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Poor Aeration Curtails Slash Pine Root Growth and Nutrient Uptake

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SUMMARY

Slash pine may absorb nutrients and water best in spring and early summer because soil moisture, soil aeration, and temperature are apparently optimum at this time.

One-year-old slash pine seedlings maintained at a high oxygen level grew about 1 ½ times as many roots as were produced at a low oxygen level. No other environmental conditions significantly influenced root growth during the 12-day test period. High oxygen level plant roots had long silvery-white tips, which graded gradually to cream, tan, and finally light brown near the base of the root segments. In contrast, new roots of low oxygen level plants were brown or tan to within a few centimeters of their tips.

At 22° C, low oxygen level plants absorbed 21 percent less water, 53 percent less phosphorus, and 54 percent less magnesium at the end than at the beginning of the 12-day observation period. In contrast, high oxygen level plants absorbed 9 percent more water, 61 percent more phosphorus, 22 percent more potassium, and 117 percent more magnesium daily at the end than at the beginning of the 12 days. At the low oxygen level, the 22° C seedlings' calcium absorption increased 152 percent by the second day but declined thereafter. Trends were about the same at 16° C and 28° C, but most differences increased with increasing temperature.

To maintain good growth rates slash pines may require more nutrients in inadequately drained and aerated soils than in well drained soils. Fertilization can possibly substitute for drainage on some sites because poor root aeration may reduce the plant's ability to absorb water and nutrients.

Additional keywords: *Pinus elliottii*, temperature, light intensity, root aeration, solution culture, pine nutrition, absorption of water, phosphorus, potassium, calcium, and magnesium.

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Slash pine (*Pinus elliottii* Engelm. var *elliottii*) grows best near ponds and poorest on poorly drained flatwoods, commonly called crawfish flats (Cooper 1957). Poor development and low yields of pines on flat, wet sites have been attributed to inadequate root aeration (McKee and Shoulders 1974), to the death of many fine feeder roots during prolonged exposure to saturated soil (Kramer 1949), to a fluctuating water table in the rooting zone (White and Pritchett 1970), and to phosphorus deficient soil (Bengtson 1968, Pritchett and Smith 1974). Probably all factors contribute. Both bedding (Bethune 1963, McKee and Shoulders 1974) and phosphorus fertilization (Barnes and Ralston 1953, Pritchett and Smith 1972, 1974) have boosted growth of slash pine on crawfish flats. Bengtson (1971) suggested that fertilization could substitute for improved drainage of less severely waterlogged soils because fertilizer stimulates additional growth and rapidly growing pines would remove some of the excess soil moisture by transpiration.

This study focused on the effects of root aeration at three temperatures and two light intensities on slash pine root growth and on the uptake of nutrients. Root growth was curtailed and nutrient uptake was modified by 9 days' exposure of roots to poorly aerated culture solutions.

MATERIALS AND METHODS

One-year-old slash pine seedlings, already acclimated to culture solutions, were observed under carefully regulated conditions to determine the effects of temperature, light intensity, and root aeration on root growth and net uptake of phosphorus, potassium, calcium, and magnesium. Absorption of water was also monitored. Plants were grown for 3 days in well aerated solutions at 22° C with daytime illumination that averaged 4,400 foot candles over the crown surface. Then they were subjected for 9 days to all possible combinations of root aerations, temperatures, and light intensities listed in table 1. A 12-hour photoperiod was used throughout the experiment. Treatments were replicated three times.

Table 1.—*Test environments. Plants were subjected to all possible combinations of these oxygen levels, temperatures, and light intensities for 9 days using a 12 hour photoperiod*

Level	Oxygen in solution: Air saturation	Oxygen in solution: Dissolved oxygen	Temperature	Light intensity (crown average)
	Percent	*- -ppm- -*	*°C*	*Foot candles*
Low	50	4 to 5 [1]	16	3,000
Intermediate	--	----	22	...
High	90	8 to 9 [1]	28	4,400

[1] In both oxygen levels, dissolved oxygen concentration was higher at low than at high temperature.

Culture solutions were replaced at the end of the second and third days of the pretested period and at 24- or 12-hour intervals thereafter. Ion uptake was reckoned by computing the quantities of individual ions that disappeared from the solution during each study interval. Initial and final root volumes were determined by water displacement.

Additional details on design and conduct of the test are given in a companion article (Shoulders and Ralston 1975).

RESULTS

High oxygen level plants grew 1.43 cm^3 of new roots per seedling, or about 2 ½ times as many as were produced by low oxygen level plants during 12 days in the growth chambers (table 2). No other element of the environment significantly influenced root growth during this period. Much of the growth of low oxygen level plant roots probably occurred during the 3 days that they were in well aerated solutions. This conclusion is supported by the fact that plants which were kept in well aerated culture solutions for 12 days grew about 0.12 cm of new roots per seedling per day.

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Table 2.—*Twelve-day root growth and 9-day uptake of nutrients per seedlings*

Temperature	Oxygen level	Root growth	Net uptake of Water	Phosphorus	Potassium	Calcium	Magnesium
C^o		Cm^3	ml.	- - - - - - - - -	Milligrams	- - - - - - - - -	
16	Low	0.55	51	.593	- .102	1.327	.261
	High	1.26	69	1.067	4.652	2.017	.527
22	Low	.40	78	.603	-1.021	2.844	.392
	High	1.68	96	1.449	7.788	3.212	.888
28	Low	.82	149	.625	-1.340	5.634	.860
	High	1.35	172	1,536	8.387	3.935	1.017

There were also differences in color between roots of high and low oxygen level plants at the end of the test (figure 1). High oxygen level plant roots had long silvery white tips. Back of these tips color graded gradually to cream, tan, and finally light brown near the base of the root segments that had developed after plants were transferred to culture solutions from soil. In contrast, new roots of low oxygen level plants were brown or tan to within a few centimeters of their tips. Many were entirely devoid of white tips as though their growth had been stopped and suberization had progressed to the root tip. There was no visual evidence, however, that root meristems were actually killed by low oxygen treatment.

Figure 1.—*Typical root systems of slash pine seedlings after exposure for 9 days to low (right) and high (left) levels of dissolved oxygen in culture solutions.*

A companion article described the effect that temperature and oxygen level had on hourly uptake of water and nutrients per unit of root volume during light and dark phases of the diurnal cycle (Shoulders and Ralston 1975). Here I wish to emphasize the effects of oxygen level on amounts of water and nutrients individual seedlings removed from culture solutions at 16, 22, and 28° C and to relate these results to conditions slash pines encounter in the field. Since light intensity had no significant effect on uptake, results for the two intensities have been averaged.

The 22° C seedlings illustrate the effects of oxygen supply on uptake of water and nutrients best because they were kept at a constant temperature for 12 rather than 9 days. Moreover, high and low oxygen level plants assigned to the 22° C temperature differed by only 0.36 cm^3 per seedling (or about 5 percent) in root volume as they entered the growth chambers. At 22° C, the low oxygen level plants absorbed 21 percent less water, 53 percent less phosphorus, and 54 percent less magnesium during the 12th day than they averaged daily during days 1 and 2 in the growth chambers at the high oxygen level. On the 12th day, the low oxygen plants "leaked" about one-third as much potassium to the

culture solutions as they had accumulated daily before the low oxygen level was imposed. In contrast to the above trends, 22° C high oxygen level plants absorbed 9 percent more water, 61 percent more phosphorus, 32 percent more potassium, and 177 percent more magnesium daily at the end than at the beginning of the 12 days.

The low oxygen level increased the 22° C seedlings' calcium uptake 152 percent by the second day; however, calcium absorption of these low level plants declined thereafter. By day 12, these plants absorbed only 69 percent more calcium than they had on day 1. Because calcium uptake of 22° C temperature high oxygen seedlings rose 112 percent during the 12-day period, low oxygen level plants each absorbed 0.368 mg less calcium during the final 9 days than high level plants.

During the 9 days, low oxygen level plants at 22° C also absorbed 18 ml less water, 0.846 mg less phosphorus, 8.809 mg less potassium, and 0.496 mg less magnesium each than high oxygen level seedlings. The large difference in net potassium uptake was due in part to the fact that low oxygen level plants surrendered 1.021 mg more of this nutrient to culture solutions than they removed.

Trends were about the same at the two other temperatures, but most differences increased with increasing temperature. Because the high temperature-low oxygen treatment so markedly stimulated calcium uptake initially, 28° C plants absorbed more calcium from low than from high oxygen level solutions during the 9 days.

DISCUSSION AND CONCLUSIONS

In the growth chambers, study seedlings encountered temperatures and root oxygen levels typical of slash pine's natural habitat at different times during the year.

The low temperature approximated the mean January temperature reported for peninsular Florida at the southern limit of typical slash pine's range (Squillace 1966). The high temperature was within 2° C of the mean July temperature throughout the sub-species' commercial range, including Louisiana and east Texas where slash pine is not native.

The low and high solution oxygen contents in table 1 correspond approximately to saturation of water films surrounding roots with atmospheres containing 10 and 19 percent oxygen. The data of Hu and Linnartz (1972) show that soil air in the surface foot of three imperfectly to poorly drained stream terrace and flatwoods soils in southeast Louisiana contained less than 10 percent oxygen for 1 to 3 months in winter and about 20 percent during the rest of the year. Soil air averaged about 20 percent oxygen yearlong in well drained Ruston soil. Soil water collected from water tables within the profiles contained 4 to 8 ppm of dissolved oxygen. Since oxygen diffuses only about 1/10,000 as fast in water as in air, oxygen concentrations at the solution-root interface were probably much lower than those of the soil air or soil water samples. Similar data on soil oxygen are not available for Coastal Plain soils further east, but flatwoods sites of Florida may be saturated with water for prolonged periods in summer because of excess rainfall in that season (McMinn and McNab 1971).

Because of these similarities between test and field conditions, results of the current study indicate that slash pine throughout much of its commercial range may be expected to absorb phosphorus, potassium, calcium, and magnesium faster in spring and early summer than at other seasons. Soil moisture as well as soil aeration and temperature, are apt to be more nearly optimum for rapid uptake then than at other times. To maintain good growth rates, moreover, slash pines may require higher levels of these nutrients in adequately drained and aerated soils than in well drained soils. The poor growth of unfertilized slash pine plantations on wet savannas in Florida and their proportionally greater response to phosphorus fertilization there than on better drained sites (Pritchett and Smith 1972, 1974) tends to reinforce this interpretation of the results.

Many experiments (e.g., Olsen 1950, 1953, Wallace and Sufi 1963, Leggett and Frere 1971, Shoulders 1972) have shown that ion uptake from weak solutions varies directly with ion concentration. Part of the reason, then, that fertilization can substitute for drainage on some sites (see Bengtson 1971) may be that poor root aeration reduces the plant's ability to absorb water and nutrients and that higher concentrations of nutrients in the soil solution are needed to compensate the plant's loss in efficiency under these conditions.

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