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Aboveground nitrogen and phosphorus use by five plantation-grown trees with different leaf longevities

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Abstract. Aboveground nitrogen (N) and phosphorus (P) requirement, retranslocation and use efficiency were determined for 28-year-old red oak (*Quercus rubra* L.), European larch (*Larix decidua* Miller), white pine (*Pinus strobus* L.), red pine (*Pinus resinosa* Ait.) and Norway spruce (*Picea abies* (L) Karst.) plantations on a similar soil in southwestern Wisconsin. Annual aboveground N and P requirements (kg/ha/yr) totaled 126 and 13 for red oak, 86 and 9 for European larch, 80 and 9 for white pine, 38 and 6 for red pine, and 81 and 13 for Norway spruce, respectively. Nitrogen and P retranslocation from current foliage ranged from 81 and 72%, respectively, for European larch, whereas red pine retranslocated the smallest amount of N (13%) and Norway spruce retranslocated the smallest amount of P (18%). In three evergreen species, uptake accounted for 72 to 74% of annual N requirement whereas for two deciduous species retranslocation accounted for 76 to 77% of the annual N requirement. Nitrogen and P use (ANPP/uptake) was more efficient in deciduous species than evergreen species. The results from this common garden experiment demonstrate that differences in N and P cycling among species may result from intrinsic characteristics (e.g. leaf longevity) rather than environmental conditions.

Introduction

In forests, individual leaves may persist from less than one year to more than 40 years (Ewers & Schmid 1981). Tree species with long leaf lifespans are commonly found growing on nutrient-poor soils and/or in very stressful environments such as subalpine and boreal forests. Hence, numerous studies have concluded that the evergreen habit is advantageous in harsh environments (Mooney 1972; Wolfe 1979; Chabot & Hicks 1982; Woodward 1987).

The dominance of evergreens in harsh environments may be related to greater carbon gain by evergreen species, which may be partially explained by smaller nutrient requirements and greater nutrient-use efficiency by evergreens (Beadle 1966; Monk 1966; Small 1972; Waring & Franklin

1979). For example, Gosz (1981) and Vogt et al. (1986) reported that N uptake and N loss in leaf litterfall were greater in temperate deciduous than in evergreen forests. Nutrient retranslocation, a possible nutrient-conserving mechanism, has been suggested to be greater in evergreen than in deciduous species (Chapin & Kedrowski 1983; van den Driessche 1984; Schlesinger et al. 1989). However other studies report equal or greater nutrient-use efficiency by deciduous compared to evergreen species (Tyrrell & Boerner 1987; Gower et al. 1989; Gower & Richards 1990).

A lack of uniform stand conditions may confound the comparison of nutrient cycling characteristics of natural evergreen and deciduous forests. For example, two major factors that influence nutrient use patterns are stand age (Turner 1975; Sprugel 1984; Gholz et al. 1985; Meier et al. 1985) and nutrient availability (Stachurski & Zimka 1975; Turner 1977; Shaver & Melillo 1984). Although Schlesinger et al. (1989) suggested that greater nutrient-use efficiency and high retranslocation appeared to be inherent to evergreen species, it is extremely difficult to ascertain from the literature whether greater nutrient-use efficiency is an intrinsic characteristic of greater leaf longevity or a phenotypic response of trees to low nutrient availability.

The overall objective of this paper was to compare N and P use by red oak (*Quercus rubra* L.), European larch (*Larix decidua* Miller), white pine (*Pinus strobus* L.), red pine (*Pinus resinosa* Ait.), and Norway spruce (*Picea abies* (L) Karst.) plantations in southwestern Wisconsin that were planted in 1961 on similar soil. The 'common garden' experimental design provides a unique opportunity to determine if nutrient requirement and nutrient-use efficiency are intrinsically correlated to leaf longevity when all other factors are relatively constant. Leaf longevity of these species ranges from 5 months for red oak to about 66 months for Norway spruce (Gower et al., submitted).

Specific objectives were to:

- estimate N and P retranslocation rates in foliage and stem wood,
- compare annual aboveground N and P requirement, uptake and retranslocation, and
- compare aboveground N and P use efficiency among the five species.

We focused on N and P because these two elements commonly limit tree growth in many temperate forest (Binkley 1986).

We anticipated that:

- N and P annual aboveground requirement was inversely related to leaf longevity,
- a greater percentage of the annual aboveground N and P requirements

of deciduous species was met by retranslocation whereas a greater percentage of the annual aboveground N and P requirements of evergreen species was met by uptake, and

- N and P use efficiency (see 'Methods' for definitions) was positively related to leaf longevity.

Methods

Study site and experimental design

The study was conducted at the Coulee Experimental Forest (43°52′N, 91°51′W) in La Crosse County, Wisconsin. The forest, which contains both natural and plantation forests, was created in 1960 to study the effect of landscape position and vegetation on soil erosion (Sartz 1978). The landscape is characterized by broad ridges dissected by narrow, steep-sided valley. The ridges are capped with dolomite, with underlying layers of Upper Cambrian Sandstones (USDA 1960). The soils are predominantly silt loams of loessal origin or a mixture of loess and sand and are classified as Typic Hapludalfs of the Dubuque, Fayette, and Gale-Hixton series (Hole 1976). Prior to settlement, the vegetation of this area was oak savanna, but a mixed deciduous forest with white and red oak (*Quercus alba* L. and *Q. rubra* L.), sugar maple (*Acer saccharum* Marsh.), red maple (*A. rubrum* L.), paper birch (*Betula papyrifera* Marsh.) and bitternut hickory (*Carya cordiformis* (Wang.) K. Koch) is common toady (Kline & Cottam 1979).

The climate is humid-continental; mean January and July monthly temperatures are −9.1 °C and 23.3 °C, respectively. The average annual precipitation is 780 mm, two thirds of which falls from May through September. The growing season, which averages 163 days, extends from late April to early October; during the winter the soil commonly freezes to a depth of 1 meter (Sartz et al. 1977).

Monoculture plantations of evergreen conifers (white pine, red pine, and Norway spruce), a deciduous conifer (European larch) and a deciduous angiosperm (red oak) were established in 1961 in a randomized complete block design with three replicate blocks. One block is located on a ridgetop and the other two blocks are located on mid and low slope positions (Fig. 1). Maximum distance between the three blocks is approximately 2 km, and the elevation of the three plots did not differ by more than 50 m. Within each block, all 5 species were planted on a similar soil, aspect, slope and elevation (Son & Gower, in press). Sartz (1972) found

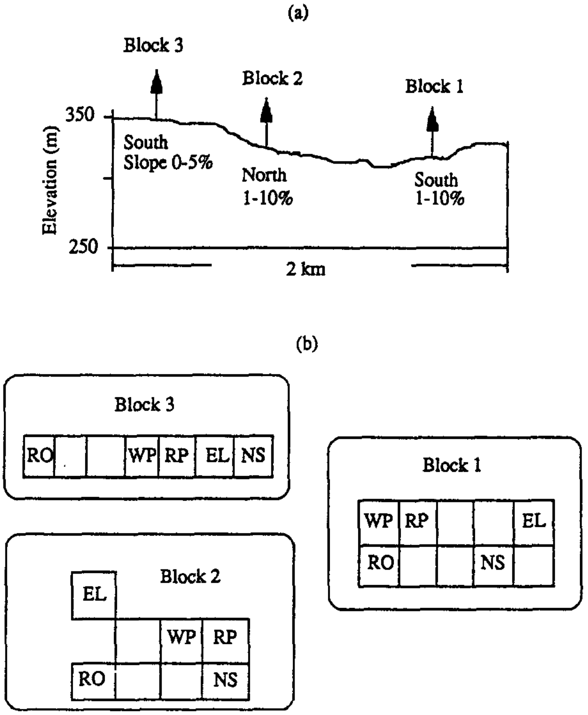

Fig. 1. Physiographic position of three study blocks (*a*) and location of individual plantations within a block (*b*). Species are RO: red oak, EL: European larch, WP: white pine, RP: red pine and NS: Norway spruce.

that precipitation and temperature differences between north and south slopes were slight in the Coulee Experimental Forest.

Seedlings were planted with 2 m × 2 m spacing in 45 m × 45 m plots. Prior to planting, European larch and red oak seedlings were grown for two years in a greenhouse, red pine seedlings were grown for two years in a greenhouse and one year in a nursery bed, and white pine and Norway spruce were grown for two years in a greenhouse and two years in a nursery bed (Sartz 1976). European larch and Norway spruce seeds came from areas of Austria that were selected to closely match the climate in Wisconsin (R. S. Sartz, pers. comm.). In May of 1988, one 25 m × 25 m plot was located in the center of each original plot (to minimize the influence of edge effect on tree growth), and the corners permanently marked. At this time all trees $\geqslant 2.5$ cm diameter at breast height (dbh, 1.37 m) were tagged and diameters (dbh) were recorded.

Stand structural characteristics are summarized in Table 1. No understory vegetation is present in the evergreen conifer plantations and under-

Table 1. Select stand structural characteristics of the 28-year-old (in the field, 1989 age) plantation-grown tree species.

Species	Mean DBH (cm)	Basal area (m^2/ha)	Trees (#/ha)	Height (m)	ANPP (kg/ha/yr)	
					Woody	Foliage
Red oak	9.3 (5.1)	11.5 (2.5)	2033 (422)	13.2 (1.6)	4500 (2000)	4500 (1300)
European larch	21.3 (5.1)	38.8 (0.5)	1045 (60)	21.0 (2.1)	6800 (1200)	3700 (20)
White pine	20.6 (5.4)	44.1 (5.5)	1248 (251)	16.5 (0.9)	5900 (900)	3600 (300)
Red pine	16.6 (3.1)	44.9 (1.9)	2032 (56)	15.2 (0.9)	2000 (700)	2100 (100)
Norway spruce	15.4 (5.6)	25.7 (2.9)	1917 (153)	15.5 (1.2)	5500 (500)	4500 (1200)

Species were planted at 2 m × 2 m spacing in 45 m × 45 m plots; all values in the paper are based on 25 m × 25 m plots located in the center of original plot. One standard error of the means is in parentheses. Net primary production data are for 1989.

story herb production comprised less than 1% of total aboveground production in the red oak and European larch plantations (S. T. Gower, unpubl. data).

Requirement, uptake and retranslocation definitions

We calculated annual aboveground nutrient use as follows: Requirement = Uptake + Retranslocation (cf. Meier et al. 1985). Nutrient requirement, as used in this study, refers to the nutrient quantity incorporated into current biomass production (woody tissue + current foliage); it is not intended to infer a minimum physiological demand that must be met. Retranslocation is the withdrawal of nutrients from an aging tissue and uptake refers to the amount of nutrient absorbed from the soil and precipitation (see Discussion).

Leaching losses may slightly affect N and P retanslocation estimates (Switzer & Nelson 1972) but accurate estimates of annual net leaching losses from the canopy are difficult (Parker 1983; Mahendrappa et al. 1986). Therefore, we did not measure leaching loss in this study (see Discussion section for the potential influence of canopy leaching losses on retranslocation estimates).

N and P Requirement

Aboveground N and P requirement (kg/ha/yr) was calculated as the product of N and P concentration and new mass of foliage, branch, stem bark, and stem wood (cf. Meier et al. 1985). Current annual foliage, branch, stem bark, and stem wood production were estimated from site-specific regression equations for each species and annual dbh measurements for all trees in the 25 m × 25 m plot. A detailed description of the field and laboratory procedures used to develop the allometric equations and to estimate aboveground net primary production for the five species is provided by Gower et al. (submitted).

Briefly, three trees from two blocks and four trees from a third block (10 trees per species) were destructively harvested in late August—early September 1988 to estimate component biomass from stem diameter (Gower et al. 1991). Trees were cut at the mineral soil surface and the length of the live canopy was measured into thirds. All live branches were removed from each canopy position (upper, middle and lower) and weighed. Two to three branches were randomly selected from each canopy position and returned to the laboratory for further analysis. In the laboratory, branches from each canopy position were separated into 1-year foliar age classes and total woody tissue and weighed to the nearest 0.1 g. The branch biomass and foliage tissue in each age class were dried at 70 °C to a constant mass and weighed to the nearest 0.1 g. Ratios of the mass of each tissue to total mass of each branch sample from each of the three canopy positions and the respective moisture content of each tissue were used to calculate total dry mass of each tissue for each canopy position. The nutrient (N and P) requirement for branch growth was estimated as the product of branch production times N and P concentration of branch tissues. This approach was taken because it was difficult to discern current branch tissue, and it may result in a conservative estimate of requirement. Current N and P foliage requirement were calculated as the product of new foliage mass times average N and P concentration of new foliage.

The stem of each tree was cut in 2-m sections and weighed (±0.1 kg). A disk (2 cm thick) was cut from the base of each 2-m section for moisture content, wood:bark ratio and N and P determination. In the laboratory, the disks were separated into wood and bark, weighed, dried to a constant mass and reweighed. Wood:bark ratios and moisture content were used to compute stem wood and stem bark dry mass for each 2-m section; these were summed for each tree to estimate total dry stem wood and stem bark mass.

A 30° wedge was cut from each disk taken from the stem and the current (1988) and 1987 wood increment were removed and composited by tree. Current stem wood N and P requirement was calculated as the product of stem wood production and N and P concentration of 1988 stem wood tissue. Stem bark tissue is also difficult to age; therefore, we calculated stem bark N and P requirement as the product of stem bark mass production and N and P concentration of a composite sample of stem bark tissue.

All tissue samples were dried at 70 °C to a constant mass and ground in a Wiley mill. Approximately 0.3 g of each tissue was digested in a sulfuric acid-lithium sulfate mixture (Parkinson & Allen 1975) and analyzed colorimetrically on a Lachat continuous flow ion analyzer (Lachat 1987, 1988).

N and P retranslocation

Retranslocation occurs in foliage prior to leaf abscission, and to a lesser degree in woody tissue (Cowling & Merrill 1966; Gholz et al. 1985; Meier et al. 1985).

Annual foliar retranslocation of N and P was calculated as the product of percent retranslocation and nutrient content of each age class of foliage. The mass of each foliage age class was obtained from site-specific regression equations (S. T. Gower, unpubl. data). Foliage N and P concentrations were obtained from the destructively harvested samples in August 1988.

Percent retranslocation from the foliage (FR) was calculated as:

$$FR = (C_{max} - C_{min})/C_{max} \times \Delta SLA \times 100.$$

C_{max} is the seasonal maximum stable N or P concentration for each age class of foliage. For persistent foliage, C_{min} is the N or P concentration for each age class of foliage in February. For deciduous leaves and for the oldest age-class of evergreen species, we used the N and P concentration in senescent foliage as an estimate of C_{min}. ΔSLA refers to statistically significant changes in specific leaf area. Senescent foliage was collected from the canopies in October and November 1989 by gently shaking branches and collecting foliage with a butterfly net. Projected (one-sided) specific leaf area was determined using a digital image analyzer (Decagon Devices Inc., Pullman, WA) and used to correct for seasonal carbon loss from the foliage (Stachurski & Zimka 1975). We only included ΔSLA in the calculations when SLA changed significantly between C_{max} and C_{min} sample periods.

One or two branches, depending upon branch size, were cut from four trees at each of the three blocks on June 3, July 19, Sept. 20, Oct. 20, 1989, and Feb. 21, 1990 to determine seasonal N and P concentrations. All of the branches were collected from the middle of the upper-third of the canopy from the same trees on each sampling date. To determine if differences in retranslocation existed among canopy positions, additional foliage samples were collected from the middle and lower canopy positions in July and October 1989, and February 1990.

To compare N and P retranslocation in stem wood, 1988 and 1987 annual rings were separated from the destructively harvested trees and analyzed. Annual stem wood N and P retranslocation between 1988 and 1987 annual rings (SWR, kg/ha/yr) was calculated as:

$$\mathrm{SWR} = \mathrm{PR} \times \mathrm{NC}$$

where PR = percent retranslocation and NC = N or P content (kg/ha). Percent retranslocation was calculated as

$$\mathrm{PR} = (C_{88} - C_{87})/C_{88} \times 100,$$

where C_{88} and C_{87} are N and P concentrations of the stem wood that was produced in 1988 or 1987, respectively. Because of the difficulty in separating annual stem bark and branch tissue, we assumed retranslocation in stem bark and branch tissue was proportional to N and P retranslocation in stem wood in each species.

N and P uptake and use efficiency

Because uptake of nutrients is difficult to measure without the use of isotopes, which was prohibited in these plantations, annual aboveground N and P uptake rates (kg/ha/yr) were calculated as the difference between N and P requirement and retranslocation (cf. Meier et al. 1985). Nutrient-use efficiency (NUE) was calculated as total aboveground net primary production divided by annual nutrient uptake (Hirose 1975).

Statistical analysis

Species and block effects of N and P concentrations for foliage and stem wood and stand-level estimates of nutrient requirement, retranslocation, uptake and use efficiency were analyzed using a general linear model procedure. A repeated measure analysis of variance procedure was used to examine seasonal N, P and specific leaf area patterns (not shown).

Regression analysis was used to examine correlations between nutrient requirement, retranslocation or use efficiency and leaf longevity. All statistical analyses were performed using SAS (SAS 1988). Unless indicated, a significance level of 0.05 was used.

Results

Seasonal foliage N and P concentrations and retranslocation

In general, current foliage N and P concentrations for deciduous species significantly decreased from June to July, remained stable through September and then significantly decreased in October (Figs 2, 3). Current foliage N and P concentrations for all evergreen conifers also significantly decreased from June to July ($p < 0.01$) and except for P concentrations for red and white pine, remained unchanged through February (Figs 2, 3). Prior to leaf senescence, the concentration of N and P in the oldest foliage of white and red pine significantly decreased. We did not observe significant differences in foliar N concentrations for leaves in the upper, middle and lower canopy for the five species.

Although leaf expansion appeared to be complete when we collected foliage in June, the specific leaf area for current foliage was significantly greater in June than July except for European larch (Y. Son, unpubl. data). Therefore, we used June foliage samples to calculate percent retranslocation for European larch and July samples for the other four species.

Percent N and P retranslocation from each foliage age class is given in Table 2. We observed a significant species ($p < 0.0001$), a needle age ($p < 0.0001$ for N, $p = 0.01$ for P), and a species × needle age interaction effect ($p < 0.0001$) (Table 3). No block effect was observed for either element ($p = 0.86$ for N, $p = 0.35$ for P). Deciduous species retranslocated more N and P from new foliage than evergreen species; red oak retranslocated the greatest percent of N (83%) from abscising current foliage whereas European larch retranslocated greatest percent of P (72%) from new foliage.

We expected maximum foliar N and P concentrations in July and the minimum concentrations in October; however, the maximum and minimum concentrations occurred in June and September, respectively, for most trees. Therefore, to calculate canopy-level N and P dynamics we assumed the same percent N and P retranslocation for foliage in the middle and lower canopy positions as the upper canopy position, for which we had foliar N and P concentration data for June and September. Because Norway spruce retained needles for only 4 years in the upper

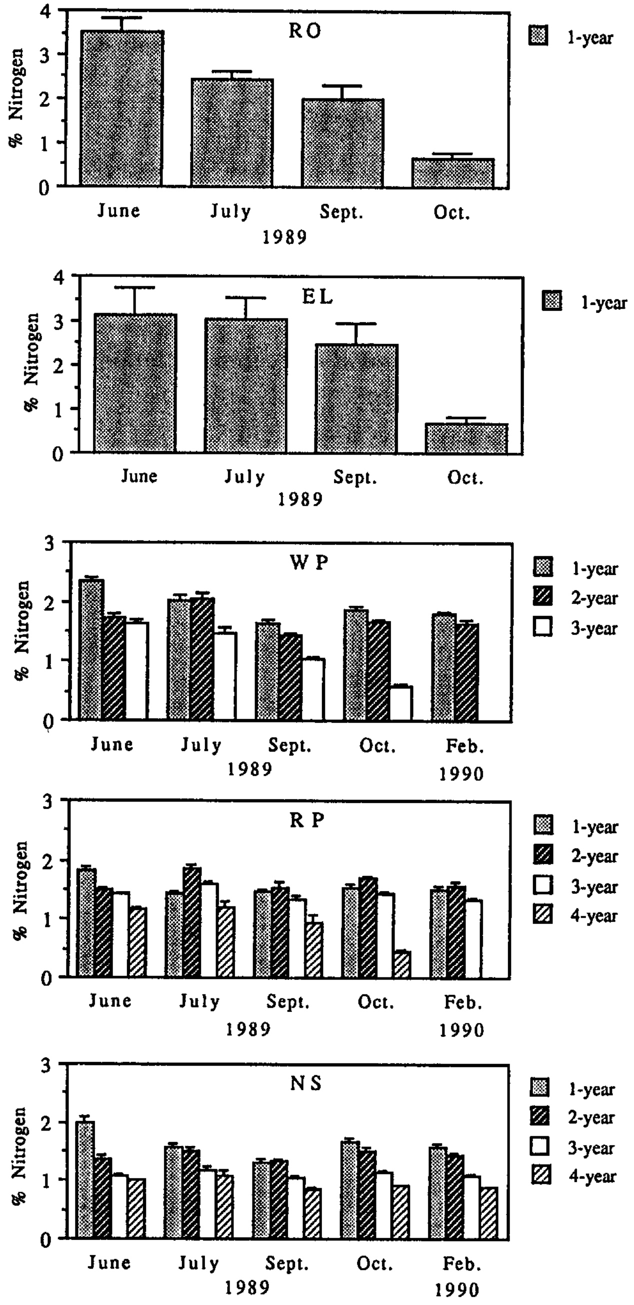

Fig. 2. Seasonal foliage N concentration (% dry weight) for 28-year-old red oak, European larch, white pine, red pine and Norway spruce. Vertical bars are 1 standard error. Symbols follow those in Fig. 1.

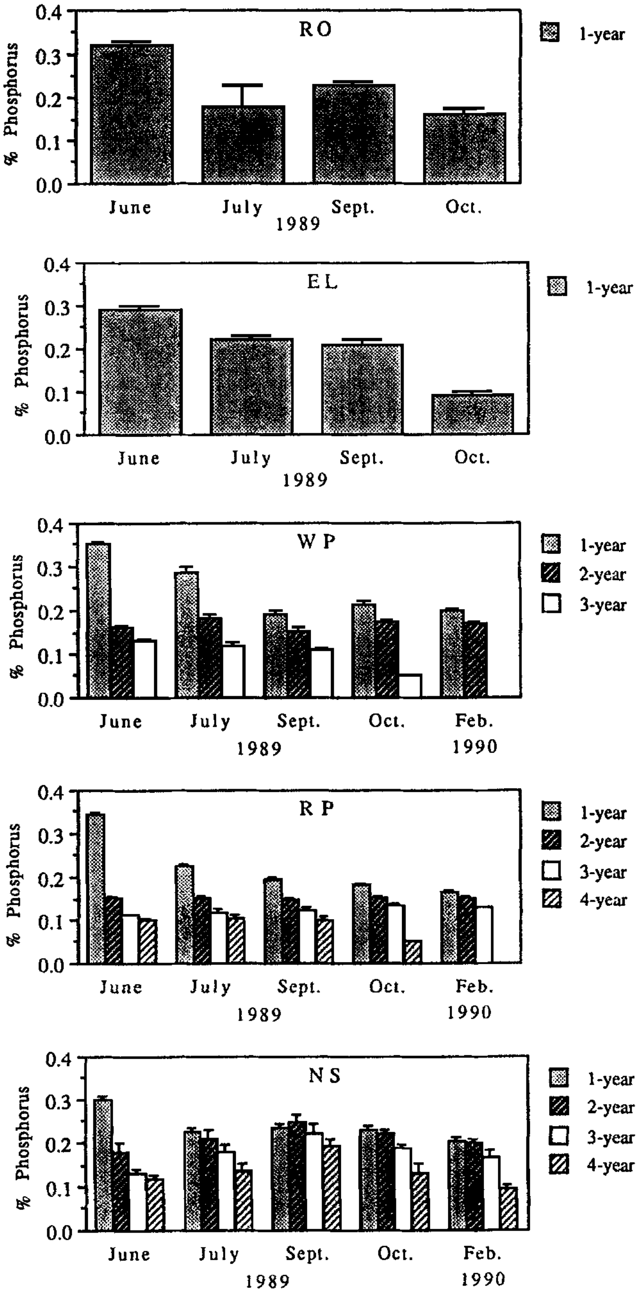

Fig. 3. Seasonal foliage P concentration (% dry weight) for the five study species. Vertical bars are 1 standard error. Symbols follow those in Fig. 1.

Table 2. Average percent retranslocation of N and P from the foliage for the five study species. Percent retranslocation = (maximum concentration − minimum concentration)/maximum concentration × ΔSLA × 100. One standard error of the means is in parentheses.

Species	Foliage age	Nitrogen	Phosphorus
Red oak	1	83(5)	47(5)
European larch	1	81(2)	72(5)
White pine	1	23(3)	35(3)
	2	32(2)	26(2)
	3	53(4)	55(4)
Red pine	1	13(2)	29(2)
	2	23(4)	18(4)
	3	21(2)	15(2)
	4	55(4)	47(5)
Norway spruce	1	22(2)	18(3)
	2	17(1)	23(1)
	3	17(2)	30(3)
	4	13(3)	26(5)

Table 3. Results of the analyses of variance for foliage N and P retranslocation for the five species.

		p-value	
Species	Source of variation	N	P
Species	Block	0.8618	0.3511
	Species	0.0001	0.0001
	Needle age	0.0001	0.0145
	Species × Needle age	0.0001	0.0001
Red oak	Block	0.9075	0.1072
European larch	Block	0.2637	0.1495
White pine	Block	0.4806	0.9906
	Needle age	0.0001	0.0001
Red pine	Block	0.8696	0.0831
	Needle age	0.0001	0.0001
Norway spruce	Block	0.0551	0.4442
	Needle age	0.0148	0.1706

canopy, we used the percent retransloction rate from 4-year-old foliage to estimate percent retranslocation in the middle and lower canopy positions.

Percent N and P retranslocation from current stem wood differed significantly among the five species. Retranslocation of N from current stem wood ranged from 35% for red oak to 60% for red pine whereas retranslocation of P ranged from 41% for red oak to 72% for red pine (Fig. 4).

Aboveground N and P requirement

Aboveground N requirement ranged from 38 kg/ha/yr for red pine to 126 kg/ha/yr for red oak, and P requirement ranged from 6 kg/ha/yr for red pine to 13 kg/ha/yr for Norway spruce (Fig. 5). Nitrogen requirement was significantly greater for deciduous species than evergreen species; however, the annual aboveground P requirement did not differ among the five species ($p = 0.10$).

Foliage production comprised the largest percentage of the total above-

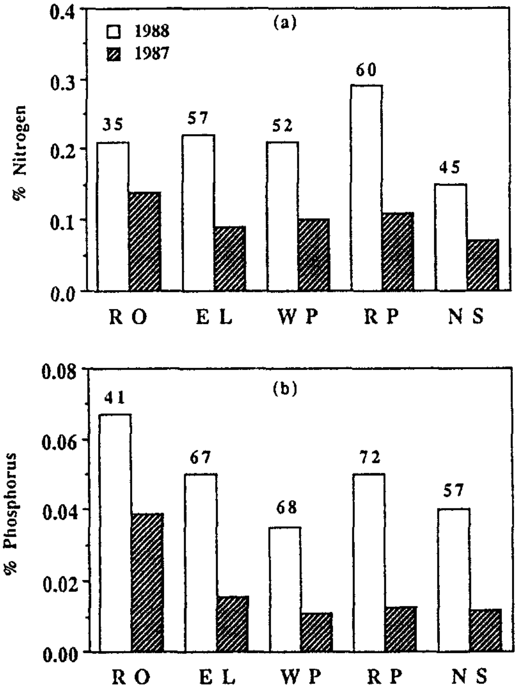

Fig. 4. Nitrogen (*a*) and P (*b*) concentrations of 1988 and 1987 stem wood. Vertical bars are 1 standard error. Symbols follow those in Fig. 1. The value above each 1988 histogram bar is the percent of N or P retranslocation out of current stem wood.

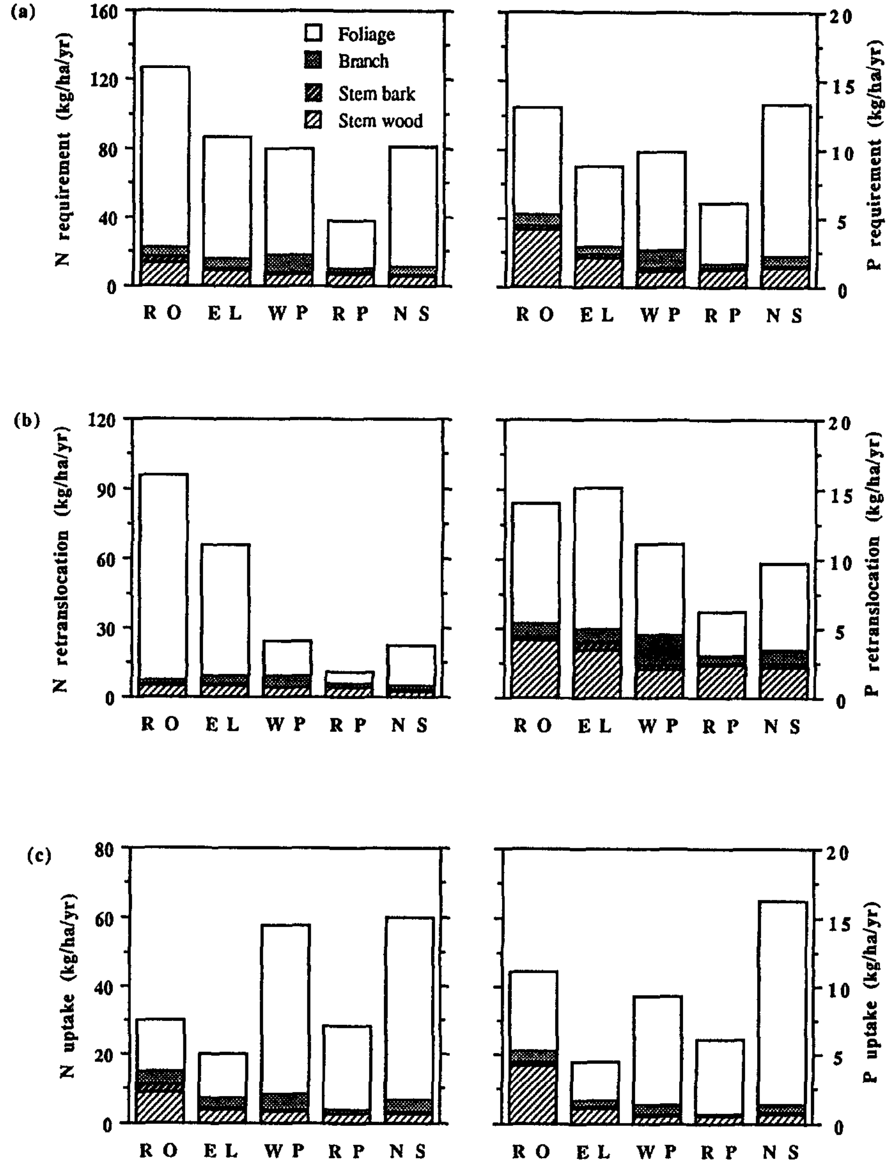

Fig. 5. Annual aboveground nutrient requirement (*a*), retranslocation (*b*) and uptake (*c*) for the five study species. Symbols follow those in Fig. 1.

ground N and P requirements followed by stem wood, branch and stem bark. The relative allocation of the total aboveground N requirement to foliage ranged from 75% for red pine to 86% for Norway spruce. Foliage production comprised from 56 to 83% of the total aboveground P requirement for red oak and Norway spruce, respectively.

Nutrient retranslocation and uptake

Nitrogen uptake differed significantly ($p = 0.01$) between evergreen and deciduous species. Average retranslocation comprised 77% of the annual aboveground N requirement for deciduous compared to 27% for evergreen species (Fig. 5). Consequently, by definition, evergreen species met a greater percent of total N requirement by uptake than deciduous species. Annual aboveground P retranslocation did not differ ($p = 0.12$) among the five species.

N and P use efficiency

Nitrogen and P use efficiency were significantly different among the five species. Nitrogen-use efficiency ranged from 136 (kg ANPP/kg-N uptake) for red pine to 471 for European larch while P use efficiency (kg ANPP/kg-P uptake) ranged from 901 for Norway spruce to 3758 for European larch (Fig. 6). Nitrogen and P use efficiency were significantly greater for the deciduous than for evergreen species we studied.

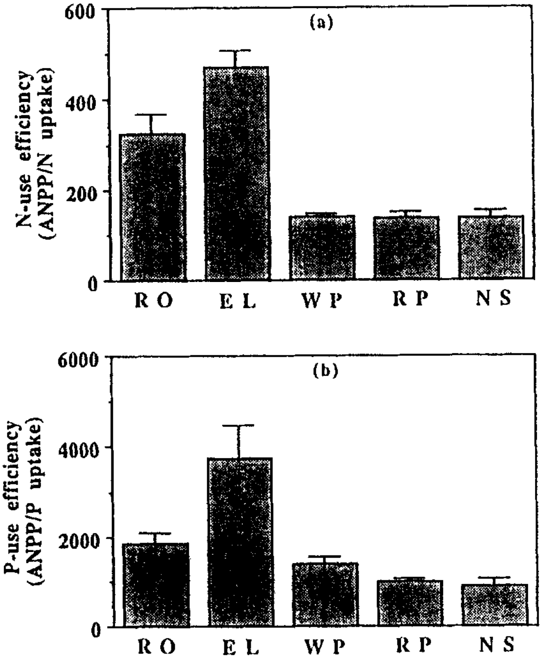

Fig. 6. Nitrogen (*a*) and P (*b*) use efficiency of the five species. Nutrient use efficiency is defined as aboveground net primary production (ANPP)/annual aboveground nutrient uptake (cf. Hirose 1975). Vertical bars are 1 standard error. Symbols follow those in Fig. 1.

Discussion

Foliage and stem wood retranslocation

Nitrogen and P concentrations in the new foliage for all five species were high compared to values commonly reported for natural forests (Binkley 1986). For example, N concentration of new foliage ranged from 1.4% for red pine to 3.0% for European larch. The high N and P concentrations are not surprising however, since the plantations were established on a fertile Alfisol.

Earlier studies have suggested that evergreens generally retranslocate N and P more efficiently from senescing foliage than deciduous species (Vitousek 1982; Chapin & Kedrowski 1983; Waring & Schlesinger 1985). If we used N and P concentrations from current foliage and senescent foliage as the maximum and minimum concentrations to calculate percent retranslocation (cf. Chapin & Kedrowski 1983), we find that deciduous species retranslocate N more efficiently. For example, we calculate that deciduous and evergreen trees retranslocate 82 and 57% N and 60 and 58% P from senescing foliage, respectively, while Chapin & Kedrowski (1983) reported that deciduous trees retranslocate 52% N and 44% P and evergreen trees retranslocate 58% N and 66% P. The percentage of N retranslocated from senescing foliage by European larch (81%) is very similar to the value (81%) reported for hybrid larch (*Larix* × *eurolepis* Henry) by Carlyle & Malcolm (1986) and to the average value summarized for larch (84%) by Gower & Richards (1990).

Several researchers have reported lower nutrient concentrations in heartwood than sapwood (Cowling & Merrill 1966; Merrill & Cowling 1966; Lim & Cousens 1986a, b; Helmisaari & Siltala 1989), but few have calculated N and P retranslocation for stem wood. Whittaker et al. (1979) reported only 3 to 10% withdrawal of N and P from stem wood for a deciduous forest. Meier et al. (1985) calculated that young and mature *Abies amabilis* forests withdrew 53 and 83%, respectively, of the N from stem wood, respectively over a five-year period. Our estimates of N retranslocation from current stem wood are similar to the values reported for the younger *Abies amabilis* stand. We did not observe a significant correlation between percent N or P retranslocation from current stem wood and leaf habit or average leaf longevity for the five species.

Aboveground N and P requirement

Increased leaf longevity may be an important mechanism to reduce annual nutrient demand (Chabot & Hicks 1982). Total aboveground N requirements (kg/ha/yr) reported in the literature range from 56—152 for temperate deciduous and 34—84 for temperate evergreen forests, while aboveground P requirements (kg/ha/yr) range from 7—11 for temperate deciduous and 0.8—9.1 for temperate evergreen forests (Ovington 1965; Nihlgard 1972; Switzer & Nelson 1972; Cole et al. 1977; Cole & Rapp 1981). Except for the large annual P requirement observed for Norway spruce, the aboveground N and P requirements calculated for the five species in this study were similar to values reported for other evergreen and deciduous forests. Our results suggest that annual aboveground N and P requirements are greater for deciduous than evergreen species; these data support speculation by Chabot & Hicks (1982) and literature reviews by Gosz (1981) and Mahendrappa et al. (1986).

Annual foliage N and P requirements comprised 56 to 86% of the total aboveground N and P requirements even though new foliage proportion comprised only 30 to 50% of total aboveground net primary production (Gower et al., submitted). The greater annual aboveground N requirement of deciduous than evergreen forests can largely be explained by the greater N concentrations of current foliage for deciduous than evergreen species. For example, we observed a significant positive relationship ($r^2 = 0.95$, $p = 0.05$) between N concentration of current foliage and annual aboveground N requirement (Fig. 7). The observed differences in annual aboveground N requirement is not related to new foliage production since

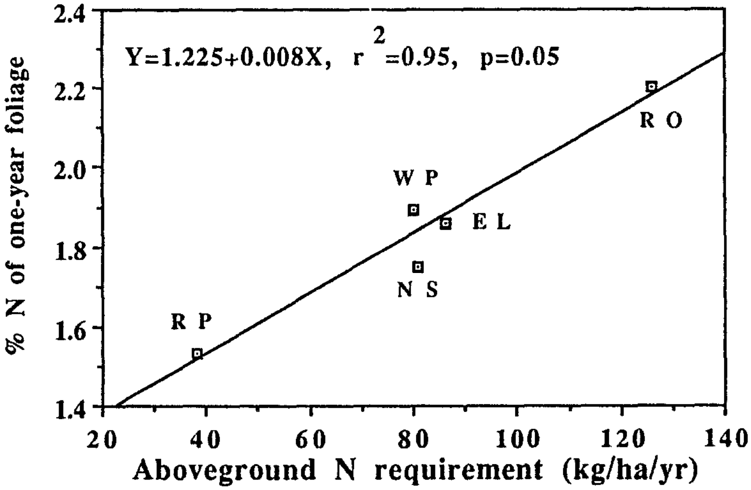

Fig. 7. Relation of current foliage N concentration to annual aboveground N requirement for the five species. Symbols follow those in Fig. 1.

foliage NPP did not differ significantly ($p = 0.76$) among the five species (Gower et al., submitted).

Foliage leaching can be an important flux in forest ecosystems for certain nutrients (e.g. K), especially in areas that receive heavy acid deposition and/or rainfall. The equation we used to calculate requirement assumes negligible amounts of canopy leaching of N or P; if this assumption is incorrect we would underestimate requirement and overestimate retranslocation. Based on estimates of canopy N and P leaching from nearby studies, we conclude that ignoring this flux should not greatly affect our results. For example, Bockheim et al. (1983) estimated that only 3.3 kg N/ha/yr were leached from the canopy of a 34-year-old red pine plantation in central Wisconsin. Lennon (1983) estimated that foliage leaching comprised $< 2\%$ of the N that was retranslocated from senescing foliage in a sugar maple stand at the University of Wisconsin Arboretum. Studies outside Wisconsin have also reported negligible or no N and/or P leaching losses (Miller et al. 1976; Gholz et al. 1985).

A second factor that could affect our estimates of uptake is canopy uptake of N from wetfall. Nadelhoffer et al. (1983) calculated that the annual precipitation input of N in forests in southcentral Wisconsin averaged 8 kg/ha/yr, and Bockheim et al. (1986) reported an annual N input of 11.6 kg/ha/yr for a red pine plantation in central Wisconsin. Using a N-uptake efficiency coefficient of 0.5 that was reported for larch and Sitka spruce (Reynolds et al. 1989), we calculate the maximum N uptake by the canopy is about 5 kg/ha/yr. Therefore, we assume that both foliar leaching and canopy uptake are minor fluxes of N and P, relative to requirement, uptake and retranslocation. This conclusion is consistent with that of Miller (1984).

Aboveground N and P uptake and retranslocation

Annual nutrient requirement of vegetation is met by uptake of nutrients from the soil and internal retranslocation of nutrients from aging tissue. The degree of reliance on retranslocation varies with site quality, species and growth rate (Cole & Rapp 1981; Birk & Vitousek 1986; Nambiar & Fife 1991). Cole & Rapp (1981) reported very little retranslocation in temperate evergreen conifer forests. However, Meier et al. (1985) estimated that 37 to 58% of N and 48 to 59% of P annual aboveground requirements were met by retranslocation in subalpine *Abies amabilis* forest, and Turner & Lambert (1986) estimated that 50 to 60% of the annual P requirement of *Pinus radiata* plantations was met by retranslocation. In this study, we estimated that retranslocation supplied 27% of the aboveground annual N requirement of evergreen forest species. The evergreen species retranslocated a smaller amount of their total annual N and P requirement than the two deciduous species. We observed a negative linear relationship between leaf longevity and annual aboveground N ($r^2 = 0.76$, $p = 0.05$) or P ($r^2 = 0.71$, $p = 0.08$) retranslocation among the five species in this study (Fig. 8).

The greater contribution of retranslocation to the annual requirement of deciduous than evergreen trees may be related to the higher foliar concentrations of N and P and high retranslocation rates prior to foliage

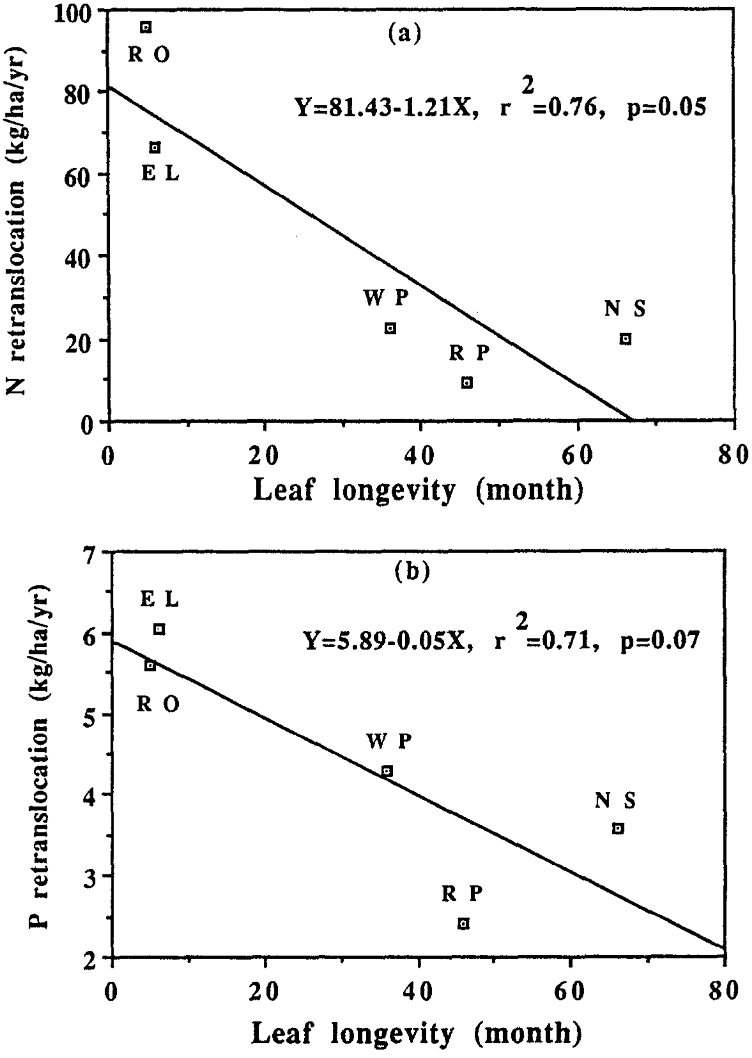

Fig. 8. Relation of N (*a*) and P (*b*) retranslocation to leaf longevity (month) for the five species. Symbols follow those in Fig. 1.

senescence. Nambiar & Fife (1991) reported a strong positive correlation between the absolute amount of N retranslocated from foliage and N content of the foliage in the spring for control and fertilized *Pinus radiata* trees.

Miller (1989) reported a strong positive correlation between annual uptake rates of N and P and annual aboveground net primary production for forests in contrasting climates. Our results do not support the relationship reported by Miller (1989); neither foliage or total aboveground NPP differed among European larch, white pine and Norway spruce (Gower et al., submitted), but N uptake rates for these three species ranged form 20 to 60 kg/ha/yr.

N and P use efficiency

Greater leaf longevity is one mechanism that has been commonly suggested to increase nutrient-use efficiency (Loveless 1961; Chabot & Hicks 1982). In this study, deciduous species used N and P more efficiently than evergreen species. We observed a negative relationship between N-use efficiency and leaf longevity ($r^2 = 0.73$, $p = 0.06$) for the five species (Fig. 9). There were no significant linear relationships between P-use efficiency and leaf longevity ($p = 0.12$, not shown).

The inverse relationship between the stand-level estimate of N-use efficiency and leaf longevity is in agreement with the inverse relationship

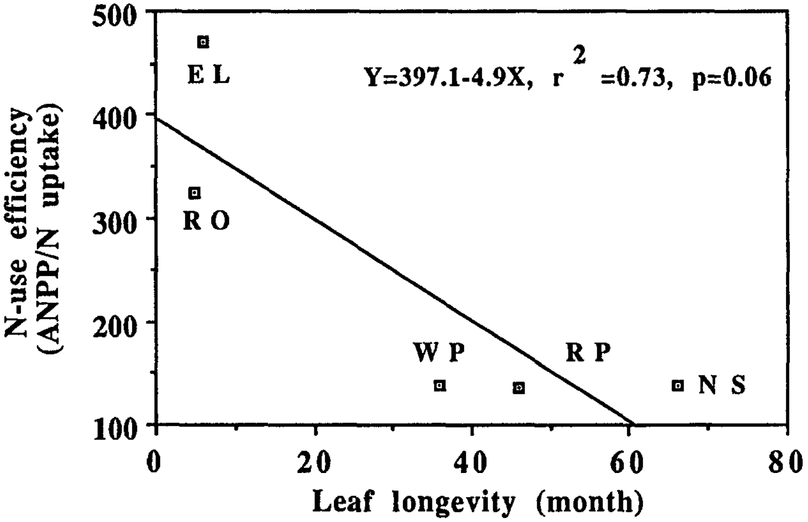

Fig. 9. Relation of N-use efficiency to longevity (month) for the five species. Symbols follow those in Fig. 1.

between instantaneous N-use efficiency (net photosynthesis/leaf N, ug[mol $N]^{-1}$ s^{-1}) and leaf longevity observed for 23 species in the northern Amazon basin (Reich et al. 1991). The more efficient use of N and P by deciduous than by evergreen species may be attributed to the greater retranslocation of N and P from current foliage in deciduous than evergreen species.

A second factor that may help explain the greater N use efficiency by species with short versus longer leaf lifespans is light attenuation through the canopy. Several researchers have calculated that in stands where leaf area index (LAI) is greater than 6 (in this study red and white pine and Norway spruce, Gower & Norman 1991) a large fraction of the canopy operates at a very low photon flux density (Field 1983; Oker-Blom 1986; Baldocchi & Hutchinson 1986). Although Hirose & Wegner (1987) demonstrated nitrogen use efficiency can be increased by partitioning leaf N content among leaves within the canopy proportional to natural field light exposure, we did not observe consistent significant difference in foliar N concentration for leaves within the canopy (Y. Son, unpubl. data). The lack of a consistent decrease in foliage N concentration (weight or area basis) is particularly surprising for Norway spruce because Field (1983) suggests the greatest advantage of N redistribution should be in species with high leaf area index.

Due to the limited number of tree species in this study, it is difficult to determine the exact form of the relationship (e.g. linear or curvelinear) between NUE and leaf longevity, therefore we chose to use a simple linear form. The important point is that these data do not support the hypothesis that nutrient-use efficiency is positively correlated to leaf longevity (Chapin 1980; Chabot & Hicks 1982).

In conclusion, the relationship we observed between leaf longevity and nutrient requirement coincides with previously reported results. However, the observed inverse relationship between N retranslocation or N-use efficiency and leaf longevity do not support the hypothesis that nutrient use efficiency is positively correlated to leaf longevity. The data from this study are inappropriate to interpret evolutionary patterns of nutrient use and leaf longevity, nor do they discount previous comparative studies. But for the first time, this study illustrates several intrinsic relationships between leaf longevity and N and P cycling in forest ecosystems.

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