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Growth and Nutrient Status of Loblolly Pine Seedlings in Relation to Flooding and Phosphorus

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ABSTRACT

Growth and total biomass of 2-year-old loblolly pine (*Pinus taeda* L.) were seriously suppressed by continuous flooding compared to dormant season flooding or drainage to a depth of 61 cm. Dormant season flooding produced larger seedlings than did maintaining the water table at 61 cm. Phosphorus added at 100 mg kg^{-1} to the surface 15 cm of topsoil increased total biomass with continuous flooding but not with other drainage treatments. Content of N, P, K, Ca, and Mg were closely associated with total seedling biomass. Sodium, Zn, and Fe concentrations were greater in roots than foliage of seedlings. Results indicate that loblolly pine required higher soil P with excessive water and suggest that P is able to at least partly alleviate the need for drainage.

Additional Index Words: **waterlogging, nutrient uptake, Coastal Plain soils.**

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PHOSPHORUS FERTILIZATION to improve growth of loblolly (*Pinus taeda* L.) and slash (*P. elliottii* Engelm.) pines on poorly drained sites in the Lower Coastal Plain has been well established (Pritchett and Gooding, 1975; Wells and Crutchfield, 1969); however, reasons for the response to P on some sites while not on others is less well understood. The tree/P relationship is even more puzzling since waterlogging increases P availability for rice and water solubility of the nutrient (Patrick and Mahapata, 1968). However, absorption of macromineral nutrients by slash pine is apparently restricted with poor aeration (Shoulders and Ralston, 1975). Results from field trials, controlled experiments, and a review of the literature led Langdon and McKee (1981) to suggest better nutrition, mainly P, may be substituted for drainage with loblolly pine on some wet sites.

The object of this study was to determine the effects of soil waterlogging, drainage, and P additions under controlled conditions on height growth, biomass production, and nutrient assimilation of loblolly pine seedlings over a 2-yr period.

METHODS AND MATERIALS

Newly germinated loblolly pine seedlings were planted in tanks (hydroedaphytron) on 31 Mar. 1978 (Hook et al., 1970) where water tables could be controlled both in terms of water depth and movement. Seed used for this study was from the National Forest Seed Orchard on the Francis Marion National Forest. Tanks were filled to a depth of 1.52 m with mixed Bt horizon sandy loam taken from the Goldsboro series (fine loamy siliceous thermic Aquic Paleudults). The sandy loam was used to represent a subsoil because of ease of handling and its low P level. This material was covered with 0.305 m A1 horizon soil (sandy clay) collected from the Bethera series (clayey mixed thermic, Typic Paleaquults) which is typical of surface soil on which a P response is expected. Both soils were obtained from a Pleistocene terrace on the Lower Coastal Plain. The sites are on the Francis Marion National Forest in Berkeley County, South Carolina. The surface soil was poorly drained, acid (pH 4.7), and contained 52% sand, 10% silt, and 38% clay. Fertility was low as demonstrated by 2.5 mg kg^{-1} extractable P, 1600 mg kg^{-1} total N, and 0.50 cmol $(p^{2+})kg^{-1}$ of Ca, K, Mg, and Na. Organic matter averaged 42.6 g kg^{-1} Loblolly pine is known to respond to P on adjacent sites indicating a deficiency in available P.

Treatments consisted of three soil moisture regimes: (i) water maintained constantly at the soil surface (flooded), (ii) a variable water table maintained at the soil surface from 1 November until 21 March after which the water level was lowered 15 cm every 2 weeks until a depth of 61 cm was reached (seasonally flooded), and (iii) maintained constantly at 61 cm below the soil surface (drained). A 61-cm water table was used to establish seedlings on all treatments, but after 60d the water levels were adjusted to treatment levels. Phosphorus, as $Ca(H_2PO_4)_2$, was mixed into the surface soil at a rate of 100 mg kg^{-1} to half of each of the water control tanks. An equal amount of Ca was applied to the unfertilized part of each tank as $CaSO_4$ to ensure that Ca was not a variable in the study. The treated portion of each tank was separated by a plywood barrier to a depth of 1.2 m. With only six tanks available, the study was limited to two replications. Eighteen seedlings approximately 3 weeks old were planted in each half tank in March 1979.

To accommodate physiological measurements of roots, one replication was harvested 20 Nov. 1980, and the other 15 April 1981 (DeBell et al., 1984). Height and diameter of seedlings at ground line were measured following the second growing season. Seedlings were harvested at ground line and segmented into stems and foliage. Roots were removed from the soil by washing with a stream of water. Biomass of individual seedlings was measured on fresh material, and subsamples of stems were taken for dry weight values after drying at 343 K for 24 h. Samples of the dried plant material were ground to pass a 40-mesh screen and analyzed for N by a modified micro-Kjeldahl procedure (Nelson and Sommers, 1973). A separate 1.0-g sample was dry ashed at 723 K for 2 h, taken up in 0.3 *M* HNO_3, and analyzed for P by the molybdovanadate procedure (Jackson, 1958). Metals were measured by atomic absorption.

Soil redox potential was measured with Pt electrodes at approximately 10 cm below the soil surface with readings corrected for the half-cell potential. Electrodes were constructed with 22 guage Pt wire as described by Letey and Stolzy (1964). Wet soil pH values were determined with a glass electrode on sample cores collected to a depth of 15 cm and mixed with an equal volume of water. Soil samples for air-dry analysis were collected at time of harvest and ground to pass a 2-mm screen. Soil pH on a 1:2 soil water mixture was measured with a glass electrode. Exchangeable bases and extractable Zn were determined by atomic absorption on 1*M* NH_4OAc extracts (Jackson, 1958). Extractable P was determined by extracting 2.5 g soil with 20 ml of Bray P2 solution (Bray and Kurtz, 1945). Organic matter

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was determined by wet oxidation (Jackson, 1958). Total soil N was measured by micro-Kjeldahl digestion of a 1.0-g sample, and NH_4 determined by the salicylate–cyanurate method (Nelson and Sommers, 1973). Data were subjected to analysis of variance and *t* test to detect differences among treatment means.

RESULTS AND DISCUSSION

Height and Diameter Growth

Drainage significantly altered seedling height, which averaged 41, 135, and 114 cm for the flooded, seasonally flooded, and drained treatments (Table 1). The average height of seedlings was greater with P addition for all moisture regimes although the effect was not significant at the 0.05 level.

Ground-line diameters averaged 8.6 mm for the flooded, 19.4 mm for the seasonally flooded, and 16.5 mm for the drained treatment. Phosphorus increased stem diameter across water table depths by 25%. The interaction of water depth and P was significant at the 0.07 level. Phosphorus increased stem diameter by 137% for the flooded tanks, 13% for the seasonally flooded tanks, and 2% for the drained tanks.

Reduced height and diameter growth of pine in response to high water tables has been reported (Burton, 1971; McKee and Shoulders, 1974; Walker, 1962). In our study, increased growth was observed with seasonal flooding compared to the drained treatment. This response suggests that either the 61-cm water table may have placed a moisture stress on the seedlings or the varied water table changed the soil nutrient status during the drainage cycle resulting in more rapid growth.

Seedling dry weight responded to flooding and P treatments similarly to height and diameter. Continuous flooding depressed dry weight of stems plus branches by 84% and foliage by 88% compared to drained plots. The average dry weight of aerial parts of trees on seasonally flooded tanks was higher but differences were not significantly different. Treatments did not significantly affect average dry weight of roots although both P and water regime appeared to have the same trends as aboveground parts.

Total weight for seedlings on the continuously flooded soils was depressed by 86% compared to seedlings grown with constant drainage. Total dry weight of seedlings with seasonally flooded soil did not significantly differ from that of seedlings with a water table at 61 cm, although weights tended to be greater. Phosphorus did not affect biomass values across flooding treatments; however, when an unpaired *t* test was run on individual trees within flooding treatments a significant response was obtained to P with continuous flooding. Here P increased total biomass by 391%. Phosphorus did not cause a significant increase in dry weight with seasonal flooding or with the drained plots but the seasonally flooded treatments tended to be more responsive to P.

The increased response to P on soils classed as having poor drainage was also observed by Pritchett and Llewellyn (1966) and Pritchett and Comerford (1982) where slash pine responded to P on poorly drained sites but not on better drained soils. They found that soil P analysis values of surface soils did not relate

Table 1—Size and biomass of 2-year-old loblolly pine seedlings, by drainage and P treatments.

Drainage treatment	Phosphorus addition	Tree height	Diameter ground line	Average tree biomass: Roots	Stems and branches	Foliage	Total
	$mg\ kg^{-1}$	cm	mm	g	g	g	g
Flooded	None	28a	5.1b	2.6a	3.3a	2.1a	8.0b†
	100	55a	12.1a	9.8a	16.1a	9.4a	35.3a
Avg.		41C*	8.6C	6.2A	9.7B	5.75B	21.7B
Seasonally flooded	None	133a	18.2b	36.4a	87.6a	65.2a	189.3a
	100	136a	20.6a	47.6a	99.9a	72.1a	219.7a
Avg.		135A	19.4A	42.0A	93.8A	68.7A	204.5A
Drained	None	105a	16.3b	29.7a	57.9a	52.4a	140.1a
	100	122a	16.7a	36.4a	64.8a	49.4a	150.6a
Avg.		114B	16.5B	33.1A	61.4A	50.9A	145.4A

* Values with the same letter in only one column are not significantly different at the 0.05 level. Capital letters denote drainage effects. Lower case represent phosphorus effects or a drainage-phosphorus interaction.
† Significance of phosphorus and phosphorus × water effect was obtained with unpaired *t* test weight of individual seedlings in treatments.

well to growth response of 3- to 5-year-old trees. Better relationships were found with foliage analysis. Mann and McGilvary (1974) observed that P did not improve growth on bedded wet sites but had a marked effect on unbedded sites due to improved aeration in the root zone. Pritchett and Gooding (1975) attributed poor growth of slash pine and P response on wet sites to poor root development and reduced root soil contact, however, data for root growth were not reported. DeBell et al. (1984) found that root metabolism of lobolly pine may be improved with P application when drainage is poor.

Nutrient Accumulation and Distribution

Nirtogen concentration in foliage was decreased 26% to 27% with flooding treatments and was 11% lower on P treated plots regardless of water table level (Table 2). The lower foliage N concentration for trees on flooded tanks indicates the nutrient level in foliage is supressed with anaerobic conditions, due perhaps to a restriction in translocation of the nutrient. Root N concentrations were 43% higher for trees with continuous flooding compared to the drained treatments. Phosphorus fertilizer had no significant effect on root N concentrations. There was about 10 times more N per tree in drained and seasonally flooded treatments than in continuously flooded treatment (Fig. 1).

Phosphorus concentration in foliage was not significantly affected by flooding alone but increased 30 to 34% with P fertilization on drained or seasonally flooded plots (Table 2). Phosphorus concentration in foliage with continuous flooding was not affected by P treatment. Continuous flooding increased P concentration in the roots by 39 and 50% compared to seedlings with the drained and seasonally flooded treatment. Thus, the continuous flooding appears to restrict P translocation in the seedling. Addition of P increased P concentration of roots 113% for all water table treatments.

Combined P content of foliage and roots increased 72% across drainage treatments by P application (Fig.

Table 2—Nutrient concentration in foliage and roots of 2-year-old loblolly pine, by drainage and P treatments.

Drainage treatment	Phosphorus addition	N	P	K	Zn	Fe
	mg kg⁻¹	g kg⁻¹			mg kg⁻¹	
			Foliage			
Flooded	None	14.4a*	1.17a	4.85a	53a	231a
	100	12.0b	1.27a	5.45a	31b	189a
Avg.		13.2B	1.22A	5.15A	42A	210A
Seasonally flooded	None	13.5a	1.08b	5.50a	48a	128a
	100	12.4b	1.40a	4.75a	47b	129a
Avg.		13.0B	1.24A	5.12A	48A	129A
Drained	None	18.7a	1.22b	5.35a	60a	151a
	100	17.1b	1.63a	5.35a	49b	128a
Avg.		17.9A	1.42A	5.35A	54A	140A
			Roots			
Flooded	None	5.9a	0.66a	2.80a	75a	5727a
	100	4.7a	1.21b	2.20a	51a	3712a
Avg.		5.3A	0.93A	2.50B	63A	4719A
Seasonally flooded	None	3.4a	0.33a	3.60a	26a	2208a
	100	3.8a	0.91b	3.50a	31a	2666a
Avg.		3.6B	0.62B	3.55A	28A	2437A
Drained	None	3.9a	0.43a	2.55a	31a	525a
	100	3.4a	0.91b	2.20a	30a	533a
Avg.		3.7B	0.67B	2.37B	31A	529A

* Columns for a given element within plant segments with the same letter are not significantly different at the 0.05 level. Capital letters refer to differences in drainage treatments, and lower case refer to differences in phosphorus treatments or a drainage-phosphorus interaction.

1). While the drainage and the P treatment interaction was not significant, P content showed a marked trend with drainage. In drained and seasonally flooded trees, total P content of trees increased 54 to 69% with added P. For trees in the continuously flooded treatment, root and foliage P content increased 456% with added P. Continuously flooded trees had nearly equal P content in roots and foliage whereas seasonally flooded and drained trees had twice the P in foliage as in roots. Without fertilization, the ratio was wider. This further supports the above observation that the continuous flooding restricts P translocation in the seedlings.

Dry weight of roots and foliage was correlated to N content in spite of widely different water regimes ($R^2 = 0.89$). Similar observations have been made in a number of pot type studies without water variation (McKee, 1973). Phosphorus concentration and uptake are complicated by the interaction of P application and water table treatment. The trend for P content of seedlings to decrease with flooding is similar to the observations in solution culture by Shoulders and Ralston (1975). Increased oxygen tension suppressed P uptake by slash pine which shows why trees become more responsive to fertilizer additions as drainage deteriorates. White and Pritchett (1970) reported similar trends with both slash and loblolly pine on a sandy soil. The decrease in N uptake in this study where N is assumed to be in a reduced form contrasts with Shoulders and Ralston's (1975) work in solution cultures where N uptake increased with increased O_2 tension. As suggested by the authors, the increased uptake of N (NO_3^-) with increased oxygen tension may be related to the use of nitrate as an oxidant under such

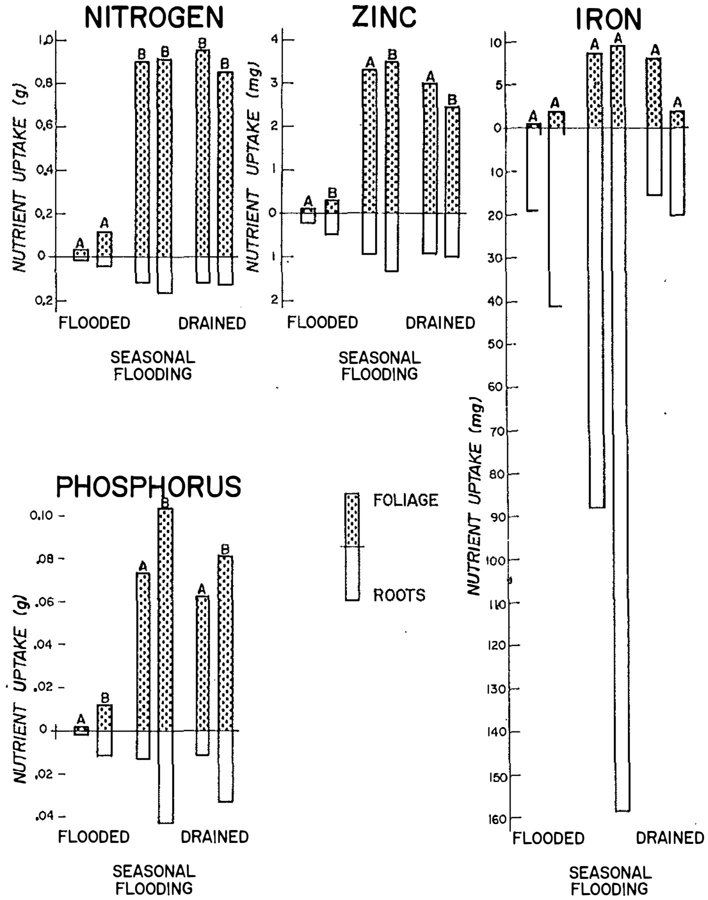

Fig. 1—Total N, P, Zn, and Fe uptake in foliage and roots of 2-year-old loblolly pine grown at three water table levels with two P treatments. Within each treatment, the right-hand bar represents plots with added P. Bars with the same capital letter are not significantly different at the 0.05 level with respect to water table level.

conditions. Measured organic intermediates in these tree roots confirmed the presence of anaerobic respiration (DeBell et al., 1984) and offers an explanation for the difference between the two studies.

Potassium concentration in foliage averaged 5.2 g kg^{-1} and was not affected by treatments. Seasonal flooding increased K concentration in roots by 50% compared to drained treatments. Subsequent studies have shown that continuous and cyclic flooding increased K in roots, stems and needles under prolonged flooding suggesting a possible adaptation of the species over time (D. D. Hook and W. H. McKee, unpublished data).

Concentration of Ca, Mg, Na, and Fe was not significantly changed in foliage or roots by treatments. Calcium concentration averaged 4.0 g kg^{-1} in foliage and 2.3 g kg^{-1} in roots, while Mg concentration averaged 1.4 g kg^{-1} in foliage and 0.7 g kg^{-1} in roots. Sodium concentration averaged 2.2 g kg^{-1} in foliage and 4.6 g kg^{-1} in roots. Iron concentration averaged 160 mg kg^{-1} in foliage and 2560 mg kg^{-1} in roots, with considerable variation between the replications. The wide variation is believed due to the apparent precipitation of iron on the surface of the root which cannot be removed by washing with water. Although

Fe concentration in foliage was not significantly different among treatments, it averaged slightly higher in foliage with soils continuously flooded. Similar results were found in a growth chamber study with loblolly pine seedlings grown under poor root aeration conditions (Hook et al., 1983).

Zinc concentration in foliage was not significantly affected by soil flooding treatments but was depressed 43% by P fertilization. Root concentration of Zn averaged 41 mg kg^{-1} for all treatments, which was similar to that of foliage (48 mg Kg^{-1}.)

Total Fe content was not altered by treatments. Much larger quantities were found in roots than in foliage. The large differences between treatment means suggest a significant response would be found. The lack of significance is caused by a onefold or larger increase in Fe concentration in both roots and foliage on seasonal or continuous flooded treatments between block 1 harvested in the fall and block 2 harvested in the spring. Iron appeared to be the only element affected by the harvest time probably because of the seasonal reducing effect.

The assumption and explanations of how P changed root growth, metabolism and nutrient uptake are given in a companion paper on the P relationship to anaerobic metabolism. (DeBell et al., 1984). The concentration of Zn and Fe (Table 2.) in the foliage and the trend to be lower with added P in the continuously flooded and drained treatments are similar to published findings where P appears to suppress uptake of these elements (Brown, 1972). Root content of these nutrients (Fig. 1) tends to increase with P independent of water tables probably as a result of root extension.

Soil properties measured at the end of the study did not relate well with nutrient content and with the exception of pH and redox potential soil properties were unaffected by treatments. On seasonally or continuously flooded plots, pH values averaged 5.5 while soil on drained plots had a pH of 4.9 when measured in the tanks. Air dry soil pH values averaged 4.5 at harvest. The change in pH reflects the soil reduction effect on soil acidity and iron reduction. Redox potential in the topsoil decreased with flooding by about 500 mV with no effect of P from 665 mV for drained soil to 160 mV for the flooded and seasonally flooded treatments. Extractable P averaged 5.6 mg kg^{-1} in the topsoil and 3.2 mg kg^{-1} in the subsoil. Phosphorus content showed no pronounced change between the beginning and end of the study, nor did it reflect significant treatment effects at least in terms of added P. The lack of a P treatment effect on the extractable P probably is the result of biological or mineral tieup of the nutrient.

Subtle differences in micronutrient distribution may alter nutrient availability and intermediate flooding may also precipitate toxic metals. Bowling (1978) reported that for naturally wet or flooded soil, drainage prior to planting loblolly pine reduced levels of soluble Al in soil resulting in increased biomass and P accumulation in a pot study. Growth and P uptake was negatively related to extractable Al. Although this study strongly indicates P utilization was altered by poor aeration from flooding, other soil changes associated with the treatments could have a similar effect.

SUMMARY

The findings indicate that the extractable mineral P supply and physiology of loblolly pine interact, allowing for opportunities to improve growing conditions for pine on wet sites by drainage or fertilization. Response of loblolly pine to P is not dependent on the amount of extractable P alone but also on the interaction of the plant to soil aeration (soil reduction) and extractable P. Seasonal flooding in the dormant season did not reduce growth of loblolly pine thru age two but indicated that the treatment may have improved uptake of nutrients on this soil.

Foliage concentration values of P alone are not totally indicative of nutrient status of trees placed under flooding stress because translocation of the nutrients from roots to foliage is restricted by lack of soil aeration.

Nitrogen increased in foliage and decreased in roots with improved drainage. When flooded, the amounts of N and P appear higher in roots.

In addition to P altering the tolerance of loblolly pine to flooding, our data suggest the possibility of manupulating flooding to better utilize existing nutrient supplies as exemplified by the slightly better growth with seasonal flooding.

REFERENCES

1. Bowling, D.E. 1978. Influence of soil phosphorus regime on loblolly pine seedlings growth. M.S. Thesis. Virginia Polytechnic Inst. and State Univ., Blacksburg, VA.
2. Bray, R.H., and L.T. Kurtz. 1945. Determination of total organic and available forms of phosphorus in soils. Soil Sci. 59:39-45.
3. Brown, J.C. 1972. Competition between phosphate and the plant for Fe^{2+} Ferozine. Agron. J. 64:240–243.
4. Burton, J.D. 1971. Prolonged flooding inhibits growth of loblolly pine seedlings. USDA For. Serv. Res. Note SW-142, 4 p. South. For. Exp. Stn., New Orleans, LA.
5. DeBell, D.S., D.D. Hook, W.H. McKee, Jr., and J.L. Askew. 1984. Growth and physicology of loblolly pine roots under various water table levels and phosphorus treatments For. Sci. 30:705–714.
6. Hook, D.D., D.S. DeBell, W.H. McKee, Jr., and J.L. Askew. 1983 Responses of loblolly pine (mesophyte) and swamp tupelo (hydrophyte) seedlings to soil flooding and phosphorus. Plant Soil 71:383–394.
7. Hook, D.D., O.G. Langdon, J. Stubbs, and C.L. Brown. 1970. Effect of water regimes on the survival, growth and morphology of tupelo seedlings. For. Sci. 16:304–311.
8. Jackson, M.L. 1958. Soil chemical analyses. Prentice-Hall, Inc., Englewood Cliffs, NJ.
9. Langdon, O.G., and W.H. McKee, Jr. 1981. Can fertilization of loblolly pine on wet sites reduce the need for drainage? p. 212–218 *In* J.P. Barnett (ed). USDA For. Serv. Gen. Tech. Rep. SO-34, South. For. Exp. Stn., New Orleans, LA.
10. Letey, J., and L.H. Stolzy. 1964. Measurement of oxygen diffusion rates with the platinum microelectrode. I. Theory and equipment. Hilgardia 35:545–554.
11. Mann, W.F., and J.M. McGilvary. 1974. Response of slash pine to bedding and phosphorus application in southeastern flatwoods. USDA For. Serv. Res. Pap. SO-99. South. For. Exp. Stn., New Orleans, LA.
12. McKee, W.H., Jr.1973. Slashpine response to nitrogen and phosphorus on imperfectly drained soil of the West Gulf Coastal Plain. Soil Sci. Soc. Am. Proc. 37:784–788.
13. McKee, W.H., Jr., and E. Shoulders. 1974. Slash pine biomass response to site preparation and soil properties. Soil Sci. Soc. Am. Proc. 38:144–148.
14. Nelson, D.W., and L.E. Sommers. 1973. Determination of total nitrogen in plant material. Agron. J. 65:109–112.
15. Patrick, W.H., Jr., and I.C. Mahapata. 1968. Transformation and availability to rice of nitrogen and phosphorus in waterlogged soils. Advan. Agron. 20:323.
16. Prichett, W.L., and N.B. Comerford. 1982. Long-term response

to phosphorus fertilization on selected Southeastern Coastal Plain soils. Soil Sci. Soc. Am. J. 46:640–644.
17. Pritchett, W.L., and J.M. Gooding. 1975. Fertilizer recommendations for pines in the Southeastern Coastal Plain of the United States. Univ. Fla. Agric. Exp. Stn., Bull. 774.
18. Pritchett, W.L., and W.R. Llewellyn. 1966. Response of slash pine (*Pinus elliottii* Engelm. var. *elliottii*) to phosphorus in sandy soils. Soil Sci. Soc. Am. Proc. 30:509–512.
19. Shoulders, E., and C.W. Ralston. 1975. Temperature, root aeration and light influence slash pine nutrient uptake rates. For. Sci. 21:401–410.
20. Walker, L.C. 1962. The effects of water and fertilizer on loblolly and slash pine seedlings. Soil Sci. Soc. Am. Proc. 26:197–200.
21. Wells, C.G., and D.M. Crutchfield. 1969. Foliar analysis for predicting loblolly pine response to phosphorus fertilization on wet sites. USDA For. Serv. Res. Note SE:128. Southeast. For. Exp. Stn., Asheville, NC.
22. White, E.H., and W.L. Pritchett. 1970. Water table control and fertilization for pine production in the flatwoods. Univ. Fla. Agric. Exp. Stn. Tech. Bull. 743.