped maple was significantly higher in the older stands, whereas that of the birches was highest in the young stands. No stand age effects on leaf size were observed.

Foliar nutrient resorption was affected by the fertilization treatment. First, to account for the effect of concurrent carbohydrate resorption, we measured the differences in SLA (Fig. 3) between live foliage and leaf litter for each species and plot (Fig. 4). Although there were no significant treatment effects on apparent carbohydrate resorption, there was a nonsignificant trend toward smaller differences in SLA of live foliage and litterfall for the fertilized than control and nutrient-depletion plots for pin cherry and beech (but not for the birches). Using resorption values corrected for carbohydrate resorption, we calculated the percentage of resorption of N, P, and K from the average of two years (1991 and 1992) of measurements of concentrations in live foliage collected in late summer and freshly collected litterfall for six of the stands (two of each age; Fig. 5). These data indicated a highly significant effect of fertilization on P resorption by pin cherry foliage, with much lower resorption in fertilized than control and depleted plots. A marginally significant ($P < 0.10$) effect of fertilization on N resorption by beech was also observed. Although no other statistically significant effects were detected, there was a trend toward a
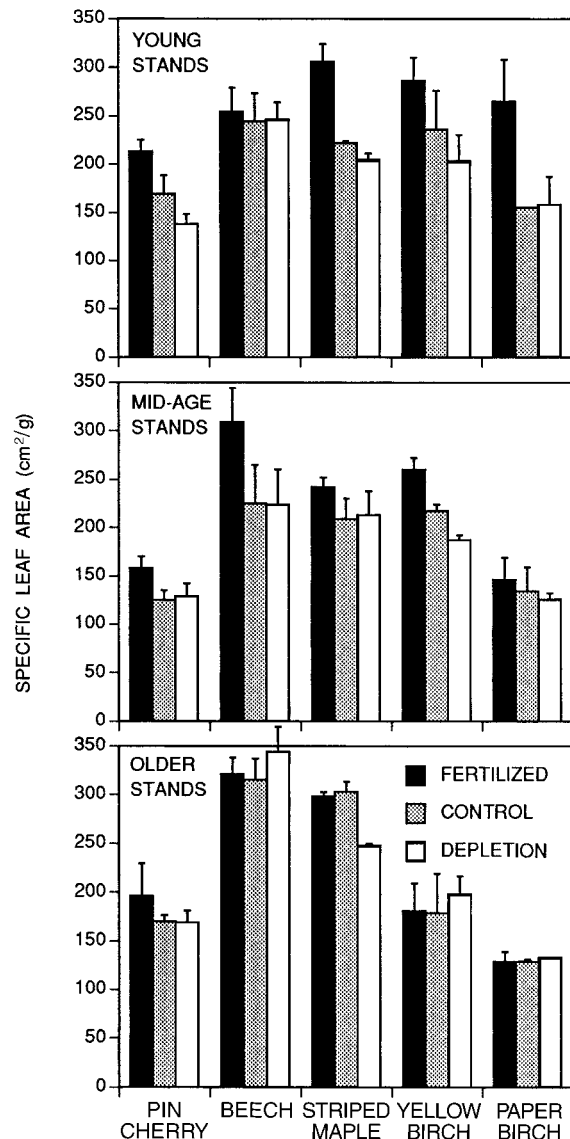
FIG. 3. Specific leaf area of mid-canopy foliage of five tree species collected in midsummer 1993 and 1994 from control and treated plots at nine sites, three of each age. Sample size for each species, plot, and year ranged from 12 to 15. Standard errors for between-stand variation are indicated.

lower percentage of resorption across all the species and nutrients in the fertilized plots (Fig. 5). Also, resorption of N and P was much higher for beech and yellow birch than for pin cherry. No stand age effects were detected.

Despite the relatively large differences in percentage of resorption between the fertilized and unfertilized trees, the mass of N and P resorbed per leaf was similar between treatments because the higher nutrient concentrations in live foliage (Table 3) largely offset the lower percentage of resorption in the fertilized plots.

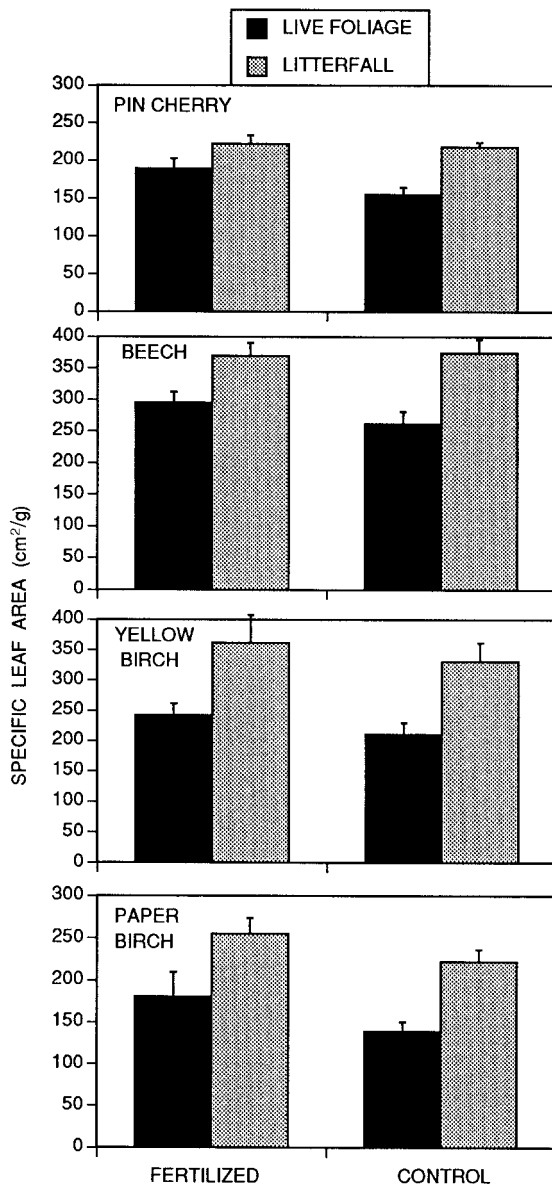*Photosynthesis and leaf respiration.*—The parame-

FIG. 4. Specific leaf area of live foliage and freshly fallen leaf litter of four species collected in 1993 from control and fertilized plots at six sites, averaged across stand ages. Standard errors for between-stand variations are indicated.

FIG. 5. Percentage resorption of nitrogen, phosphorus, and potassium from foliage of three species (corrected to a unit area basis to account for organic matter resorption) in control and treated plots, averaged across six sites (two of each age) and two years (1991 and 1992).

ters of the hyperbolic function (Eq. 2), describing the light-response curve for photosynthesis of pin cherry and paper birch, were compared between fertilized and control plots (Table 4). Expressed on a leaf area basis, pin cherry in the fertilized plots had much higher values for the slope of the light response (a), and this pattern was highly significant in stand M-1. In contrast, there were no significant differences in the light-saturated photosynthetic rate, A_{max} (on a leaf area basis), between the control and fertilized plots at either site. A direct comparison of photosynthetic rates above the light saturation point for pin cherry (500 μmol·m^{-2}·s^{-1}; Amthor

et al. 1990) also indicated no differences between treated and control plots. Hence, the principal photosynthetic response of pin cherry to fertilization was to increase assimilation rates at low light levels and thereby raise the apparent light compensation point.

When assimilation was expressed on a leaf mass basis, values of a were much higher ($P < 0.01$) for pin cherry in the fertilized plots in both stands, reflecting

TABLE 4. Nonlinear regression statistics using a hyperbolic function (Eq. 2) fitted to light-response data for (A) pin cherry in 1993 and (B) paper birch in 1994 in control and fertilized plots from early successional hardwood sites in New Hampshire.

Stand no.	Treatment	Parameter†	Parameter value	95% CI	r^2
A) Pin cherry					
Y-2	Control	a	0.033	0.023–0.042	0.43
		A_{max}	12.84	10.43–15.25	
	Fertilized	a	0.062	0.036–0.088	0.25
		A_{max}	9.01	7.52–10.51	
M-1	Control	a	0.033	0.024–0.042	0.35
		A_{max}	9.73	8.28–11.17	
	Fertilized	a	0.067	0.046–0.089	0.25
		A_{max}	8.84	7.88–9.79	
B) Paper birch					
Y-2	Control	a	0.054	0.043–0.064	0.27
		A_{max}	10.84	9.92–11.76	
	Fertilized	a	0.048	0.037–0.059	0.25
		A_{max}	10.11	9.09–11.13	

† a = the slope of the light-limited part of the light-response curve; A_{max} = the light-saturated photosynthetic rate, measured in $\mu mol \cdot m^{-2} \cdot s^{-1}$.

the significantly higher specific leaf areas in the fertilized trees (Fig. 3). In contrast, no significant differences in A_{max} were observed. The treatment effects on net assimilation apparently were not driven by differences in dark respiration, which were very similar in the control and fertilized plots (0.0113 and 0.0116 $\mu mol \cdot g^{-1} \cdot s^{-1}$, respectively).

To investigate potential causes of the high variation around our light-response curves for pin cherry, linear regressions were applied to the residuals. Multiple linear regressions were run using the residuals from both the mass-based and area-based light curves as dependent variables and relative humidity, air temperature, vapor pressure deficit, day of year, and sample SLA as independent variables. In stand M-1, air temperature and sample SLA both accounted for a significant amount of the variation for both treatments by area and by mass. In stand Y-2, variation in SLA explained a significant amount of variation in net photosynthesis when expressed on a leaf mass basis. Other variables did not account for significant amounts of variation.

For paper birch in stand Y-2, there was no evidence of any treatment effect on the light-response curve for photosynthesis. The slope (a) and asymptote (A_{max}) of the hyperbolic function were very similar between trees in the fertilized and control plots (Table 4). Thus, the significantly higher concentrations of N and P in paper birch foliage (Table 3) did not result in substantially increased photosynthetic capacity on a unit leaf area basis. However, as in the case of pin cherry, the larger leaf size and higher specific leaf area of fertilized paper birch (Fig. 3) probably allowed higher overall photosynthetic efficiency because of the lower unit area respiratory costs during periods unfavorable for carbon assimilation (e.g., nighttime, poor weather).

Fine roots and soil respiration.—Relative root growth was measured using in situ root screens (Fahey and Hughes 1994) in the treatment plots in three stands during the first and second years of treatment. During the first summer (1989) root growth appeared to be stimulated in the organic horizons and depressed in the mineral horizons of the fertilized plots, but the differences among treatments were not significant. By the end of the first growing season, the trend toward higher root growth in forest floor horizons of the fertilized plots was significant in all three stands, suggesting that the surface application of fertilizer had stimulated surface roots. During the second year, however, this treatment effect was not observed, and no significant root growth differences were detected.

Fine root biomass was measured in late summer 1991 in fertilized and control plots at each stand. The overall analysis of variance revealed no significant age or treatment effects on fine root biomass. However, in four of the individual stands, significant differences were observed between fertilized and control plots. In two cases (stands Y-1 and M-2), root biomass was higher in fertilized plots, while in stand Y-3 and O-2 the reverse was true. In all the other stands, fine root biomass was similar between control and fertilized plots.

Fine root biomass was measured again in 1994, this time with all three treatment plots being assessed in all the stands except O-2. Again, there were no significant overall age or treatment responses in fine root biomass (Table 2); although fine root biomass was much higher in control than fertilized plots in five of the stands, the reverse was observed for two stands. Moreover, in only one case (stand Y-1) was the trend observed in 1991 repeated, whereas in stand M-2 it was reversed (i.e., much lower root biomass in the fertilized plot). Thus, although there appeared to be a trend toward lower fine root biomass in the fertilized plots, no general response of fine root biomass to fertilization can be ascribed to these early successional northern hardwood stands.
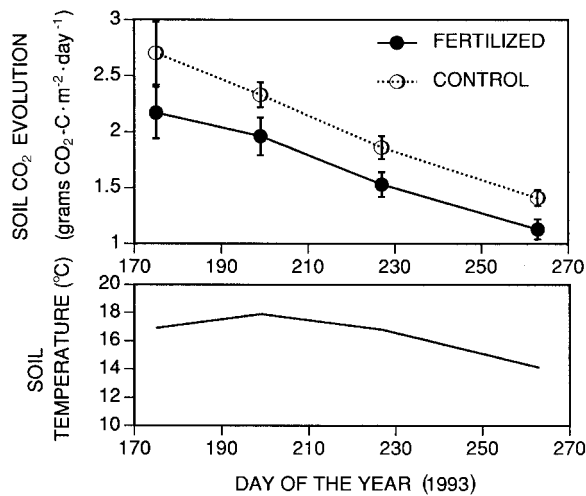
FIG. 6. Seasonal pattern of soil CO_2 evolution and soil temperature (at 15 cm depth) in control and fertilized plots averaged across seven sites in 1993. Standard errors for between-stand variation are indicated.

Soil CO_2 evolution was measured monthly from June through September 1993 in fertilized and control plots at seven of the stands (excluding stands Y-1 and O-2). Based on repeated-measures ANOVA, soil CO_2 flux was significantly lower in the fertilized plots, and no age effect was observed. Peak fluxes of CO_2 generally occurred in late June prior to the peak in soil temperature (Fig. 6). The differences in soil CO_2 flux between control and fertilized plots were usually <25% (with the exception of stand Y-2), but the high replication with this technique allowed us to detect much smaller differences than would be possible for fine root biomass. In all cases where fine root biomass appeared to be higher (though not statistically) in control than fertilized plots (stands Y-2, M-2, M-3, O-1, and O-3), significantly higher soil CO_2 evolution was observed for those control plots. However, an overall regression model relating fine root biomass and CO_2 evolution, and including effects of site and treatment, proved to be nonsignificant. Thus, at this point there is no conclusive evidence that soil CO_2 evolution was an effective proxy for fine root biomass to evaluate fertilization responses in these young northern hardwood forests.

The community-wide response to fertilization in the chemistry of fine roots (which could not be separated by species) was similar to that of foliage. In 1992, macronutrient concentrations were higher in fertilized plots for fine roots from both the organic and mineral horizons (Table 3). As was observed for foliage, the N:P ratio of fine roots was markedly lower in the fertilized than control plots.

Population-level responses

Tree growth and survivorship.—The treatment effect on tree survivorship was consistent across stand ages and species: survivorship was significantly decreased by the fertilization treatment (Fig. 7). In general, this effect of fertilization became significant in the third year of treatment, and by the fourth and fifth year it was highly significant ($P < 0.01$) for all species except paper birch ($P < 0.05$). The fertilization effect on survivorship appeared to be strongest for yellow birch and striped maple and for the mid-age stands (Fig. 7). A significant stand age effect on survival also was observed during the last two years of study for beech, yellow birch, and striped maple.

Relative growth rates of stems that survived through 1993 were analyzed by repeated-measures ANOVA. For the overall model, significant treatment effects were observed only for pin cherry, which grew faster in the fertilized than the control or nutrient-depletion plots (Fig. 8). Two further observations about the pin cherry growth response to fertilization are notable. First, the growth response was delayed until the second full year of treatment (1990). Second, the relative magnitude of the response appeared to be largest for the young stands, intermediate for the mid-age stands, and smallest for the old stands (Fig. 8). However, only the difference between the oldest and the youngest stand ages was statistically significant. Other overall effects on tree growth were inconsistent across stands; however, there was a weak (but nonsignificant) trend toward slower growth of paper birch in the fertilized plots, particularly in the mid-age stands.

Among the individual stands, there were many observations of significant treatment effects on growth. In particular, in two of the mid-age stands (M-1 and M-2), there were clear signs of suppressed growth of all the species other than pin cherry (Table 5). However, these trends were not consistent across all the replicate stands within an age class, and could have resulted in part from uncontrollable initial differences in stand structure between plots within a stand. Another distinctive pattern was much higher growth of all species except paper birch in one of the young stands (Y-3).

A case-control study approach was used to examine the interactive effects of the fertilization treatment, stand age, and tree growth rate on survivorship. The functional relationships between relative growth rate (RGR) and survivorship were examined for pin cherry in control plots of the three different age classes and for pin cherry in fertilized and control plots in each age class (Fig. 9). In the control plots of the mid-age and older stands, the likelihood of survival declined sharply below annual RGR of ~3%, while in the young stands a gradual decline in survival probability accompanied decreases in RGR from 6 to 2% per year. The effect of fertilization was to markedly decrease survivorship at intermediate growth rates in the young and mid-age stands. In contrast, in the older stands fertilization caused a significant increase in mortality, mostly in the slowest growing pin cherry trees (Fig. 9). The shape of the growth–survivorship relationship was sur-
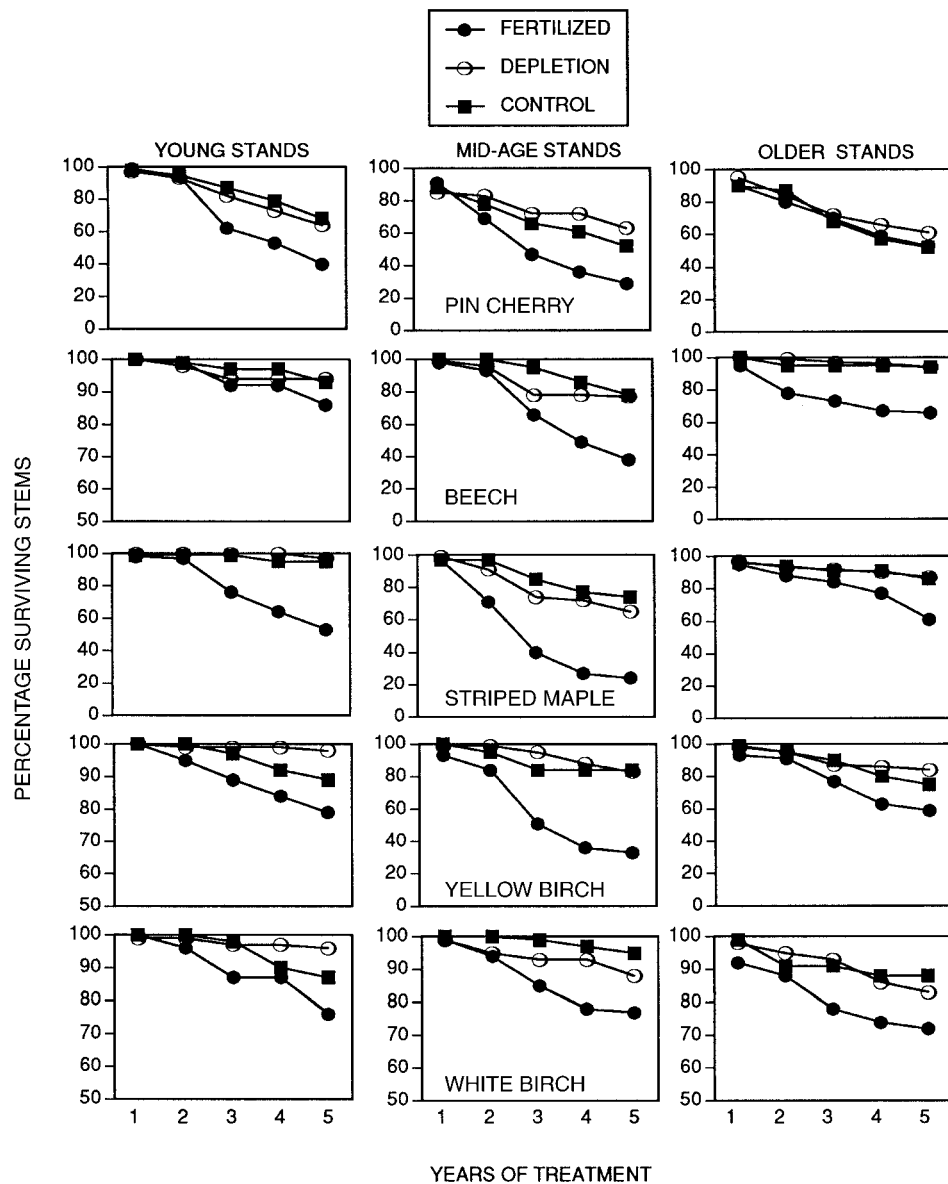
FIG. 7. Survivorship curves over 5 yr of treatment for five tree species in control, fertilized, and nutrient-depletion plots of three different ages (averages of three replicates of each age).

prisingly similar across ages, although relative growth rates were much higher in the young stands.

Seed deposition.—Seeds of maple, beech, and pin cherry were sorted from the litter traps in each year. Except for pin cherry, seed fall was small and erratic in all years. For pin cherry, two very large seed years were observed among the five years of collection, years 3 and 5 of treatment (1991 and 1993). Overall, pin cherry seed fall was much greater in the former year, the average across all the control plots being 124.0 seeds/m^2 in 1991 and 10.9 seeds/m^2 in 1993. In both of these years, highly significant effects ($P < 0.01$) were detected in the ANOVA model: in 1991 there was an age effect on pin cherry seed fall (higher seed fall

in the oldest stands), while in 1993 a treatment effect was observed (Fig. 10). Although in both years most stands showed highest seed production in the fertilized plots, this pattern was significant only in 1993, largely because the pattern was reversed in two of the mid-age stands in 1991. Also, whereas in 1991 peak seed fall was observed in the older stands, in 1993 the young stands showed marginally higher ($P < 0.10$) seed fall than the other ages. The relative increases in pin cherry seed fall in the fertilized plots in 1993 greatly exceeded the relative increases in pin cherry basal area (Fig. 1) and leaf area (Table 2), indicating higher reproductive allocation. No differences were observed between the control and nutrient-depletion plots.

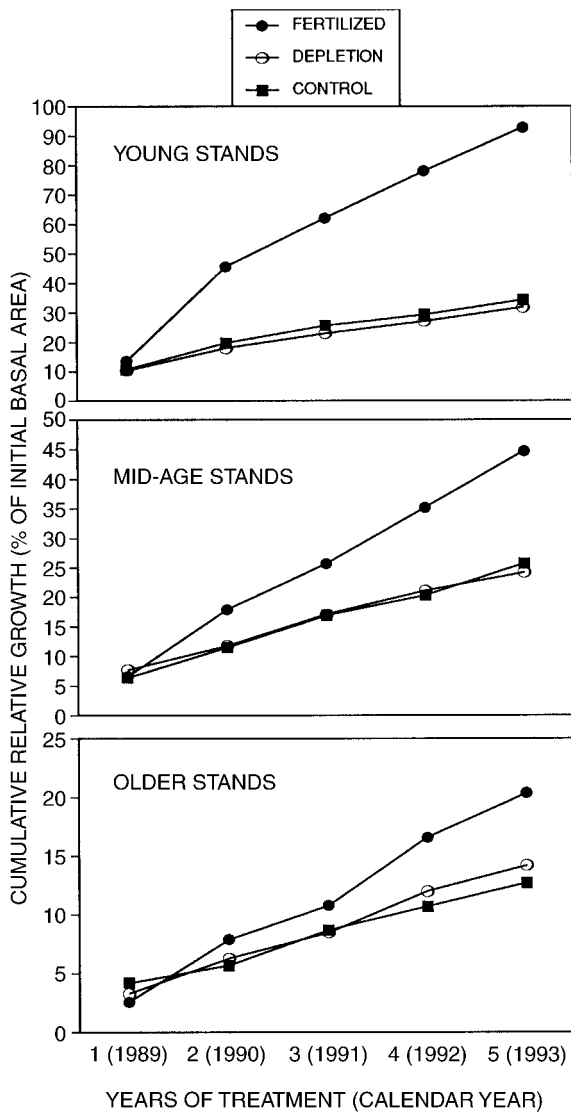FIG. 8. Cumulative relative growth through 5 yr of treatment of surviving pin cherry trees in control, fertilized, and nutrient-depletion plots of three ages (average of three replicates per age).

Canopy architecture response

Canopy height increased significantly along the age sequence (Table 2). There was also a clear trend in the vertical foliage profiles, which shifted from unimodal in the young stands to increasingly bimodal in the older stands (Fig. 11). Fertilization appeared to accelerate and accentuate these trends. In particular, fertilization greatly stimulated the height growth of dominant pin cherry trees and also significantly increased the plot half-way heights (as defined above in *Stand structure and canopy architecture*) (Table 6). Also, the relative response of half-way height to fertilization decreased significantly with stand age.

Pin cherry and paper birch exhibited major differences in the response of canopy architecture to fertil-

ization. Pin cherry trees grew taller, had a greater leaf area, and had proportionately more of their leaf area in the upper canopy in the fertilized plots (Fig. 12). In contrast, the height and leaf area of paper birch were similar in control and fertilized plots, and proportionally less birch leaf area was in the upper canopy of the fertilized plots. These patterns are particularly evident from the calculation of leaf area dominance, defined as the species-specific leaf area above the plot half-way height divided by the total leaf area above that height. Leaf area dominance of pin cherry was increased by fertilization, whereas that of paper birch was greatly reduced (Table 6). One final note on canopy architecture concerns quaking aspen (*Populus tremuloides* L.), which was present in four of the nine stands. When present, aspen was usually the tallest tree in both control and fertilized plots, and it also appeared to increase in height by 1.5–2.0 m in response to the fertilization treatment.

Other community and ecosystem responses

Size structure.—The effects of fertilization on tree growth and mortality resulted in changes in the size structure of the community. Histograms of size-class frequency distributions (Fig. 13) suggested a decrease in skewness in the fertilized plots for all three stand ages. We calculated Gini coefficients to better characterize the size inequalities after 5 yr of treatment (Weiner and Solbrig 1984). A weak trend of increasing size inequality was observed with increasing stand age in the control plots, with average G values of 0.326, 0.344 and 0.368 in the young, mid-age and older stands, respectively. Fertilization increased G values in the young (0.361) and mid-age (0.415) stands but not in the older stands (0.365). The size inequality tended to be increased by fertilization despite the apparent decrease in skewness of the size-frequency histogram (Fig. 13) because of the large growth response of the dominant canopy stems.

Ground vegetation.—Forty-two herb taxa and 32 woody taxa were identified in the permanent quadrats across all stands and plots, but many species were uncommon, occurring sporadically in only a few quadrats. During 1994–1995, herb species richness in the control plots ranged from 0 to 16 across all stands. There was no clear trend in herb abundance or diversity along the gradient in stand age; in one mid-age (M-3) and one old (O-1) stand, herb abundance was negligible, so that treatment effects could not be evaluated there. These two stands were omitted for the analysis of treatment effects.

The diversity of forest herbs was strongly affected by the fertilization treatment: after 7 yr of treatment (1995) average herb species richness was twice as high in the control as in the fertilized plots (11.7 vs. 5.6 species/plot, respectively). This difference was a consequence of the combination of declining herb abundance and diversity on the fertilized plots and increas-

TABLE 5. Significance and direction of relative growth rate responses of dominant species in fertilized plots compared to growth in control plots.

Stand no.	Stand age (yr)	Species					
		Pin cherry	Paper birch	Yellow birch	Beech	Striped maple	Sugar maple
Y-1	10	++	0	NA	NA	NA	NA
Y-2	10	(+)	0	0	0	0	0
Y-3	9	+	0	++	++	++	NA
M-1	16	+	(−)	NA	−−	(−)	(−)
M-2	16	+	0	(−)	−		
M-3	16	++	0	NA	0	0	0
O-1	22	+	0	0	0	NA	NA
O-2	22	0	0	0	0	0	0
O-3	22	++	0	0	0	++	0

Notes: For positive growth responses: ++, $P < 0.01$; +, $P < 0.05$; (+), $P < 0.10$; 0, NS; symbols are analogous for negative (−) responses. Notation of NA signifies that the species was too uncommon to measure growth response.

ing abundance and diversity on most of the control plots (Fig. 14). Trends in the nutrient-depletion plots were similar to those of the control plots.

Wood ferns (*Dryopteris* sp.) were the only herbs that were common enough across all sites to allow a statistical analysis of overall treatment effects on abundance; the frequency of wood fern was significantly reduced by fertilization (Fig. 14), whereas temporal trends in the nutrient-depletion and control plots were not significantly different. Another common herb that showed the same trend as wood fern was *Trillium* sp.: in five of the stands it increased in frequency in the control and nutrient-depletion plots, whereas there was no increasing trend in the fertilized plots. In contrast, *Trientalis borealis* Raf. and *Dennstaedtia punctilobula* (Michx.) Moore appeared to be unaffected by treatments, exhibiting similar temporal patterns across all the plots within those sites where they were abundant. Among other herb taxa exhibiting trends in some of the stands, the following were particularly prominent: (1) *Monotropa uniflora* L. was not observed in any of the plots during the first two years, and in subsequent years it appeared in the control and nutrient-depletion plots (six of the former and four of the latter) but not in any of the fertilized plots; (2) there was a strong trend of increasing frequency of *Lycopodium* sp. in the control and nutrient-depletion plots and decreasing frequency in the fertilized plots in two of the stands (Y-1 and M-2); (3) *Maianthemum canadense* Desf. also appeared to be depressed by fertilization but was not common enough to justify any firm conclusions about this possible effect.

Among the woody taxa, the most consistent pattern was the declining abundance of both *Rubus allegheniensis* Porter and *Rubus idaeus* L. through time within the young and mid-age plots and their rarity in the older plots. The only treatment effect of note was the sporadic occurrence of pin cherry seedlings in many of the fertilized plots.

Litter decomposition and mineralization.—The effects of litter quality and incubation site on litter decay

were examined with a reciprocal transplant study at several of the stands. Fertilization markedly altered both leaf morphology and chemistry, and these responses were expected to result in changes in the rate of release of nutrients from decaying litter in the fertilized plots. Besides increasing the macronutrient concentrations in foliage and fresh litterfall, the fertilization treatment also consistently reduced the concentration of lignin in litter; hence, the ratio of lignin : N was greatly reduced in leaf litter on the fertilized plots (Fig. 15). As a consequence, leaf litter from the fertilized plots tended to decay more rapidly than litter from the control plots; this fertilization effect was significant on at least one collection date for four species, the exceptions being beech and pin cherry (Table 7). No effects of the incubation site (fertilized vs. control) on decay rates were observed.

After one year of decay, nutrient release from decaying litter was strongly influenced by the fertilization effect on foliar chemistry (Table 7). In particular, whereas N and P were strongly immobilized in decaying litter from the control plots, these nutrients were released from the fertilized litter (with the exception of beech). Thus, recycling of N and P was greatly accelerated in the fertilized plots.

Microbial biomass and N availability.—Microbial biomass and its nitrogen content and the availability of soil C to microorganisms did not change significantly along the age sequence of stands. A significant overall treatment effect ($P < 0.05$) on the concentration of microbial biomass in the organic horizons was observed, with the highest values in the nutrient-depletion plots and lowest in the fertilized plots. Although the same trend was observed for the mineral soil, it was not significant ($P = 0.13$).

Forest production and production efficiency.—After 4–5 yr of treatment (1992–1993), ANPP was significantly higher in the fertilized than the control and nutrient-depletion plots. For the unfertilized plots, no trend in ANPP was observed across the age sequence. Moreover, although there appeared to be a greater stim-
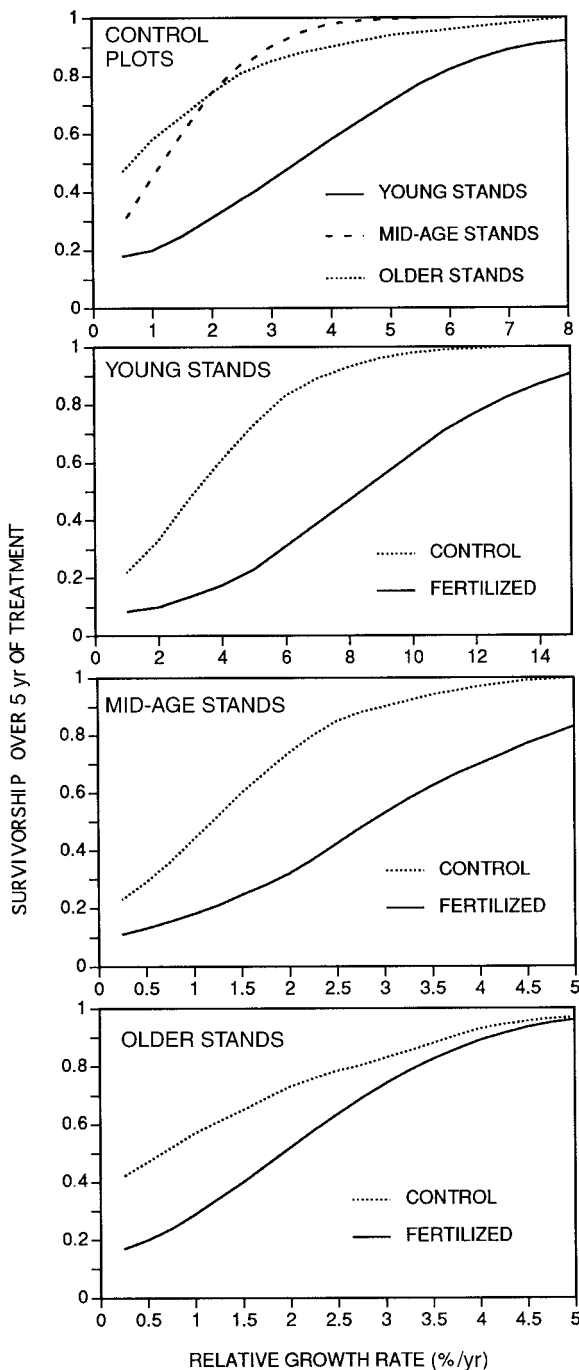
FIG. 9. Survivorship vs. relative growth curves for pin cherry trees growing in control and fertilized plots of three different ages. Curves represent best fits to a logistic model calculated by pooling data across replicates and applying a simplex algorithm. The curves for the control plots (top panel) are reproduced in the lower three panels.

FIG. 10. Deposition of pin cherry seeds for two years in control and treated plots, averaged across three replicates of each age. Standard errors for between-stand variation are indicated.

threefold) in one of the young stands (Y-1, Table 2). Thus, although the fertilization treatment did not affect live basal area because of the high losses to mortality, it did strongly affect ANPP in these early successional stands. Finally, production efficiency was calculated as the ratio of woody biomass production to leaf area. As expected, production efficiency increased markedly in the fertilized plots, in parallel with the increase in ANPP (Fig. 16B).

DISCUSSION

In an attempt to describe the nature of the relationships among four levels of ecological organization (physiological, population, community, and ecosystem), Clark (1990) analyzed the connections between individual plant growth, mortality, and resource availability during the development of monospecific stands of vegetation. The connections among these levels may be most prominently exhibited by the process of interspecific competition during stand development, but an analytical treatment is intractable because of interspecific variation in the plant traits that contribute to competitive performance. However, empirical approaches to demonstrate these connections may be feasible and instructive even in forest ecosystems (Cannell and Grace 1993). Ideally, such experiments would be conducted in natural field settings and in forests with

ulation of ANPP in the fertilized plots of the youngest stands compared with the mid-age and older stands (Fig. 16A), this trend was not significant and resulted primarily from the very large ANPP response (nearly
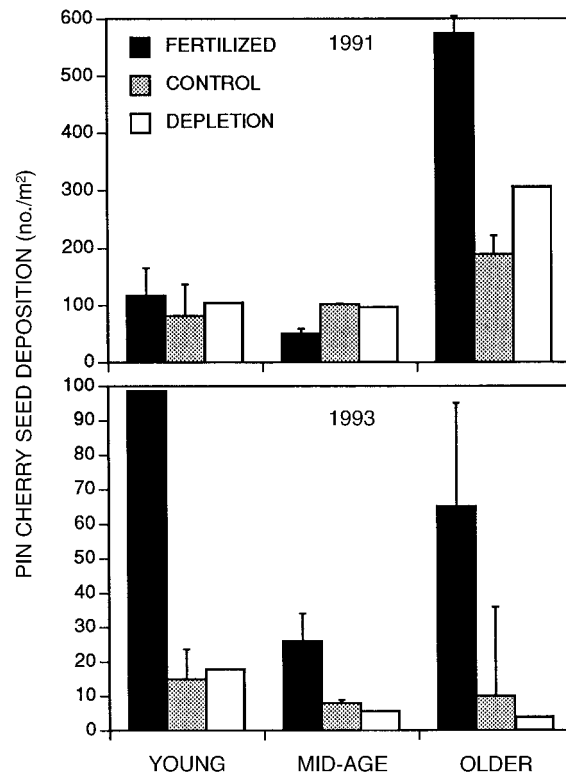
TABLE 6. Tree heights of the overall canopy (mean of 16 tallest trees) and the tallest pin cherry and paper birch trees (at least four individuals per plot), and half-way height and leaf area dominance of pin cherry and paper birch averaged by stand age and treatment.

	Young		Mid-age		Older	
Parameter	Control	Fertilized	Control	Fertilized	Control	Fertilized
Tree height (m)						
Canopy	8.3	10.8	10.1	12.3	13.2	14.3
Pin cherry	8.0	10.7	9.8	11.6	12.7	14.5
Paper birch	8.2	8.4	9.9	10.4	13.5	13.9
Half-way height	0.46	0.66	0.56	0.68	0.73	0.78
Leaf area dominance						
Pin cherry	0.48	0.88	0.75	0.74	0.30	0.63
Paper birch	0.24	0.02	0.16	0.09	0.37	0.08

Notes: In each plot, half-way height is the relative height in the canopy at which an equal area of leaves is held above and below. Leaf area dominance of a species is defined as the species-specific leaf area above the plot half-way height divided by the total leaf area above the half-way height.

a limited number of species that exhibit contrasting life history strategies. The well-studied northern hardwood forest ecosystem (Bormann and Likens 1979) presents such a setting, and has provided a number of insights into the nature and interactions of various autoecological and synecological processes regulating ecosystem development following large-scale disturbance.

This experiment provided conclusive support for our hypothesis about the relationship between soil resource availability and forest succession in northern hardwoods: that the competitive ability of the exploitive species, pin cherry, would be favored by high soil resource availability, and hence the interval of pin cherry dominance in early successional stands of northern hardwoods would be prolonged under resource-rich conditions (Fig. 1). This result supports the contention that pin cherry decline during the second and third decades of forest succession is due in part to the species' poor ability to compete effectively for limited soil resources, particularly N and P, with more conservative species such as beech, maples, and birches.

In contrast, the logical converse of our hypothesis, that nutrient depletion would hasten the demise of pin cherry, was not supported: trees in the nutrient-depletion plots exhibited patterns of nutrition, morphology, growth, and mortality that were very similar to the control plots. This result is probably explained by the fact that the magnitude of nutrient removal was only 20% as great as that of nutrient addition. Apparently, the capacity of soil nutrient pools to buffer the effects of the depletion treatment was sufficient to overcome individual, population, and community effects. Thus, alterations in nutrient availability in the fertilization treatment overcame the stand-to-stand variation in responses; and in a less intense treatment any site quality differences would likely confound the detection of treatment effects. Finally, in the present experiment the remarkable similarity of the control and depletion plot responses helped to convince us of the sufficiency of the controls. We anticipate that nutrient removal at a

rate roughly equaling annual atmospheric deposition of N will eventually affect tree growth, biological diversity, and species interactions, and the treatments are continuing.

Responses of individuals to changes in soil resources

Foliage chemistry.—One of the principal mechanisms that imparts competitive ability in plants is effective resource acquisition (Goldberg 1990). Although all the dominant species responded to fertilization with significant increases in foliar N, P, and K, the largest proportional increase was observed for pin cherry, especially for N (Fig. 2). During the initial stage of col-
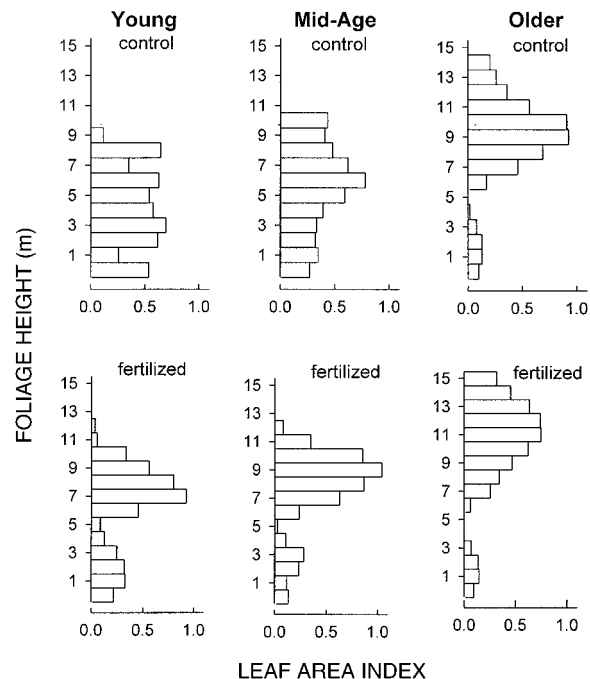
FIG. 11. Foliage-height profiles in control and fertilized plots of three different ages in 1994, averaged across three replicates of each age.
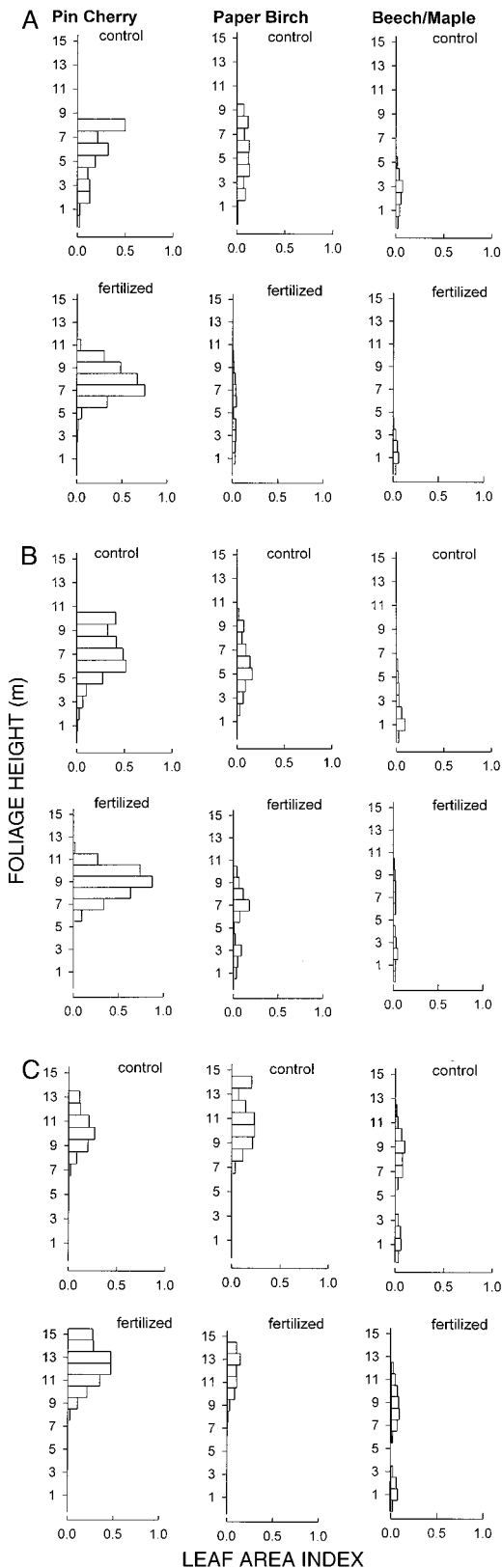
FIG. 12. Foliage-height profiles of pin cherry, paper birch, and sugar maple plus beech in control and fertilized plots of three different ages in 1994, averaged across three replicates per age, for (A) young stands, (B) mid-age stands, and (C) older stands.
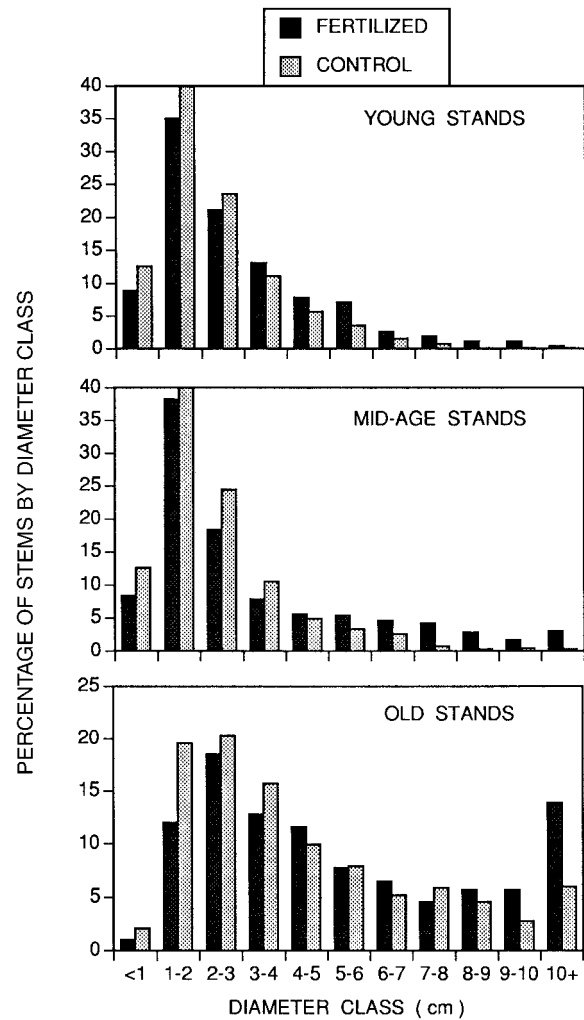
FIG. 13. Size structure histogram in 1993 for tree stems in control and fertilized plots of three ages, averaged across three replicates per age.

onization following large-scale disturbances, when nutrient availability is at a maximum, young pin cherry trees exhibit very high tissue nutrient concentrations (Mou et al. 1993), higher than observed in the present study. This probably represents in part luxury uptake, providing the capacity to supply some future growth when soil nutrient levels decline. However, it also seems likely that optimal physiological performance of pin cherry depends upon relatively high foliar N and P levels. That is, pin cherry seems to be effective at co-opting soil resources when they are abundant, but its ability to respond to consequent low resource availability is severely limited. Although the other species also have been observed to exhibit high foliar N and P concentrations in the first few years of colonization after clearcutting (Mou et al. 1993), these concentrations were much lower than for pin cherry. Conversely, in these 6- to 23-yr-old stands (i.e., control plots) foliar N concentrations were quite similar across all the dom-
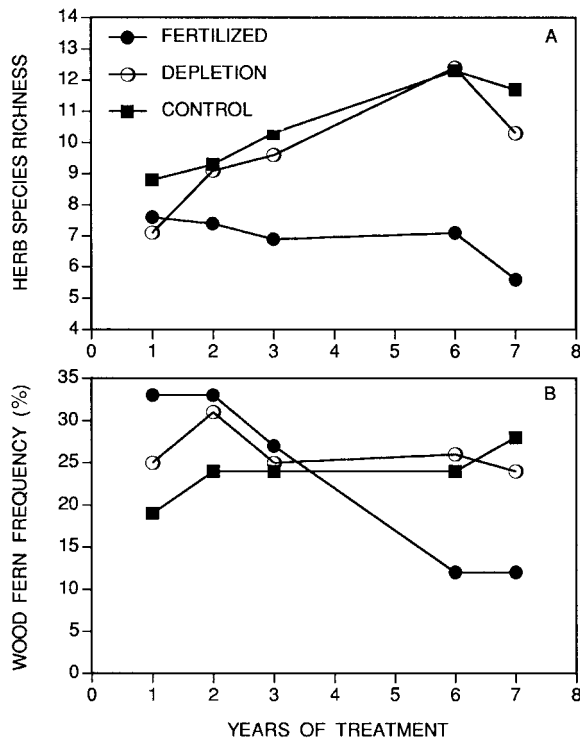
FIG. 14. (A) Species richness of herbaceous plants in permanent quadrants (total area = 20 m²) over 7 yr of treatment in control and fertilized plots, averaged across seven sites (two sites had virtually no herb cover). (B) Frequency of occurrence of wood fern (*Dryopteris* spp.) in 20 quadrats (each 1.0 m²) per plot, averaged across seven sites.

inant species (Table 3); hence, physiological performance of pin cherry may be impaired by low foliar N at this stage of succession whereas that of its competitors is not. The photosynthetic and foliar morphology responses seem to support this contention. That is, the foliar morphology response of pin cherry to higher nutrient availability led to an enhancement of its photosynthetic performance and probably contributed to increased growth.

Nutrient resorption.—One effective response to low resource availability is conservation of previously acquired resources, for example with long-lived leaves (Chabot and Hicks 1982). An alternative mechanism, particularly in these deciduous forests, is high resource resorption. Chapin and Kedrowski (1983) concluded that there is no clear connection between nutrient stress and the efficiency of nutrient resorption by foliage (i.e., percentage resorbed). Although we observed significant decreases in the percentage of nutrients resorbed by leaves in the fertilized plots, the magnitude of these decreases was small, and the total mass of nutrients resorbed was similar in the control and fertilized plots. Resorption of N and P was significantly lower for pin cherry than for beech and birch (Fig. 5), matching the results of Ryan and Bormann (1982) and supporting the suggestion that resorption may confer a competitive
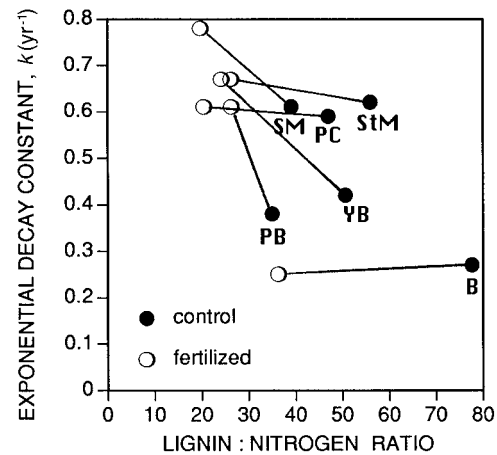
FIG. 15. Exponential decay coefficients, k, plotted against initial lignin : nitrogen ratios for six litter types (B = beech, SM = sugar maple, StM = striped maple, YB = yellow birch, PB = paper birch, and PC = pin cherry) collected from control and fertilized plots.

advantage on these species when nutrients are limited. Thus, although phenotypic plasticity in resorption does not appear to be an important mechanism conferring a competitive advantage under nutrient limitation, in these forests interspecific differences may be important. These results appear to contradict those of Chapin and Moilanen (1991), who observed that the efficiency of resorption was similar for trees of differing N and P status. Their results also suggested that the efficiency of nutrient resorption depends primarily upon carbohydrate resorption. Our results do not contradict that possible interaction, as we observed that higher carbohydrate resorption (as indicated by the difference in

TABLE 7. One-year mass loss and nutrient release from decaying litter of six species, collected from control and fertilized plots.

Species	Treatment	Percentage of original remaining		
		Dry mass	N	P
Beech	Control	79.5 (5.5)	143.6	192.1
	Fertilized	82.8 (8.0)	144.3	115.5
Yellow birch	Control	69.0 (8.0)	131.2	130.0
	Fertilized	59.1 (3.1)**	77.7	77.3
Paper birch	Control	68.9 (4.6)	104.7	95.0
	Fertilized	60.4 (7.9)***	84.2	68.9
Pin cherry	Control	62.7 (4.9)	107.3	103.9
	Fertilized	59.0 (15.5)	81.4	42.6
Sugar maple	Control	62.7 (4.3)	124.0	182.5
	Fertilized	55.2 (7.6)***	70.8	99.2
Striped maple	Control	64.3 (9.9)	141.0	126.9
	Fertilized	56.4 (7.0)**	92.7	74.9

Notes: Data are averaged across incubation sites that exhibited no influence according to ANOVA. Significant differences for mass loss between control and fertilized litter are indicated (**$P < 0.01$; ***$P < 0.001$), and standard errors are in parentheses.

FIG. 16. (A) Aboveground net area production over 5 yr of treatment of trees (>2 cm dbh) in control and fertilized plots of three different ages, averaged across three replicates per age. (B) Aboveground production efficiencies, calculated as the ratio of aboveground production (measured in $g \cdot m^{-2} \cdot yr^{-1}$) to leaf area index. Standard errors for between-stand variation are indicated.

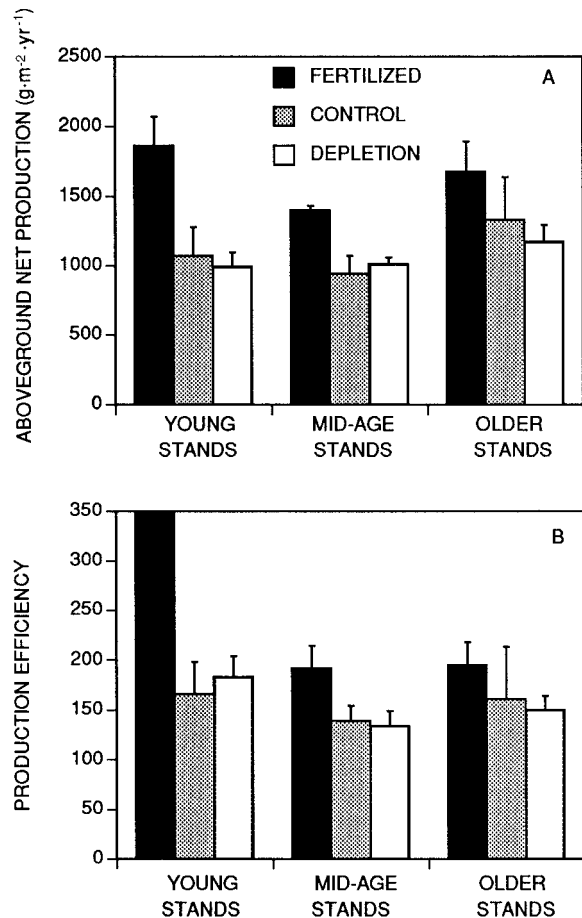SLA between live foliage and fresh litter) was associated with higher N and P resorption (Fig. 4 and 5).

For both carbohydrates and the limiting nutrients (N and P), active resorption probably accounts for most of the measured changes during senescence. Ryan and Bormann (1982) demonstrated that leaching by late summer rainfall did not contribute significantly to these changes in foliar N and P in young and mature northern hardwoods at Hubbard Brook Experimental Forest (HBEF). Similarly, our calculations based upon throughfall concentrations of dissolved organic carbon at HBEF (G. M. Lovett and T. J. Fahey, *unpublished data*) discount the importance of leaching losses to apparent organic matter resorption. However, another possible mechanism of organic matter losses in senescent foliage is respiration, and this mechanism has not been investigated in northern hardwoods.

Foliage morphology.—The fertilization treatment appeared to result in changes in foliage morphology,

as mid-canopy foliage of several species exhibited higher SLA and area per leaf in the treated plots (Fig. 3). The interpretation of this effect is complicated by coincident effects on the distribution of light in the canopy because leaf morphology responds markedly to the light environment to which leaves are exposed (Kira 1975). A more detailed analysis of light availability and foliage morphology through height in the canopy in two of the study sites (M-1, O-3) indicated that SLA decreased steadily with increasing height (and light availability) in the canopy for all species (J. Cramer et al., *unpublished manuscript*). Surprisingly, the only significant differences in SLA between the control and fertilized plots were observed for the most shaded foliage of pin cherry and the two birch species, and SLA was actually lower for the nutrient-rich fertilized leaves (the opposite of the present results). Hence, a straightforward interpretation of the SLA responses observed for the mid-canopy foliage is not possible, although connections with physiological activity seem likely (Ellsworth and Reich 1993).

Photosynthesis and respiration.—Obviously, the efficiency of carbon assimilation in photosynthesis plays a crucial role in determining competitive outcomes. Our measurements of mid-canopy foliage from two of the sites suggested that the photosynthetic activity of pin cherry responded to fertilization, whereas that of a principal competitor (paper birch) did not. However, the causes of these differences and their role in changing the competitive balance are not clear from this study. The most prominent response of pin cherry photosynthesis to fertilization was an increase in the slope of the light-limited portion of the light-response curve (Table 4). If this response was associated with increased foliar nutrient concentrations and changes in leaf morphology (higher SLA), then it is surprising that similar changes in paper birch did not cause an analogous photosynthetic response. However, it is notable that foliar N:P in the fertilized plots was altered profoundly for paper birch but not pin cherry (Fig. 2). A simple interpretation of the effect of this photosynthetic response on the growth of pin cherry would be that partially shaded foliage might fix more carbon in the fertilized plots. However, this interpretation should be viewed with caution. In particular, we were able to quantify photosynthetic responses only for mid-canopy foliage; large differences in photosynthesis and leaf morphology, as well as their responses to fertilization, can be expected within tree crowns (Ellsworth and Reich 1993; J. Cramer et al., *unpublished manuscript*). Quantifying the implications for carbon balance of photosynthetic and morphological responses to fertilization would require detailed examination of within-crown variations in light availability and leaf responses; this was beyond the scope of the present study.

Surprisingly, the light-saturated rates of net photosynthesis were not significantly different between fertilized and control trees of either pin cherry or paper

birch. Although the higher foliar N concentrations might be associated with higher activity of RuBP carboxylase, which should stimulate light-saturated (dark-reaction-limited) photosynthesis (Evans 1989), it is possible that much of the additional N in leaves was in the form of amino acids (Billow et al. 1994). Moreover, although the lack of response of photosynthetic capacity is not consistent with many literature observations (Evans 1989, Mitchell and Hinckley 1993), there is some precedent in studies of forest trees. For example, Teskey et al. (1994) detected no increase in photosynthesis of fertilized *Pinus elliottii* Englem, and the growth increases they observed apparently resulted mostly from increased stand leaf area. Also, although Linder and Troeng (1980) observed higher maximum photosynthesis in fertilized than in unfertilized *Pinus sylvestris* L., the increase was much too small to account for observed stand growth responses. No analogous studies on broadleaf deciduous species have been reported.

As noted for nutrients, one effective strategy under resource limitation is the conservation of acquired resources, and for fixed carbon such a strategy might involve modulation of the rate of respiration. We observed that dark respiration rates of foliage for fertilized and unfertilized pin cherry and paper birch were similar on a unit mass basis; hence, the higher SLA in the fertilized plots might result in lower respiratory costs during unfavorable weather when expressed on a unit photosynthetic area basis. Thus, besides effects on photosynthetic activity, changes in leaf morphology of fertilized trees may also confer some energy conservation benefits.

Canopy architecture.—Architectural responses could confer important benefits to individuals in the competition for the light resource, and such a response is particularly important to extremely shade-intolerant species like pin cherry. There was a marginally significant trend in the overall ANOVA ($P = 0.10$) toward higher leaf area per unit basal area of pin cherry in the fertilized vs. control plots (0.164 vs. 0.116 m²/cm², respectively). Thus, the strategy of the dominant pin cherry trees usually was to increase the size of the crown relative to its supporting stem. Some of this response would be attributed to the increase in foliage SLA (Fig. 3), but the foliage height profiles also illustrate an increase in pin cherry canopy height (Table 6, Fig. 13). One expected risk associated with this strategy is mechanical stress, and, in fact, there was a large pulse of pin cherry mortality associated with windthrow; stem breakage occurred in three of the fertilized plots in 1995 and 1996 (stands M-3, O-1, O-2).

Carbon allocation.—Physiological and morphological responses of individuals and species to changing resource availability may be overshadowed by changes in plant carbon allocation. For example, Gower et al. (1992) observed that large reductions in belowground C allocation in fertilized Douglas-fir (*Pseudotsuga*

menziesii Franco) resulted in higher aboveground production. Although this pattern of response is logical, it does not appear to be universal for forests, as Safford (1974) observed a large increase in fine root biomass in a fertilized northern hardwood forest in New Hampshire. The present results indicated that the response of fine root biomass to fertilization in young northern hardwoods is not uniform across sites. Although there was good evidence for an initial stimulation of fine root growth, especially in the surface organic horizons, thereafter the response was variable, i.e., some fertilized plots showed stimulation of fine root biomass, whereas in others it was depressed. Stimulation of fine root biomass in the fertilized plot was most dramatic (>50% increase) and consistent (i.e., both years of measurement) in stand Y-1, which was the poorest site; soils at Y-1 developed on coarse glacial outwash, whereas all the others were on glacial till. The mechanism of response to fertilization in this stand may have been fundamentally different than in the others.

With the clear exception of stand Y-1, the results suggested that belowground C allocation was probably reduced in the fertilized plots after 5 yr of treatment. This conclusion is based upon the highly significant differences in soil respiration (Fig. 6) and the nonsignificant but largely consistent trends in fine root biomass. Because leaf area index increased in most of the fertilized plots (Table 2), the ratio of fine root biomass to leaf area usually was much lower (but not significantly different in the overall ANOVA), and this response probably contributed to higher productivity. However, it should be noted that total belowground C allocation also would be influenced by the rate of root tissue respiration, and Burton et al. (1996) observed that the respiration rate of sugar maple fine roots increased with root N concentration.

In sum, at the individual plant level, limited access to soil resources constrains the development of the pin cherry canopy soon after canopy closure in successional northern hardwood forests. Improved access to soil nutrients favors pin cherry in competition and stimulates its basal area growth by allowing an increase in photosynthetic surface area. The responses of foliar chemistry, LAI, and resorption by pin cherry strongly suggest that improved access to soil N allows this species to greatly improve its physiological performance. Three mechanisms could contribute to the increase in the production of pin cherry: (1) rapid height growth of fertilized pin cherry may release more of the foliage from competition with neighboring stems (Fig. 12); (2) leaf biomass and area may respond directly as a result of the larger pool of nutrients available to be allocated to those tissues; and (3) some of the increase in leaf area might be attributed to the morphological and photosynthetic response of individual leaves, permitting positive C gain at lower light levels and hence tolerance of greater self-shading. Resolving the relative importance of these three explanations of the architectural

and growth response of pin cherry to fertilization would necessitate quantitative modeling of light interception and utilization by the competing canopies in these stands.

Competition and structure of populations and communities

General.—The effects of changes in soil resource availability on plant morphology and physiological performance would be expected in turn to alter the size structure of populations and the composition and species structure of the overall forest community. These population and community responses would result directly from changes in growth and mortality within the component populations, as affected by shifts in competition. Cannell and Grace (1993) classified two extremes of competition in forests. At one extreme, in purely two-sided competition for soil resources, the size of individuals is not directly related to competitive ability because both access to and requirement for soil resources is usually directly proportional to plant size. In contrast, at the other extreme, large plant size confers a tremendous advantage in purely one-sided competition for light. In most forest settings, some degree of co-limitation by both light and soil resources exists, and competition falls somewhere along the continuum between these extremes.

Increasing soil resource availability would be expected to alter competition toward the one-sided extreme (more intense competition for light), placing smaller individuals at a greater disadvantage. Clark (1990) predicted on theoretical grounds that for even-aged monospecific stands, increased nutrient availability would result in higher mortality, owing to the higher competition associated with increased individual growth rates. He also predicted that these effects would be less for older stands. Our experiment confirmed that these two predictions may hold for even-aged multispecies stands. That is, growth rates increased more in the younger than older fertilized plots (Fig. 6); increased mortality was observed in smaller, slow-growing individuals of all the dominant species in the fertilized plots (Fig. 7); and this effect was less for the older stands. Hence, growth and dominance were concentrated in a small number of individuals in the community, and the chronology of stand development was accelerated. Tome et al. (1994) argued that the effect of one-sided competition on population structure should be to increase size variability, whereas two-sided competition should have little influence on size variability. In the present experiment, size inequality of the community, as indicated by the Gini coefficients (Weiner and Solbrig 1984) increased through time in the unfertilized plots, illustrating the strong competition for light. Fertilization increased this size inequality, at least in the young and mid-age stands. Although the increased light competition reduced survivorship of suppressed stems and hence reduced the skewness

of the size-frequency distribution (Fig. 13), size inequality as represented by Gini coefficients still responded positively to fertilization because of the large growth response of the dominant stems.

Each population exhibited a similar survivorship response to soil resource additions, so that the overall species structure of the community was not greatly altered after 5 yr, except to the extent that the dominance of pin cherry was increased (Fig. 1), and the process of transfer of canopy dominance (especially to paper birch) was delayed (Fig. 12). Apparently, the development of the competitive hierarchy for the light resource (i.e., the distribution of tree heights) that is established during the initial phases of secondary succession was only slightly altered by the higher soil resource availability. We suspect that if soil resources were more acutely limiting during the establishment of the competitive hierarchy for the light resource, then the species structure of a forest community might be altered to a greater extent by an experimental shift in fertility. An experimental test of this hypothesis would help to establish how the species composition of natural forest communities is determined by the balance between one-sided and two-sided competition under co-limitation.

Canopy structure and light competition.—The essence of the competition for light is represented in foliage height profiles. In a previous study of secondary succession in northern hardwoods, Aber (1979) observed patterns of development of canopy architecture similar to those in our chronosequence: (1) increases in canopy height with age, (2) rapid recovery of LAI after cutting with steady increases between age 10 and 30 yr, and (3) increasing stratification of the canopy into overstory and understory layers. The latter pattern also was noted for a *Liriodendron tulipifera* L. forest association in Maryland (Brown and Parker 1994). Aber's (1979) results also suggested that LAI was responsive to water and nutrient availability, and he speculated that on nutrient-rich sites, leaf area would tend to be concentrated in the upper canopy. The increase in nutrient availability on the fertilized plots accelerated the process of development of canopy architecture—height growth, LAI increase, and stratification and concentration of foliage in the upper canopy (the latter pattern concurring with Aber's [1979] speculation about nutrient-rich sites). Although the LAI increase was not statistically significant, it was somewhat consistent (7 of 9 stands) and hence supportive of current dogma (Waring and Schlesinger 1985).

More important to the competitive interactions was the apparent contrast in patterns of light capture by pin cherry and its principal competitor, paper birch (Fig. 12, Table 6). In the control plots, the leaf area dominance of pin cherry declined markedly between age 16 and 22, largely as a result of increasing leaf area dominance by paper birch (despite only moderate mortality of pin cherry; Fig. 7). Fertilization maintained leaf area

dominance of pin cherry at the expense of paper birch (Table 6). Taken together, these results indicate that the transfer of canopy dominance from pin cherry to birch (and other more conservative species) during the third decade of stand development results primarily from the poor ability of pin cherry to compete for soil nutrients and the consequent effect on its ability to compete effectively for light. Thus, in this instance of interspecific competition under conditions of co-limitation, the outcome is determined primarily by the influence of the two-sided competition for nutrients upon the one-sided competition for light. The simplicity of this sequence seems to be largely a result of the extreme life history strategy of pin cherry; in less extreme competitive interactions among trees, the interplay of light and soil resource competition may be more complex and much more difficult to discern.

Plant growth and mortality.—The relationship between individual plant growth and survivorship is central in regulating population responses to environmental change and variation, but limited information is available on this connection. In northern hardwoods, Mou and Fahey (1993) observed that the ability of a spatially explicit model of forest development to track observed successional patterns was limited by poor predictions of survivorship derived from theoretical relationships to growth. Pacala et al. (1996) based a successful model of northeastern forest succession on an empirically derived relationship between growth and survivorship in the recruitment stage of tree life history. One principal mechanism whereby growth influences the likelihood of surviving (besides the obvious competitive interactions) is through the ability of fast growers to repair injuries and resist pathogen damage (Waring 1987). However, this mechanism of protection may increase the risk of catastrophic damage owing to the structural deficiencies of the trunk and root systems (Loehle 1988), particularly for a pioneer species like pin cherry. Another possible cause of variation in the growth–survivorship function among forest stands for a particular species would be differences in the distribution of pest or pathogen populations.

We observed significant variation in the relationship between relative growth rate and survivorship of pin cherry between the control and fertilized plots in the present study (Fig. 9). In all except the older stands we observed much lower survivorship of pin cherry at intermediate growth rates in the fertilized plots. Although a pathogen of cherry, the black knot fungus (*Apiosporina morbosa*), was usually present on dying trees, a quantitative survey of black knot incidence indicated no differences between control and fertilized plots.

Hence, it was surprising to observe significant variation in the relationship between relative growth rate and survivorship between the control and fertilized plots in the present study (Fig. 9). Except in the oldest stands, we observed much lower survivorship of pin cherry at intermediate growth rates in the fertilized plots. It seems that at this stage in its life history (i.e., between ages 6 to 16 yr), pin cherry continues to invest in stem growth, probably at the expense of energy storage and root growth, and suddenly dies if this strategy is unsuccessful (i.e., if it does not effectively co-opt the light resource). At later stages (age >18 yr), increased mortality risk in fertilized plots only applied to the slowest-growing individuals. In fact, at this stage, overall pin cherry survivorship was not significantly lower in the fertilized plots (Fig. 7). Higher survivorship among the largest individuals, probably owing to the higher growth rates (Fig. 8), counterbalanced higher mortality in the smaller size classes. These complex results for pin cherry illustrate some of the difficulties that will be encountered in attempting to model population and community responses to environmental change.

Seed production.—The longer term population and community responses to changes in soil resource availability depend also upon changes in regeneration and recruitment. The present study focused upon the thinning stage of succession, where competition is most intense and new recruitment is minimal (Peet and Christensen 1987), and where most forest species are investing resources primarily in growth rather than reproduction. However, the life history of pin cherry is marked by early and high investment in sexual reproduction to re-supply the soil seed bank prior to its early senescence (Marks 1974). Besides increasing the vegetative growth of this extreme exploitive species, augmentation of soil resource availability also stimulated pin cherry seed production (Fig. 10). Certainly, such an increase in seed production should result in subsequent increases in the species' abundance, but the recurrence interval of large-scale disturbance will also profoundly influence the long-term abundance of pin cherry (Peterson and Carson 1996; G. L. Tierney and T. J. Fahey, *unpublished manuscript*).

Other community and ecosystem responses

Ground vegetation.—The effects of disturbance and resource availability on the abundance and diversity of herbaceous vegetation have been widely studied. In northern hardwoods, as in most forests, large-scale disturbance increases the abundance and diversity of ground vegetation by increasing resource availability (Bormann and Likens 1979, Hughes and Fahey 1991), but after several decades of stand development, the patterns of abundance of herbs appear to resemble those of the pre-disturbance forest (Reiners 1992). Because of the high between-stand variation that exists in ground vegetation, the age sequence in our study is not suitable for examining these successional trends; however, comparisons between control and treated plots provide insights into the regulation of herb abundance and diversity during an important interval of forest recovery from disturbance.

The effect of resource availability on the abundance and diversity of ground vegetation has received considerable attention, both theoretical (Wright 1992, Tilman and Pacala 1993, Houston 1994) and empirical (Grubb 1986, Gentry and Emmons 1987). Most researchers predict a modal relationship of ground vegetation diversity and abundance along the soil fertility gradient, with peaks at intermediate fertility, as increased shading leads to competitive exclusion on richer sites. Alternatively, the diversity and abundance of ground vegetation might increase monotonically with fertility if soil fertility has little effect on stand LAI, so that on more fertile soils, understory plants could benefit by shifting allocation from roots to shoots (Gentry and Emmons 1987). In our study the response of LAI to fertilization was moderate, averaging 0.7 units (or ~12% increase) across the nine stands (Table 2). Apparently the consequent reduction in light availability was sufficient to override any gains to understory plants in soil resource availability, as the fertilization treatment consistently reduced herb diversity and the frequency of common herbaceous species (Fig. 14). We suggest that the mechanism of Gentry and Emmons (1987) will not operate unless the LAI response is even smaller than ~10%, as might occur in forests that are closer to some physiologically or morphologically determined LAI limit.

Productivity and production efficiency.—Aboveground net primary production (ANPP) in these young northern hardwood forests increased significantly in response to fertilization (Fig. 16A), indicating that there was some degree of soil resource limitation on productivity in the control and nutrient-depletion plots. The mechanism of this ecosystem-level response to fertilization differed from monospecific conifer forests, where increases in photosynthesis and total leaf area (Linder et al. 1987), leaf area duration (Gholz et al. 1991), or decreases in belowground C allocation (Gower et al. 1992) have been cited as the principal causes of ANPP increases. In these dense, mixed-species stands, our evidence indicates that the large ANPP response resulted primarily from an increase in the growth rate and dominance of the exploitive species, pin cherry, and from a change in its population structure and canopy architecture. In particular, the increase in the area of pin cherry foliage exposed to relatively high levels of PAR (Table 6) probably resulted in the large ANPP response to fertilization in these northern hardwood stands. This conclusion is supported by the observation that the highly significant increase in stand production efficiency of the fertilized plots (Fig. 16B) was strongly associated with the increase in pin cherry dominance; for example, across all the plots, over half of the variation in production efficiency was explained by a regression on the percentage of total leaf area comprised of pin cherry ($r^2 = 0.51$; one outlier plot removed). Accelerated mortality of smaller trees in the fertilized plots also shifted the size structure of the

community (Fig. 13), probably reducing the respiratory load associated with shaded, slow-growing individuals. Thus, we conclude that the ecosystem-level carbon flux response was connected primarily to a shift in the competitive balance under high soil resource availability.

Unfortunately, our results do not contribute toward clarifying the age-related pattern of decline in forest ANPP (Ryan et al. 1997). The variations in site quality and stand composition apparently confused any temporal trends in ANPP across the successional sequence, and the timing of maximum LAI and ANPP probably varied across sites. These results illustrate that it will be difficult to discern age-related patterns of ANPP in mixed-species stands using a chronosequence approach. However, our results clearly suggest that the dynamics of individual populations in mixed-species stands can be important in modulating age-related patterns of ANPP.

We should point out that in many of the stands, a reduction in carbon allocation to roots may also have contributed significantly to increased ANPP, but this response was not consistent across the entire study. In particular, in the lowest fertility stand (Y-1), where the largest ANPP response to fertilization was observed (about threefold; Table 2), we also observed a significant and consistent increase in fine root biomass. Hence, in this stand the elimination of severe nutrient limitation probably resulted in such a large increase in net photosynthesis that C availability for belowground allocation was stimulated as well. These results suggest the possibility that it is primarily at intermediate soil fertility levels that a reduction in allocation to fine roots stimulates ANPP in these forests (e.g., our stands Y-2, M-2, M-3).

Excluding stand Y-1, the increase in ANPP in the fertilized plots, compared to the control and depleted plots, averaged 455 ± 72 g dry matter·m^{-2}·yr^{-1}. It is instructive to compare this response on a C flux basis with other ecosystem fluxes. Assuming 50% C concentration in dry matter, C flux in ANPP averaged ~227 g·m^{-2}·yr^{-1} higher in the fertilized plots in 1992–1993. The average difference (across seven stands) in soil C emissions between the fertilized and control plots during the growing season (June–October) was estimated at ~50 g C·m^{-2}·yr^{-1} (Fig. 6); if late fall differences were maintained during winter and spring, an additional 50 g difference in C flux would result. Hence, differences in belowground C allocation probably contributed significantly to the ANPP response in many of the stands.

Litter decomposition and nutrient recycling.—The apparent nutrient limitation to pin cherry that accompanies stand development is associated primarily with decreasing nutrient supply from soil as the forest floor pool declines (Covington 1981, Federer 1984) and the live biomass pool increases (Bormann and Likens 1979). Nutrient-poor conditions can be reinforcing: as plant litter becomes more resistant to decay, nutrient

recycling is delayed and certain nutrients (especially N and P) may be immobilized by the soil microbial community. Through its effect on plant tissue chemistry, the increase in soil resource supply to these young northern hardwood forests was further reinforced by more rapid decomposition and nutrient recycling of plant litter (Table 7). The effect on the soil microbial community was to lower microbial biomass per unit organic matter, suggesting a more metabolically active heterotroph assemblage. These effects probably resulted from lower tissue lignin concentrations as well as higher nutrient concentrations. Except for pin cherry and beech, decreased lignin : N ratios in litter were correlated with significantly increased decay rates (Fig. 16), roughly following the relationship expected from previous work in these forests by Melillo et al. (1982). Surprisingly, large declines in the lignin : N ratio of beech and pin cherry did not stimulate more rapid decay, but the recycling of P was greatly accelerated even in these litters (Table 7). These results illustrate how the indirect effect of plant traits on soil resource availability can be regulated by a feedback at the ecosystem level, thereby influencing the outcome of interspecific competition. Because decay of litter from all the competing species would be expected to respond in the same direction to increasing or decreasing nutrient supply (Table 7), the effect should be ecosystem-wide and it should favor the more extreme strategists (as in the present case, pin cherry). Whether such a mechanism actually becomes significant in mediating interspecific competition would seem to depend upon three factors: (1) the sensitivity of foliage chemistry to changing soil resource supply, (2) the sensitivity of decomposition and nutrient mineralization to changes in litter chemistry, and (3) the relative role of recycling from litter in supplying plant nutrient uptake. If all three factors are high, then the outcome of competition could be influenced by such a feedback.

Conclusion

Goldberg (1990) viewed competition as the central process wherein the interactions among the physiological, population, community, and ecosystem levels of ecological organization are played out. Physiological, morphological, architectural, and allocational traits of individuals and their responses to changing availability of resources (light, water, and nutrients) determine competitive abilities, and population size and structure are altered by consequent patterns of growth and mortality. In turn, the contrasting traits among populations lead to differential success, depending upon the nature of resource constraints, and hence to shifts in community structure and composition as succession proceeds. In most forest settings, competition for light is expected to be intense, but varying degrees of co-limitation by soil resources might influence that primary resource constraint by differential limitation to height growth. Finally, feedbacks to resource availability at the ecosystem level result from changing patterns of material recycling and energy flow owing to differences among constituent populations in resource utilization, retention, and conversion efficiency. Our experiment exhibited each of these types of interaction and in some cases illustrated which of a variety of possible responses played the most important role in determining the effects of soil resource availability on competition during secondary succession in northern hardwood forests.

On the basis of the response to experimental alteration of soil resource availability, we conclude that the successional shift in dominance from pin cherry to birch–maple–beech in the third decade following large-scale disturbance results primarily from the poor competitive ability of pin cherry for soil resources (mostly N and possibly P). However, the effect of this signal seems to be transmitted through competition for light, as nutrient limitation impairs the height growth and canopy development of pin cherry, permitting paper birch (and possibly other species) to co-opt the light resource. Thus, we propose that interspecific competition influences the longevity of pin cherry in northern hardwood forests. Although pin cherry is constrained by its suite of life history features (e.g., weak wood, small root system) to a short life span in these closed forests, its poor capacity to compete for limited soil nutrients and consequent inability to compete for light hastens its demise. Further evidence in support of this hypothesis might be found in the relationships between the growth of paper birch and the mortality of pin cherry in coming years in the control plots and in the responses of pin cherry longevity to thinning (an experiment is in progress in these stands).

The mechanism of response of pin cherry to increased nutrient availability included changes in morphological, architectural, and physiological traits, all of which probably contributed to increasing and prolonging its dominance and permitting higher allocation to seed production. Enhanced foliar nutrition resulted in significant changes in leaf morphology across all species (increased leaf size and area : mass ratio), and these changes were particularly prominent for pin cherry. Architecturally, the ratio of leaf area : basal area for fertilized pin cherry increased by ~40%, and this species' proportion of stand LAI increased from 26 to 41% across all sites. Finally, the altered foliar nutrition and morphology may enhance photosynthesis at low light levels; in contrast, paper birch photosynthesis clearly did not respond to fertilization, possibly because of foliar nutrient imbalances. Thus, at the individual tree level the improved performance of pin cherry with high soil resource supply resulted from canopy expansion made possible by nutrient allocation to foliage, which in turn altered foliar nutrition, adaptive morphology, and photosynthesis. Although reductions in C allocation to roots probably occurred, this response was nei-

ther very large nor uniform across all sites: in fact, it was reversed in the most infertile site.

The changes in canopy architecture and increased dominance by the largest trees in the fertilized plots resulted in more intense one-sided competition for light and placed suppressed individuals at a greater disadvantage, accelerating their mortality. The relationship between individual tree growth and mortality was also altered, at least for pin cherry, as slow-growing individuals were much more likely to survive in the control than fertilized plots. Although the increased mortality reduced the skewness of the size-frequency distribution in the community, size inequality increased in the fertilized plots, owing to the stimulation of growth of dominant individuals. The reduction in light availability in the understory was sufficient to override possible stimulating effects of high fertility on the diversity and frequency of forest herbs. The connection between competitive responses of individuals and populations and the emergent property of stand-level primary productivity was unexpected: increases in primary production (or volume growth) in the fertilized plots seem to have resulted primarily from the increased dominance of fast-growing pin cherry and from a shift in the size structure of all populations resulting from greatly increased mortality of suppressed stems. Both a decrease in the respiratory load associated with small, slow-growing individuals and enhanced light capture by the foliage of dominant pin cherries probably contributed to the near-doubling of stand basal area growth in fertilized plots.

The connection between resource availability and the individual, population, and community responses in the intensely competitive situations of mesic forest ecosystems would seem to be adequately conceptualized in terms of the continuum between purely one-sided and purely two-sided competition. Explicit quantification of where a particular competitive setting falls upon this continuum would seem to be necessary to predict the outcome of competition, and experimental alteration of resource limitation might permit this quantification. In the present experiment, the shift toward one-sided competition was large enough to alter some aspects of community organization; however, the size hierarchy established prior to the shift was probably not disrupted enough to greatly alter the eventual composition of the overstory. We suggest that if either soil resources were more acutely limiting or the size hierarchy less well-established at the initiation of treatment, fertilization of a young, mixed forest would be likely to alter the eventual composition by similar mechanisms to those observed here. By extension, the composition of natural forests probably depends on site quality for similar reasons.

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