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# Effects of Light, Nitrogen, and Phosphorus on Red Pine Seedling Growth and Nutrient Use Efficiency

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**ABSTRACT.** Growth and nutrient use efficiency were determined for red pine (*Pinus resinosa* Ait.) seedlings grown at various levels of light, nitrogen, and phosphorus. Nutrient use efficiency was estimated for nitrogen (NUE) and phosphorus (PUE) and was calculated as biomass production divided by total nutrient content. Seedlings grown in high light had four to five times more biomass than those in the low light treatment. Nitrogen supply had a significant effect on total biomass as well as other biomass components. Phosphorus supply did not have a significant effect on any of the biomass components. NUE and PUE decreased with increased supply of N and P, respectively. The results of this study suggest that red pine seedlings can adjust their nutrient use efficiency, particularly for N, when light and nutrient availability are varied. NUE was highest with high light and low N-high P supply in nutrient solutions. FOR. SCI. 40(1):47-58.

**ADDITIONAL KEY WORDS.** *Pinus resinosa* L., nutrient use efficiency, nitrogen, phosphorus, light.

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**R**ED PINE (*Pinus resinosa* Ait.) is commonly planted in the northeastern United States on clearcut sites previously occupied by northern hardwoods. Typically, these northern hardwood sites are more productive than sites where red pine naturally occurs. If allowed to regenerate naturally, clearcuts are usually colonized by fast-growing hardwoods. From a management perspective, it is important to know how a planted tree seedling will respond in environments outside the nutritional range where that species occurs in nature. Knowledge of whether red pine adjusts nutrient use efficiency in response to changing environmental conditions would provide useful information to forest managers.

High nutrient use efficiency by plant species could be an adaptive strategy to tolerate nutrient stress on sites of low soil fertility. A phenotypic adjustment in nutrient use efficiency may allow red pine to tolerate nutrient depletions caused by faster growing competitor species. Species often exhibit the highest nutrient use efficiency at low levels of nutrient availability based on studies with varying nutrient availability (Gray and Schlesinger 1983, Shaver and Melillo 1984, Boerner 1984, Boerner 1985, Birk and Vitousek 1986, Lajtha and Klein 1988). Birk and Vitousek (1986) determined that the nitrogen use efficiency (NUE) of loblolly pine (*Pinus taeda* L.) seedlings increased as N availability decreased. Pastor et al. (1984) estimated NUE of eight tree species by using the inverse of nutrient concentration in litterfall. They found that red pine had the highest NUE and

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phosphorus use efficiency (PUE) of the eight species studied (three coniferous, five deciduous) and typically grew on sites with the lowest N availability. Although in Pastor et al.'s study, mature red pine had a high NUE and PUE compared to other tree species, it is not known if red pine can alter its nutrient efficiency in response to changes in environmental conditions. The purpose of this study was to determine (1) if red pine seedling growth rate and biomass were affected by different levels of light, nitrogen (N), and phosphorus (P) supply, and (2) if red pine has the ability to shift nutrient use efficiency in response to changes in nutrient and light availability.

A greenhouse experiment was designed to determine the growth and nutrient use efficiency of red pine seedlings in response to varying levels of N, P, and light. Growth conditions in the laboratory cannot duplicate field conditions. However, experiments under controlled conditions can identify the potential of red pine seedlings to utilize available nutrients and to change nutrient use efficiency in response to changes in nutrient supply and light. This study estimated nutrient use efficiency of red pine seedlings, including total root production and nutrient content of the whole plant.

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## METHODS

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Six-month-old containerized red pine seedlings were transplanted, one per pot, into 7.6 L pots containing a mixture of sand, peat, and perlite (2:1:1 sand:peat:perlite by volume). Plants were watered by hand at the soil surface to minimize foliar leaching. Immediately after transplanting, green shade cloth was installed over half of the 40 seedlings of each block. Pots were repositioned monthly along the greenhouse bench within the two light treatments to minimize location effects within blocks.

The experimental design was a split-plot factorial with N (high and low), P (high and low), and light (open and shaded) as the factors. The eight treatment combinations were replicated ten times in a split-plot design. The light treatment was the main plot factor and the location of the light treatments in the greenhouse was the blocking factor. Each block consisted of 40 seedlings, 20 seedlings under shade cloth (73% light exclusion,  $190 \mu\text{mol m}^{-2} \text{s}^{-1}$ ), and 20 seedlings in the open (full greenhouse light,  $>800 \mu\text{mol m}^{-2} \text{s}^{-1}$ ). Of the 20 seedlings, 5 replicates of each nutrient addition were randomly positioned within the main plot factor. Nitrogen and P were crossed factors with each potted seedling receiving a combination of either high N-high P, high N-low P, low N-high P, or low N-low P (Table 1).

Four nutrient treatments were applied, differing in the amount and concentration of N and P (Table 1). A ratio of 36% N as  $\text{NH}_4$  and 64% N as  $\text{NO}_3$  was maintained for the high N solutions whereas a ratio of 20% N as  $\text{NH}_4$  and 80% N as  $\text{NO}_3$  was applied in the low N solutions. Because there was a ten-fold difference between the high and low N addition, the effect of  $\text{NH}_4/\text{NO}_3$  ratios between treatments was assumed minimal. The concentrations of potassium (K), calcium (Ca), magnesium (Mg), sulfur (S), and micronutrients were identical in all treatment solutions. Nutrient solutions were formulated following guidelines suggested by Tinus and McDonald (1979) for *Pinus* spp. One liter of nutrient solution for each treatment was applied once a week for both growth periods. All seedlings were watered with distilled water twice a week.

TABLE 1.

Elemental composition of treatment solutions applied to red pine seedlings.

Nutrient compounds	High nitrogen-high phosphorus		High nitrogen-low phosphorus	
	Concentration (mg/L)	Total element (mg/L)	Concentration (mg/L)	Total element (mg/L)
KNO <sub>3</sub>	401	N (224)	401	N (224)
Na <sub>2</sub> (HPO <sub>4</sub> )	183	P (40)	18.3	P (4)
NH <sub>4</sub> NO <sub>3</sub>	480	K (155)	480	K (155)
MgSO <sub>4</sub>	412	S (102)	412	S (102)
CaSO <sub>4</sub>	259	Ca (60)	259	Ca (60)
		Mg (40)		Mg (40)
	Low nitrogen-high phosphorus		Low nitrogen-low phosphorus	
KNO <sub>3</sub>	115	N (20)	115	N (20)
Na <sub>2</sub> (HPO <sub>4</sub> )	165	P (40)		
NH <sub>4</sub> (HPO <sub>4</sub> )	18.86		18.86	P (4)
KCL	211	K (155)	211	K (155)
MgSO <sub>4</sub>	412	Mg (40)	412	Mg (40)
CaSO <sub>4</sub>	259	Ca (60)	259	Ca (60)

Note: Micronutrients were added monthly (50 mg/L) as Soluble Trace Element Mix (S.T.E.M.) derived from boric acid, copper sulfate, iron sulfate, manganese sulfate, sodium molybdate, and zinc sulfate.

In October 1989, after the first 4-month growing period, seedlings were stored in a greenhouse with natural light at temperatures below 4°C for 1000 hr to fulfill cold requirements. Seedlings were watered as needed to prevent soil drying during storage. Subsequently, seedlings were returned to the greenhouse at 27°C to break dormancy and resume growth (December 1989) for an additional 4 months until bud set. During the second 4-month growing period, artificial light (fluorescent bulb, 1000  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) was applied for an additional 4 hr/day to extend the photoperiod.

All seedlings were harvested at the end of the experiment and separated into the following components: (1) 1-yr-old needles; (2) 2-yr-old needles (2 growth periods of 4 months each); (3) stems; and (4) roots. Plant components were dried at 60°C for 48 hr prior to weighing. Three to four seedlings per treatment combination were ground in a Wiley Mill to pass a 20-mesh screen and then pooled by tissue type (1-yr-old needles, 2-yr-old needles, stems, and roots) to assure that enough dry sample was available for nutrient analysis and to reduce the total number of nutrient analyses. Plant tissue samples were analyzed by the Plant and Soil Analysis Laboratory at the University of Maine for total N and P content per component. Total N of all plant tissue was determined by block digestion using a sulfuric acid-hydrogen peroxide solution for total N and analyzed on a Wescan 360 Ammonia Analyzer (Wescan Instruments, Santa Clara, CA). To determine total P, ground plant tissue samples were dry-ashed at 550°C for 5–6 hr and dissolved in 50% HCL. Total P was analyzed by inductively coupled plasma emission spectrometry (ICP, model 975 Atomcomp) (Thermo-Jarrel Ash, Franklin, MA). Precision and accuracy for the tissue nutrient analysis were all within 5%.

Nutrient use efficiency was calculated as biomass production/total plant nutrient content (Agren 1985) using the average weight of the seedlings pooled for nutri-

ent analysis. We calculated biomass production by subtracting average initial biomass from each seedling per treatment. Initial biomass was estimated with a subsample of 20 seedlings from the seedling stock used in the experiment. Average seedling biomass ( $1.55 \pm 0.10$  g), foliar nitrogen ( $1.19 \pm 0.05\%$ ) and phosphorus ( $1991 \pm 59 \mu\text{g/g}$ ), and root nitrogen ( $0.99 \pm 0.04\%$ ) and phosphorus ( $2393 \pm 80 \mu\text{g/g}$ ) were very similar prior to treatment.

#### STATISTICAL ANALYSIS

A split-plot analysis of variance was used to analyze the biomass data in PROC GLM of SAS (SAS Institute Inc. 1987). Block and shade were the main plot factors with N and P as the split-plot factors. An example of a complete ANOVA table for the split-plot design is provided for total seedling biomass (Table 2). Because red pine seedlings were composited for nutrient analysis, nutrient use efficiencies and nutrient concentrations were analyzed with a two factor (N and P) analysis of variance using PROC GLM of SAS (SAS Institute Inc. 1987). It was not possible to test for the shade effect since seedlings were composited across blocks. When the results from analysis of variance of nutrient data were significant ( $P < 0.05$ ), a Ryan-Einot-Gabriel-Welsch multiple range test was used to separate means (SAS Institute Inc. 1987).

## RESULTS AND DISCUSSION

Total biomass of red pine seedlings was significantly higher in the full light than the shade treatment (Table 3). High nitrogen significantly increased total biomass in the full light treatment but had no effect in the shade treatment resulting in a significant light x nitrogen interaction. Phosphorus supply had no significant effect on total biomass or the other biomass components (Table 3). Similar significant trends follow for the other biomass components except that the 2-yr-old needle

TABLE 2.

Analysis of variance table for red pine seedling total weight.

Total weight	df	Mean square	F	p
Shade	1	6576.6896	775.97	0.023*
Error (BLK*Shade)	1	8.4755		
N	1	364.4920	3478.21	0.011*
Error (BLK*N)	1	0.1048		
P	1	26.2836	0.21	0.726
Error (BLK*P)	1	124.8916		
N*P	1	25.9096	3.48	0.313
Error (BLK*N*P)	1	7.4492		
Shade*N	1	268.2718	558.52	0.027*
Error (BLK*Shade*N)	1	0.4803		
Shade*P	1	21.0852	0.19	0.0738
Error (BLK*Shade*P)	1	110.6329		
Shade*N*P	1	17.5769	2.04	0.389
Error (BLK*Shade*N*P)	1	8.6032		

Note: df, degrees of freedom; p, significance of effect (\* $P < 0.05$ ).

TABLE 3.

Probabilities of statistically significant effects of shade, nitrogen, and phosphorus generated by analysis of variance for seedling component dry weight and shoot:root ratios.

Source	NDL1	NDL2	Stem	Root	Sht:Rt
Shade	ns	ns	ns	0.035	ns
N	0.041	0.022	ns	ns	ns
P	ns	ns	ns	ns	ns
Shade*N	0.017	ns	0.026	0.021	ns
Shade*P	ns	ns	ns	ns	ns
N*P	ns	ns	ns	ns	ns
Shade*N*P	ns	ns	ns	0.053	ns

Note: ns,  $P > 0.05$ . NDL1 = 1-yr-old needles; NDL2 = 2-yr-old needles; Sht:Rt = shoot:root ratio.

component was affected only by the N treatment (Table 3). Total seedling biomass was five times greater in the full light-high N treatment than in the shade-high N or shade-low N treatments (Table 4).

Most studies have found that shoot:root ratios are lower under nutrient stress (Gray and Schlesinger 1983, Shaver and Melillo 1984, Linder and Rook 1984, Cromer et al. 1984, Birk and Vitousek 1986, Timmer and Armstrong 1987, Cromer and Jarvis 1990), or under low light intensity (Bourdeau and Laverick 1958, Logan 1966, Margolis and Vezina 1988). In contrast to other studies, we found no significant differences in shoot:root relationships under nutrient stress or with changes in the level of light intensity (Table 4).

TABLE 4.

Average values (by treatment combination) of red pine seedling biomass by components (g) and shoot:root ratio. Values in parentheses are standard errors of the mean.

Light	N	P	TOTWT	NDL1	NDL2	Stem	Root	Sht:Rt
High	High	High	29.13 (2.57)	11.95 (1.68)	7.51 (0.99)	4.08 (0.37)	5.59 (0.34)	4.12 (0.31)
		Low	24.54 (2.42)	12.48 (1.31)	4.40 (1.00)	3.17 (0.28)	4.48 (0.44)	4.51 (0.24)
	Low	High	18.89 (1.27)	<b>7.94</b> (0.95)	4.03 (0.37)	2.76 (0.28)	4.16 (0.30)	3.61 (0.22)
		Low	18.88 (1.45)	8.53 (0.77)	3.70 (0.49)	2.76 (0.25)	3.88 (0.35)	3.92 (0.22)
Low	High	High	4.82 (0.32)	1.34 (0.27)	1.51 (0.16)	0.69 (0.04)	1.27 (0.16)	2.80 (0.25)
		Low	4.44 (0.32)	1.04 (0.22)	1.47 (0.08)	0.66 (0.04)	1.26 (0.08)	2.54 (0.26)
	Low	High	3.99 (0.25)	0.91 (0.15)	1.32 (0.08)	0.55 (0.03)	1.21 (0.08)	2.29 (0.13)
		Low	4.07 (0.28)	1.02 (0.16)	1.28 (0.09)	0.61 (0.05)	1.18 (0.09)	2.46 (0.15)

Note: TOTWT = total weight of the seedling; other column abbreviations as in Table 3.

In both light treatments, NUE was significantly higher with low N supply but was only significantly affected by P supply in the full light-low N treatment (Figure 1). In the shade treatment, PUE was not significantly affected by nutrient supply. In the full light, PUE was significantly higher at low levels of phosphorus supply than at high phosphorus supply with high N-low P treatment having the highest PUE (Figure 1). The highest NUE occurred when light and P were not limiting plant growth. NUE and PUE decreased with increased supply of N and P, respectively, similar to results of other studies (Gray and Schlesinger 1983, Shaver and Melillo 1984, Birk and Vitousek 1986, Lajtha and Klein 1988). Reich and Shoettle (1988) suggested that the relative efficiency of use of N in photosynthesis and growth is directly dependent on the availability of other nutrients, particularly P. If so, photosynthetic capacity and leaf N content should be closely correlated only when other nutrients are available in nonlimiting quantities.

Suboptimal N:P ratio (Ingestad 1979b, Reich and Shoettle 1988), or an increase in proportion of leaf N allocated to structural or defense compounds rather than photosynthesis, may explain the decrease in NUE as nutrient availability increased. Reich and Shoettle (1988) indicated that both leaf P and N were important determinants of maximum leaf photosynthetic capacity and photosynthetic nutrient use efficiency. The ability of white pine (*Pinus strobus* L.) seedlings to efficiently utilize N in photosynthesis was best correlated with leaf N:P ratio, and decreased linearly with this ratio, regardless of absolute N or P levels. At N:P ratios above about 10:1, a relative lack of P apparently interfered with the ability of white pine to utilize N for photosynthesis. In this study, the ability of red pine seedlings to efficiently use N decreased linearly with plant N:P ratio for seedlings grown in the shade or full light ( $r = -0.689$ ,  $r = -0.839$ , respectively,  $P < 0.05$ ). As N:P ratio declined NUE increased, suggesting that a critical level of P was necessary for efficient use of N. Reich and Shoettle (1988) found similar results for white pine seedlings where potential photosynthetic N use efficiency was well correlated with foliar N:P ratio ( $r^2 = 0.71$ ), and NUE was also well correlated to whole plant N:P ratio ( $r^2 = 0.61$ ).

The mean N:P ratio in whole plants for the high N-low P nutrient treatment was about 14:1 while the solution N:P ratio for this treatment was about 56:1 (Table 1). The average N:P ratio for seedlings with high N-high P treatment was 12:1 with a corresponding solution N:P ratio of 6:1. The highest mean growth was observed for the high N-high P treated seedlings even though the N:P ratio of the solution was much higher in the high N-low P treatment. These results are similar to those found by Lajtha and Klein (1988), who observed highest growth with the N:P ratio of *Larrea* plants at 12:1. Even at the lowest N and highest P supply in solution, the N:P ratio in red pine plants was near the optimum level (i.e., 100:14) reported by Ingestad (1979a) for *Pinus silvestris* L., while the maximum growth was observed at N:P ratios of 12:1 for red pine in this study. This pattern of optimum N:P ratio suggests that the uptake of N and P is dependent on each other.

Nitrogen concentrations were significantly higher in the high N than the low N treatments for all biomass components in the full light (Figure 2) and shade (Figure 3) treatments. Phosphorus had no significant effect on N concentration (Figures 2 and 3). Concentrations of N were higher in the shade treatment (Figure 3) than the full light treatment (Figure 2) for all biomass components.

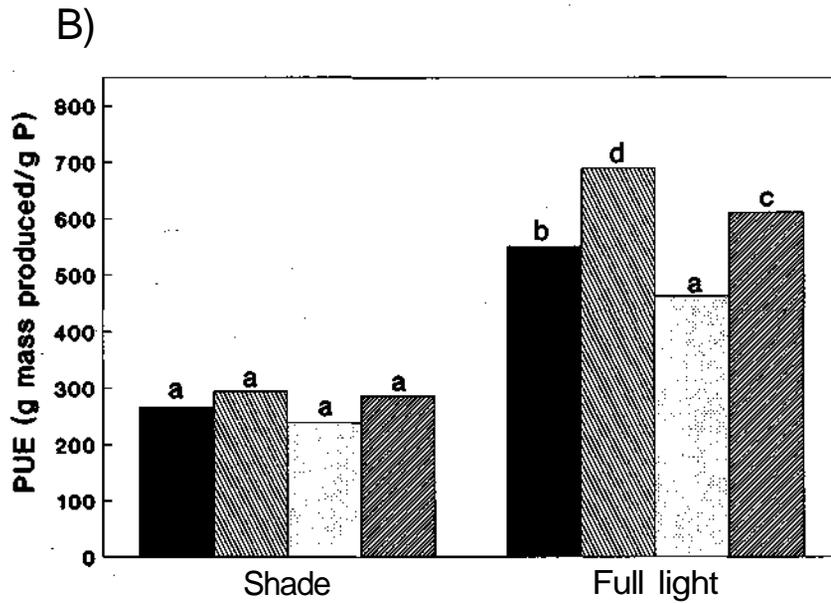
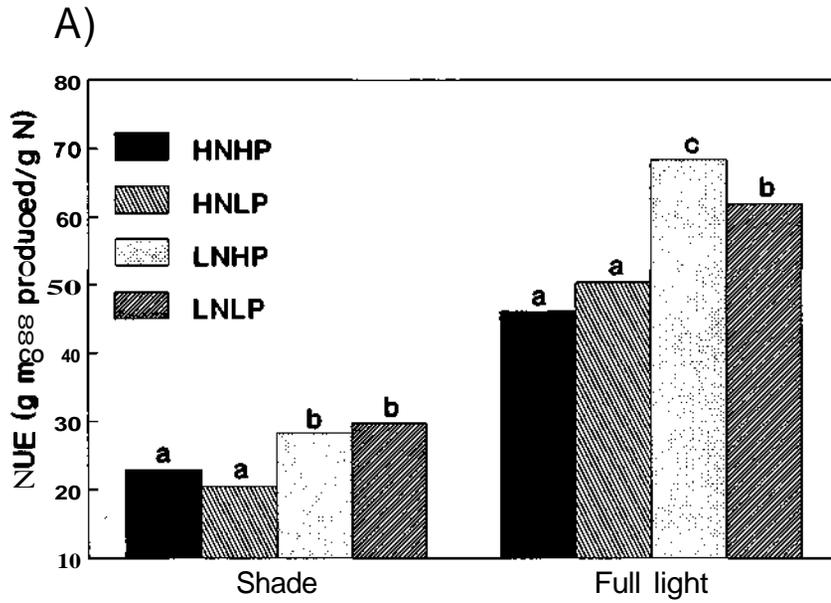


FIGURE 1. Nutrient use efficiencies of red pine seedlings for: (A) nitrogen (NUE), and (B) phosphorus (PUE). Nutrient treatments are: HNHP = high nitrogen-high phosphorus, HNLP = high nitrogen-low phosphorus, LNHP = low nitrogen-high phosphorus, and LNLP = low nitrogen-low phosphorus. Different letters within a light treatment are significantly different ( $P < 0.05$ ) according to Ryan-Einot-Gabriel-Welsch multiple range test.

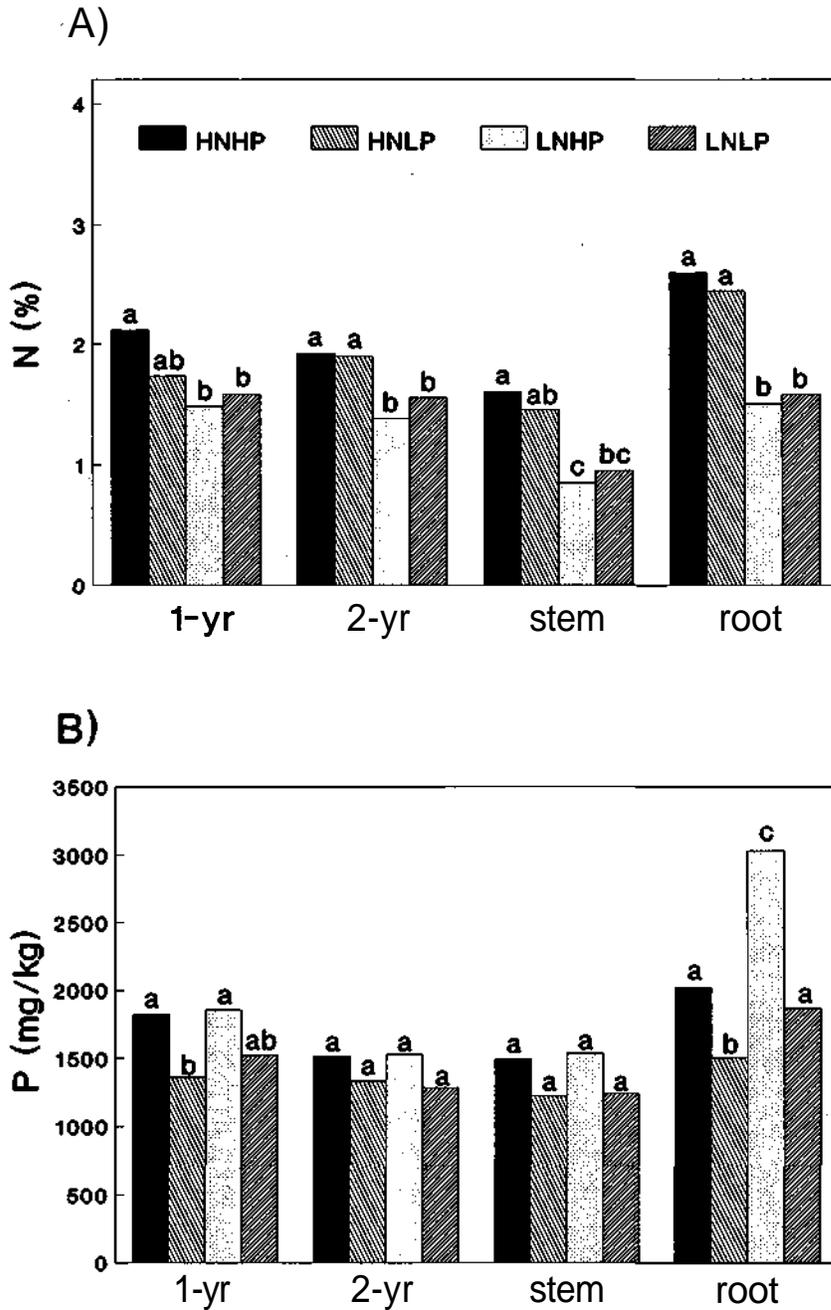


FIGURE 2. Concentrations of: (A) nitrogen (N), and (B) phosphorus (P) of red pine seedlings by biomass component: 1-yr = 1-yr-old needles, 2-yr = 2-yr-old needles, stems, and roots; for the open (high light) treatment. Nutrient treatments are: HNHP = high nitrogen-high phosphorus, HNLP = high nitrogen-low phosphorus, LNHP = low nitrogen-high phosphorus, LNLP = low nitrogen-low phosphorus. Different letters within biomass component are significantly different ( $f < 0.05$ ) according to Ryan-Einot-Gabriel-Welsch multiple range test.

Although P concentration was significantly higher for all tissue types in seedlings treated with high P, the total weight of the seedlings and weight of the other seedling components were not affected by the level of P supply. Adequate light and N supply appear to be the overriding factors controlling growth. Perhaps P was not limiting growth of red pine seedlings. Foliar P concentrations in the full light treatment were above 0.20–0.25% for all nutrient treatments, but were below 0.20% for the shade-low P treatment. Swan (1972) found growth depressions in red pine seedlings with foliar P concentrations below 0.19%.

In this study, N and P concentrations in the high nutrient supply treatments were twofold higher in the shade treatment (Figure 2) than the full light treatment (Figure 3) but did not improve the growth of the seedlings. Margolis and Vezina (1988) reported that N assimilation enzymes became saturated in yellow birch (*Betula alleghaniensis* Britt.) in low light but did not become saturated in jack pine even under conditions of low light and high N (Margolis et al. 1988). In studies from fertilized trees and crop plants (Mengel and Kirkby 1982, Bielecki and Fergusun 1983), inorganic P comprised 50–95% of total P, suggesting luxury consumption. Slowly growing species that absorb nutrients in excess of immediate growth requirements (i.e., luxury consumption) during nutrient flushes may use these reserves to support growth after soil reserves are exhausted (Chapin 1987). This conservation strategy may infer nutrient use efficiency in the long term but would result in a calculation of low efficiency (g mass/g nutrient). Luxury consumption and large vacuolar storage reserves have lower energy costs compared to the production of enzymes and proteins (Mooney and Gulman 1982, Margolis and Brand 1990), but would have the potential to contribute to future productivity.

The results of this study indicate that nutrient use efficiency of red pine seedlings is affected when light and availability of other nutrients are varied. NUE was highest with full light and low N-high P supply. Differences in NUE may also result from differences in N allocation. Leaves with high maximum photosynthetic rates may invest a large proportion of the leaf N in rubisco (Field and Mooney 1986). Low NUE may result from inefficient allocation of N among photosynthetic compounds, such that some compounds are present in excess, while the rate-limiting compounds are underrepresented. For example, shade plants invest large quantities of N in light-harvesting pigments and proteins but make only small investments in rubisco and other CO<sub>2</sub>-processing enzymes (Bjorkman 1981, Evans 1989).

Results from this study, as well as others (Birk and Vitousek 1986, Reich and Shoettle 1988), indicate that increasing nutrient use efficiency is a phenotypic response of pine seedlings to low nutrient availability. This contrasts with Prescott et al. (1989) and Pastor et al. (1984) who suggested that differences in NUE among tree species were due to the inherent nutrient use efficiencies of the species dominating the stand rather than a phenotypic response to nutrient availability. However, despite the phenotypic response of red pine, greater nutrient use efficiency with decreasing nutrient availability did not maintain its growth rate. In contrast, Boemer (1984) found that all four of the deciduous species in his study exhibited physiological plasticity, which allowed maintenance of relative growth rates, despite low soil nutrient availability, by increasing the efficiency of nutrient use.

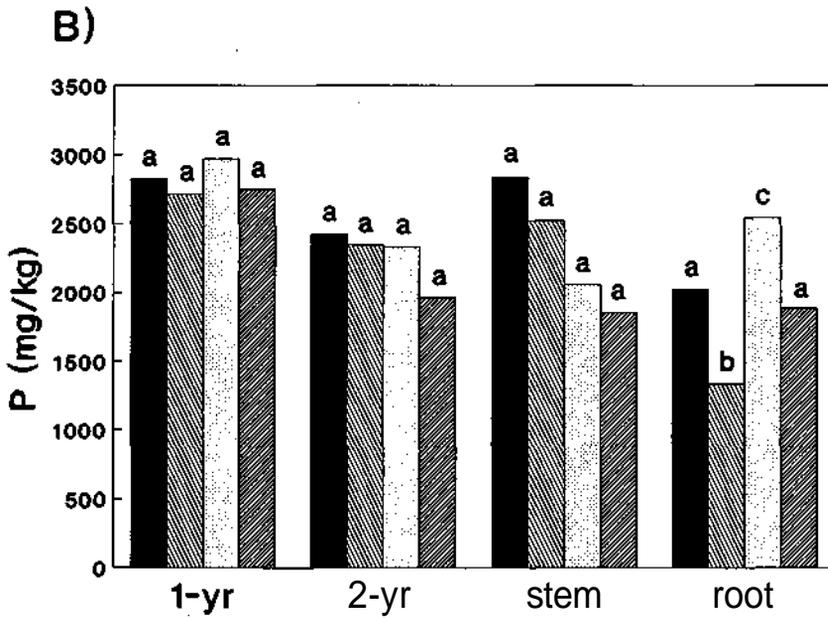
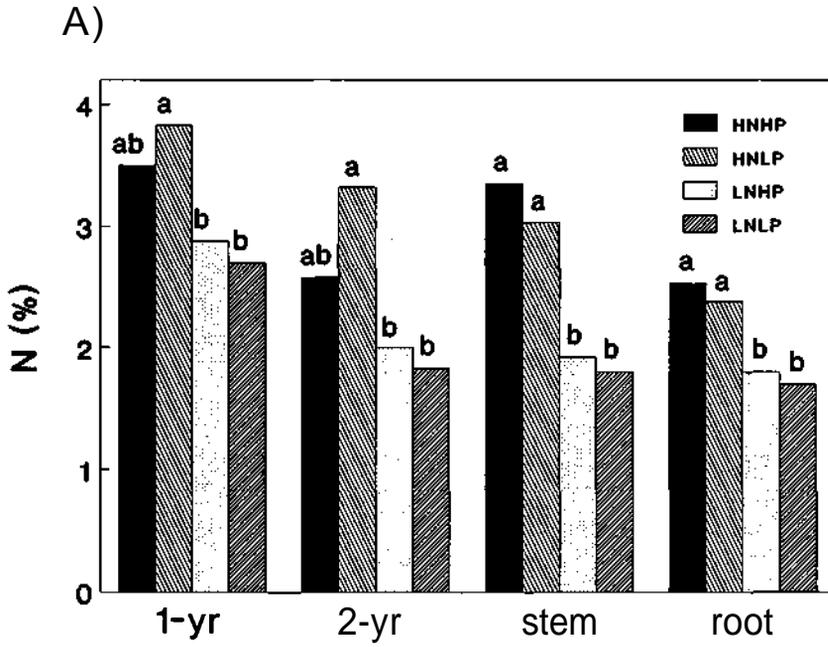


FIGURE 3. Concentrations of: (A) nitrogen (N), and (B) phosphorus (P) of red pine seedlings by biomass component: 1-yr = 1-yr-old needles, 2-yr = 2-yr-old needles, stems, and roots; for the shade (low light) treatment. Nutrient treatments are: HNHP = high nitrogen-high phosphorus, HNLP = high nitrogen-low phosphorus, LNHP = low nitrogen-high phosphorus, LNLP = low nitrogen-low phosphorus. Different letters within biomass component are significantly different ( $P < 0.05$ ) according to Ryan-Einot-Gabriel-Welsch multiple range test.

Although phenotypic adjustment of nutrient use efficiency did not maintain the growth rate of red pine, it may allow it to tolerate nutrient depletions caused by faster growing competitor species. Red pine may be able to adjust NUE within a certain range of N availabilities as long as other variables, such as light and P, are not limiting. However, if deciduous species have a greater physiological plasticity than evergreen species (Gray and Schlesinger 1983), these differences may have important implications, particularly when planting red pine outside of their natural range. If resources are distributed differently in space and/or time, or are in greater supply than in red pine's native habitat, red pine may not be able to utilize these nutrients as efficiently as competitors. The competition from deciduous species for mineral nutrients may have a greater impact on red pine growth if the deciduous species can maintain a constant growth rate across a broader range of nutrient availabilities than red pine seedlings. Further studies are needed to test the competitive interactions of planted red pine and hardwood competitors in field conditions to understand the role of phenotypic adjustments in nutrient use efficiency.

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