

Phosphorus allocation in flooded loblolly pine seedlings in relation to iron uptake

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To determine whether P allocation in loblolly pine (*Pinus taeda* L.) seedlings is related to uptake of Fe^{2+} and its subsequent oxidation and precipitation out of the transpiration stream, newly germinated and 1-year-old loblolly pine seedlings were grown in flooded and drained pots in a glasshouse for 24 to 28 weeks. The foliage of the younger seedlings grown in flooded pots exhibited P deficiency symptoms and had lower P concentrations, averaging 63% of those for drained seedling foliage. The older seedlings did not develop P deficiency symptoms but flooding resulted in P concentrations in the foliage averaging only 66% of those for drained seedlings. In both newly germinated and 1-year-old seedlings, P concentrations of the roots from flooded pots were 158 and 25% higher, respectively, than those of the roots from drained pots. Flooding also resulted in significantly higher Fe concentrations in all seedling components. Fe concentrations in roots were positively correlated with P concentrations in roots and negatively correlated with P concentrations in stems and foliage. Implications are that excessive concentrations of Fe in and on the roots interfered with the movement of P into stems and foliage.

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En vue de déterminer si la disponibilité du P dans les semis de *Pinus taeda* L. est reliée à l'assimilation de Fe^{2+} à son oxydation et à sa précipitation subséquente à l'extérieur du flux de la transpiration, des plantules et des semis de 1 an de *P. taeda* ont été cultivés dans des pots inondés et drainés en serre durant 24 et 28 semaines. Le feuillage des plantules cultivées dans les pots inondés a exhibé des symptômes de déficience en P et avait des concentrations plus faibles en P, équivalant à environ 63% de celles du feuillage des semis drainés. Les semis âgés de 1 an n'ont exhibé aucun symptôme de déficience en P, mais l'inondation a eu pour résultat que la concentration en P du feuillage n'égalait en moyenne que 66% de celle des semis drainés. Dans les deux classes de semis, la concentration en P des racines dans les pots inondés était de 158 et de 25% supérieure, respectivement, à celle des racines dans les pots drainés. L'inondation a aussi eu pour résultat des concentrations significativement plus élevées de Fe dans toutes les parties des semis. La concentration en Fe dans les racines était corrélée positivement avec la concentration en P dans les racines et négativement avec la concentration en P dans la tige et le feuillage. On en déduit que des concentrations excessives de Fe dans et sur les racines entravent la mobilité du P dans la tige et le feuillage.

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Introduction

Flooding can lead to anoxic soil conditions, a decrease in soil redox potentials, and a subsequent increase in iron (Fe^{2+}) availability to plants. Excessive Fe^{2+} uptake has been shown to have negative effects on some plant species growing in flooded soils (Jones 1971a, 1971b; Sanderson and Armstrong 1978, 1980; Hendry and Brocklebank 1985; Wheeler *et al.* 1985). These effects include Fe-induced deficiencies of nutrients, particularly phosphorus (P) (Armstrong and Boatman 1967; Tanaka and Tadano 1972; Jones 1975; Trought and Drew 1980).

Growth of loblolly pine (*Pinus taeda* L.) seedlings is reduced by flooded soil conditions and uptake of Fe is greatly increased. Foliage of such seedlings often appears deficient in P. However, if P is applied to the soil prior to flooding, growth is improved and Fe uptake seems to be reduced (Hook *et al.* 1983). Hence, application of P appears to mitigate some of the negative effects of flooding, and P nutrition appears to be closely related to Fe concentration in young loblolly pine seedlings grown in flooded soil. The study described here was initiated to determine

whether a relationship exists between excessive Fe uptake (induced by soil flooding) and P allocation and growth of young loblolly pine seedlings established on wet sites.

Materials and methods

Establishment and maintenance

Potting medium was prepared by mixing 1:2 v/v builder's sand and soil from the A₁ horizon of a Bethera soil (clayey mixed thermic Typic Paleaquults; Soil Survey Staff 1975), which is typical of soils with pine establishment problems due to poor drainage. Sand was added to avoid puddling. Four-litre plastic pots were lined with plastic bags to prevent loss of soil, water, and nutrients, and 4.1 kg of medium (dry weight basis) and 60 $\mu\text{g Pg soil}^{-1}$ as $\text{Ca}(\text{H}_2\text{PO}_4)_2$ were added.

Loblolly pine seeds were germinated in the pots and thinned to 10 seedlings per pot. Loblolly pine seedlings, one growing season old, were root-pruned to 15 cm and planted in similar pots with three seedlings per pot. Using newly germinated (NG) and 1-year-old (1Y) seedlings, data were collected on seedlings varying in age from germination to 2 years old during a single growing season. Pots of both age groups were randomized on benches in a greenhouse as a factorial experiment with four replications.

TABLE 1. Growth parameters of newly germinated (NG) and 1-year-old (1Y) loblolly pine seedlings averaged across treatment periods

Age	Treatment	Height (cm)	Hanging root length (cm)	Root- collar diam. (mm)	Growth rate (cm week ⁻¹)	Dry weight (g)				
						Foliage	Stem	Root	Total	F:R
NG	D	20.6a	33.9a	3.7a	1.15a	1.18a	0.47a	0.69a	2.34a	1.71
	F	11.5b	13.1b	3.6a	0.39b	0.37b	0.17b	0.20b	0.74b	1.85
1Y	D	46.2a	32.0a	9.4b	0.57a	8.83a	6.00a	7.15a	21.98a	1.23
	F	46.5a	29.0a	12.6a	0.62a	8.82a	6.32a	5.39a	20.72a	1.64

NOTE: D, drained. F, flooded; F:R, foliage to root ratio. Values within columns and age groups followed by the same letter do not differ significantly at the 0.05 level.

An establishment period of 4 and 8 weeks was allowed for NG and 1Y seedlings, respectively. During this time pots were given one application of Hoagland's solution (Hoagland and Arnon 1950); NG seedlings received 35 mL of 0.1 strength and 1Y seedlings received 120 mL of 0.5 strength solution. After establishment, treatments consisting of well-drained soil (25% moisture by weight) and flooded soil (2 cm standing water above soil surface) were imposed on the pots with distilled water. Maintenance weights (total weight of pot, seedlings, soil, and soil moisture to allow 25% soil moisture by weight) of drained pots were increased twice to allow for increases in seedling biomass. Greenhouse benches, as well as pots on each bench, were moved weekly to avoid positioning effects. Greenhouse temperatures did not exceed 45°C.

For the first 12 weeks after initiation of treatments, one flooded and one drained pot of NG seedlings per replication were harvested every 4 weeks. Thereafter, harvests were made every 8 weeks for a total of five harvests during 28 weeks of treatment. The 1Y seedlings were harvested every 8 weeks from initiation of treatments yielding three harvests during 24 weeks of treatment. At harvest, soil was gently washed from root systems and seedlings from each pot were iced in plastic bags until completion of the harvest. The seedlings were then separated into roots, stems, and foliage, which were dried in a forced air oven at 70°C for 24 h to obtain dry weights for each component.

Nutrient analysis

Nutrient concentrations of N, P, K, Ca, Mg, Na, Mn, Zn, and Fe on a gram dry weight basis were determined for roots, stems, and foliage after grinding to pass a 40-mesh screen. N was determined by the salicylate-cyanurate method (Nelson and Sommers 1973). A separate 1.0 g sample was dry-ashed at 450°C for 2 h, taken up in 0.3 M HNO₃ and analyzed for P by the molybdovanadate procedure (Jackson 1958) and for metals by atomic absorption.

Statistical analysis

Since this study was initially designed as a single experiment, the two age groups were not randomized separately. The data from each group were analyzed separately, however, using analysis of variance. It is acknowledged that separate analysis may have introduced additional variation.

The data for the NG seedlings were analyzed as a 2 × 5 factorial (2 water regimes and 5 treatment periods) and the data for the 1Y seedlings were analyzed as a 2 × 3 factorial (2 water regimes and 3 treatment periods). Statistical significance was measured at the 0.05 level. Treatment period effects are discussed only where a treatment period by treatment interaction was present. Data presented are averages across treatment periods. Correlation coefficients were also run on Fe- and P-related variables across drainage treatments.

Results

Growth

Flooding significantly limited NG seedling height and weekly height growth rate (Table 1). These traits were only 56 and 34%, respectively, of those of seedlings from drained treatments. Root length was less with flooding, with the greatest differences

occurring after 12 weeks when drained seedling root length was 34.5 cm compared with 9.8 cm for flooded seedling root length. After 8 weeks of treatment, flooded seedlings had larger root-collar diameters of 3.1 mm compared with 2.8 mm for drained seedlings. As length of treatment increased, however, root-collar diameters of drained seedlings were either larger than or not different from those of flooded seedlings.

Seedling biomass production was also limited by flooding, averaging 34% of that of seedlings in drained treatments (Table 1). The longer the duration of flooding, the greater the reduction in seedling dry weight production. After 4 and 20 weeks of flooding, NG seedling dry weights were 57 and 27%, respectively, of those of drained seedlings.

Unlike that of NG seedlings, height, growth rate, root length, and seedling biomass of 1Y seedlings were not affected by flooding; however, root-collar diameter was increased by flooding (Table 1). Average root weight appeared to be lower with flooding than without, but the difference was significant only at the 0.07 level.

Foliage weight:root weight ratios for both NG and 1Y seedlings were higher initially with flooding, but by the last harvest there was no significant difference. During the course of the experiment, leaf production decreased after long-term flooding in relation to root production.

Nutrient concentrations

Foliage

The concentration of P in the foliage of NG seedlings from flooded treatments was only 63% of that in drained seedlings, but the concentration of Fe was 125% greater than that in drained seedlings (Table 2). Foliar concentrations of all other observed nutrients were significantly lower in flooded than in drained NG seedlings; hence, foliage concentration ratios of Fe to all observed nutrients were significantly increased by flooding.

Foliar concentration of P in flooded 1Y seedlings was 66% of that in drained seedlings, whereas the concentration of Fe was 69% greater than that in drained seedlings. These results are similar to those of the NG seedlings. Concentrations of all other observed nutrients, except N and K, were also lower with flooding, and the ratio of foliage Fe concentration to all observed nutrients increased with flooding.

Stem

P concentration in the stems of NG seedlings tended to be lower with flooding, but the difference was significant only at the 10% level (Table 2). Stem Fe concentrations were more than five times as high in flooded seedlings than in drained seedlings. Concentrations of other observed nutrients were generally lower with flooding, but there were some treatment × treatment

TABLE 2. Nutrient concentrations of newly germinated (NG) and 1-year-old (1Y) loblolly pine seedling foliage, stems, and roots averaged across treatment periods

Age	Seedling component	Treatment	Nutrient concentrations			
			N (mg g ⁻¹)	P (mg g ⁻¹)	K (mg g ⁻¹)	Fe (µg g ⁻¹)
NG	Foliage	D	1.57a	0.178a	0.47a	47b
		F	0.93b	0.112b	0.38b	106a
	Stem	D	0.63a	0.144a	0.32a	57b
		F	0.47b	0.127a	0.28a	290a
	Root	D	1.06a	0.144b	0.30a	1541b
		F	0.89a	0.371a	0.34a	4053a
1Y	Foliage	D	0.63a	0.105a	0.28a	63b
		F	0.61a	0.069b	0.27a	106a
	Stem	D	0.27a	0.056a	0.17a	98b
		F	0.30a	0.047b	0.16a	164a
	Root	D	0.63a	0.097b	0.20a	1153b
		F	0.69a	0.121a	0.19a	3258a

NOTE: D, drained; F, flooded. Values for each component within columns and age groups followed by the same letter do not differ significantly at the 0.05 level.

TABLE 3. Concentration ratios of shoot:root Fe for newly germinated (NG) loblolly pine seedlings

Treatment period (weeks)	Treatment	
	Drained	Flooded
4	0.039	0.035
8	0.047	0.041
12	0.036	0.031
20	0.017	0.058
28	0.026	0.046
Mean	0.033	0.042

NOTE: Means differ significantly at the 0.05 level.

period interactions. Ratios of Fe concentration in relation to all observed nutrients increased with flooding. The Fe:P concentration ratio peaked at 0.53 after 20 weeks of flooding and decreased to 0.44 after an additional 8 weeks of flooding. Drained seedling values did not change with harvest date. Stem Fe concentration peaked in flooded seedlings after 20 weeks of treatment at 524 µg g⁻¹ and declined after an additional 8 weeks of treatment to 353 µg g⁻¹. These results may indicate a process of slow adaptation to the flooded soil conditions whereby the seedlings were able to limit Fe uptake somewhat, or they may simply be due to a dilution effect where growth rate increased disproportionately to Fe uptake rate.

Concentration of P in the stem of flooded 1Y seedlings was 84% of that in drained seedlings, whereas stem Fe concentration was 67% greater than that in drained seedlings. Concentrations of other nutrients were either lower (Ca, Mg, Mn, Zn) or unaffected (N, K, Na) by flooding. Ratios of Fe concentration to all observed nutrients increased with flooding.

Root

Roots were rinsed with distilled water prior to analysis. Therefore, any nutrients on the root surface that were not dislodged by water were included in the analysis, and the root data represent a combination of internal and external nutrients.

Concentrations of P in and on the root systems of NG

seedlings averaged over 2.5 times greater with flooding than with drainage and peaked after 20 weeks of flooding at 0.578 mg g⁻¹, compared with 0.128 mg g⁻¹ with drainage. P concentrations dropped to 0.377 mg g⁻¹ after an additional 8 weeks of flooding but were still 2.8 times greater than those for drained seedlings. P concentration of drained seedling roots did not change over the length of the study. Root Fe concentration also increased over 2.5-fold with flooding, whereas all other observed nutrients either decreased in concentration (Ca, Mg, Na, Zn) or did not change (N, K, Mn). Flooding did not significantly increase the ratio of Fe:P concentration in the roots; the Fe and P concentrations increased proportionately with flooding. Ratio values of Fe to all other observed nutrients did, however, increase with flooding.

In 1Y seedlings, root P and Fe concentrations were increased by 25 and 183%, respectively, with flooding, whereas all other observed nutrient concentrations were either lower with flooding (Mg, Na, Mn, Zn) or unaffected (N, K, Ca). Unlike NG seedlings, the ratio of Fe concentration to all observed nutrients including P was increased by flooding. Apparently, in older seedlings the accumulation of Fe and P in or on the roots is not a one-to-one relationship.

Shoot:root nutrient ratios

The ratio of shoot:root P concentration (shoot concentration is a weighted average of foliage and stem concentrations) averaged 0.38 for flooded and 1.19 for drained NG seedlings. Apparently, relatively less of the total P accumulated was being distributed to the shoots of flooded seedlings. There was a significant interaction between treatment and treatment period for the ratio of shoot:root Fe concentrations (Table 3). When NG seedlings were flooded for less than 20 weeks, excess Fe was concentrated in the roots and distribution to the shoot was limited. After 20 weeks of treatment, relatively more Fe was distributed to the shoots of flooded seedlings. This corresponds to Fe concentration values in the stem peaking at 20 weeks of flooding. At 28 weeks of treatment, the ratio was less than at 20 weeks of treatment but was still greater than the drained seedling ratio. The decrease in the ratio at 28 weeks may have been due to root adaptation to Fe accumulation as mentioned above.

Flooding decreased shoot:root ratios in 1Y seedlings for P and Fe as well as all other observed nutrients except K, Na, and Zn. The P and Fe shoot:root ratios were reduced by 44 and 47%, respectively.

Discussion

Concentrations of Fe and P in NG loblolly pine seedlings reported in this paper are in agreement with those reported for 17-week-old seedlings by Hook *et al.* (1983), but values for 1Y seedlings are somewhat less than those reported for 2-year-old seedlings by McKee *et al.* (1984). Foliage of flooded NG seedlings exhibited P deficiency symptoms (Lyle 1969) as early as 4 weeks after initiation of treatment. Concentrations of P in foliage of flooded NG seedlings ($0.07\text{--}0.24\text{ mg g}^{-1}$) and 1Y seedlings (0.07 mg g^{-1}) reported here are below levels considered to be optimal for Scots pine (*Pinus sylvestris* L.) (Ingestad 1962). P concentrations in roots ranged from $0.24\text{--}0.58\text{ mg g}^{-1}$ for NG flooded seedlings and $0.12\text{--}0.13\text{ mg g}^{-1}$ for 1Y flooded seedlings. These values are well below those reported by Hacskeylo *et al.* (1969) for Scots and loblolly pine roots, but they are significantly higher than P concentrations for drained NG seedling roots ($0.19\text{--}0.12\text{ mg g}^{-1}$) and 1Y seedling roots ($0.09\text{--}0.10\text{ mg g}^{-1}$). P deficiency symptoms were not present, however, in drained seedlings.

Drained seedling roots contained 26% of the P and 29% of the biomass, whereas flooded seedling roots contained 54% of the P and 27% of the seedling biomass. This indicates that in flooded seedlings, P was concentrated in the roots at the expense of the foliage. McKee *et al.* (1984) suggested that flooding reduced P movement from roots to foliage in loblolly pine seedlings. Since flooding depressed growth of NG seedlings and caused P deficiency in foliage, it is reasonable to assume that, among other factors, P deficiency induced by flooding could be a partial cause of the reduced growth of seedlings.

Fe was the only other nutrient whose concentration increased in the root with flooding. The correlation coefficient for root Fe and P concentrations for NG seedlings after 8 weeks of flooding was 0.97 and the correlation coefficients for root Fe, and foliage and shoot P concentrations for the same seedlings were -0.95 . When root Fe concentrations were high, root P concentrations were also high and foliage P concentrations were low. There was also a strong negative correlation between the root Fe concentration and the shoot:root P concentration ratio ($r = -0.98$). This negative correlation suggests that Fe may have immobilized P in or on the roots, preventing its translocation to the shoot.

Under aerobic conditions Fe^{3+} and phosphate will combine to form insoluble iron phosphate compounds ($\text{FePO}_4 \cdot \text{H}_2\text{O}$), which can precipitate out of solution. Phosphate can also be adsorbed on surfaces of oxides and hydroxides of Fe (adsorbed phosphate) and calcium and magnesium phosphates can coprecipitate with insoluble ferric oxyhydroxides (occluded phosphate) (Patrick 1978; Kuo and Mikkelsen 1979; Bradley *et al.* 1984; Richardson 1985). In a companion paper, McKevlin *et al.* (1987) found large accumulations of Fe^{3+} in certain root tissues and on the root surface of flooded loblolly pine seedlings and large aerenchyma zones that extended to within $<1\text{ mm}$ of the root tip. Using oxygen microelectrodes, Hook and McKevlin (1987) found high oxygen levels in roots from flooded treatments, but oxygen appeared to be highly compartmentalized across the root. Hence, it seems likely that the aerenchyma zones and associated aeration allowed for the oxidation of Fe^{2+} in their vicinity. Thus, the interrelations of Fe and P concentra-

tions in roots, soil chemistry of Fe and P, and Fe location and anatomy of roots supports the hypothesis that the large accumulations of Fe in or on the root immobilized P in or on the root and thus limited its distribution to the shoot. The following sequence of events is suggested: (i) a limited internal aeration system in roots of loblolly pine oxidizes Fe^{2+} primarily within the roots; and (ii) free phosphate comes in contact with Fe^{3+} to form insoluble FePO_4 , which is immobile in the root. Therefore, free phosphate is reduced and phosphate transport to the foliage is limited. Such interactions could account for the P deficiencies in the foliage of NG seedlings and, in combination with other detrimental effects of soil waterlogging, account for reduced growth. This root Fe-P relationship was not as pronounced in the 1Y seedlings. Although the same general relationships were evident, they were not as strong and P deficiency symptoms were not noted in these seedlings. Older seedlings may be less sensitive because of lower P requirements in the foliage and larger root systems to supply P needs. Therefore, one of the important beneficial effects of P fertilization on some waterlogged soils (Hook *et al.* 1983; DeBell *et al.* 1984; McKee *et al.* 1984) may be to provide a concentration of P in the soil solution sufficient to overcome Fe interference in and on the root and still provide excess P to the foliage.

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