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Response of Loblolly Pine (Pinus Taeda L.) Seedlings to Various Levels and Combinations of Nitrogen and Phosphorus.

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RESPONSE OF LOBLOLLY PINE (*Pinus taeda* L.) SEEDLINGS TO VARIOUS LEVELS AND COMBINATIONS OF NITROGEN AND PHOSPHORUS

A Dissertation

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by
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PLEASE NOTE:
Several pages contain colored illustrations. Filmed in the best possible way.

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TABLE OF CONTENTS

LIST OF TABLES

Number Page

LIST OF FIGURES

LIST OF PLATES

ABSTRACT

Loblolly pine (Pinus taeda L.) seedlings were treated with all combinations of four levels of nitrogen -- 0, 100, 200, and 300 ppm -- and eight levels of phosphorus -- 0, 10, 20, 30, 40, 50, 60, and 70 ppm -- in sand culture. Sources of nitrogen and phosphorus were NH_4NO_3 and $NaH_2PO_4 \cdot H_2O$. Treatments were assigned factorially in a completely randomized block design with three replications. Nutrient solutions were cycled through the cultures daily and renewed every three weeks. Five seedlings per pot were grown for a period of nine months after treatments were begun.

In a separate test, additional rates of 25 and 75 ppm N and 0.5, 5, 150, and 200 ppm P were tested with a single replication. For the nitrogen series, phosphorus was held constant at 30 ppm, and in the phosphorus series nitrogen was supplied at 100 ppm.

Measurements of certain shoot and root variables were made at the termination of the study. Concentrations of nitrogen, phosphorus, potassium, calcium, and magnesium were determined for mature needles, immature needles, mature stem, immature stem, taproot, and lateral roots. Treatment effects were evaluated by analysis of variance, and individual means were compared by orthogonal comparisons.

In terms of net biomass production of shoot material, 100 ppm N was found to be the optimum level of this element. The two higher

rates of nitrogen had a growth-depressing effect. Increasing the level of nitrogen also decreased shoot-tissue maturity. The greatest mass of roots was also produced at 100 ppm N; however, all levels of applied nitrogen reduced root length and numbers of primary lateral roots. Root/shoot ratio was found to be largely a function of nitrogen supply, with largest ratios occurring for plants grown without nitrogen.

Phosphorus significantly increased both shoot and root growth; however, 10 ppm P appeared to be as effective as the other rates of this element.

Orthogonal comparisons revealed virtually all the interaction effects to be due to the inclusion of treatments lacking nitrogen and phosphorus. No significant interaction was observed on the response surface beyond the minimum applied rates of each element. According to these results, therefore, the optimum combination was found to be 100 ppm N - 10 ppm P. However, trends from the supplementary test indicated optimum levels may be somewhat lower, perhaps near 25 to 75 ppm N and 6 to 8 ppm P.

Concentrations of nitrogen and phosphorus in all tissues increased with increasing increments of these elements; however, concentrations of potassium, calcium, and magnesium generally decreased with increased supply of nitrogen and phosphorus.

Nitrogen and phosphorus deficiency symptoms typical of most conifers were observed in plants grown in the absence of these elements. Nitrogen deficiency was characterized by poor shoot growth and pale green foliage. Phosphorus-deficient plants were severely stunted, and

needles were bluish-green in the terminal region and brown on the lower portion of the plant.

The results of this study indicate that young loblolly pine seedlings grown in sand culture under greenhouse conditions have relatively low N and P requirements -- less than 100 ppm N and less than 10 ppm P.

INTRODUCTION

Fertilization of forest trees is a relatively new concept. In fact, for many years man had the idea that trees were different from other members of the plant kingdom in that nutrient elements were not necessary for their growth. Perhaps this concept had its origin in Van Helmont's now-classical willow twig experiment from which he concluded that tissues "arose from water alone" (Russell 1961). Or more likely, since for ages trees were available in apparently inexhaustible supplies, man simply never considered that trees were sensitive to inorganic nutrients. Now, in the twentieth century, man has fully realized two seemingly unrelated facts--that nutrients are essential to trees and that trees are not available in an everlasting quantity.

The American timber industry is, as are virtually all phases of society, being affected by the population "explosion." The additional numbers of human beings are demanding more forest products, while at the same time requiring additional land on which to dwell. Although the ratio of supply to demand for wood is generally good now, by the year 2000 projected supplies will fall considerably short of the projected timber cut. The U. S. Forest Service (1965) has estimated that demands for timber products will increase by 80 percent by the turn of the century. The timber industry is, therefore, faced with the challenge of producing a greater quantity of wood products from a

smaller land area. To meet this challenge land managers must seek means by which per-acre production can be significantly increased during the next 30 years.

Site amelioration by the addition of inorganic nutrients is recognized as one of the possibilities for achieving increased timber production. In some European countries forest fertilization is rapidly becoming a facet of intensive silviculture. In Sweden, for example, calculations indicate that 3.5 million acres per year can be profitably fertilized. In Norway about 1 million acres could be fertilized each year, and estimates indicate that beginning in 1975, 2.5 million acres per year should be fertilized in Finland (Hagner 1967). In the United States the need for fertilization is not now and perhaps will never be as great as in the Nordic countries.

Nonetheless, in anticipation of the need for some degree of fertilization in this country, forest scientists have recently developed an interest in the nutrition of leading commercial species, particularly the southern pines. Much of the research has been conducted in a greenhouse environment for the purpose of determining so-called nutrient requirements in terms of growth and nutrient composition of the tissue. Of the macronutrients, nitrogen and phosphorus have received most of the attention. Potassium has been studied to a lesser extent, possibly because for good tree growth few areas of the country are known to be deficient in this element. This is especially true within the natural range of the southern pines.

In the case of loblolly pine (Pinus taeda L.), nitrogen and phosphorus nutrition has been investigated generally without testing combinations of the two elements. Various rates of nitrogen or

phosphorus have been tested in experiments that have held the other element at a constant level (Fowells and Krauss 1959; Thompson 1965). These studies have furnished worthwhile information concerning the nutrition of loblolly pine, but there is the need for additional knowledge concerning the effects of combinations of various levels of nitrogen and phosphorus on this species. The present study was designed to contribute to this area of knowledge.

Specifically, the objective was to measure the response of loblolly pine seedlings to four levels of nitrogen, 0, 100, 200, and 300 ppm, eight levels of phosphorus, 0, 10, 20, 30, 40, 50, 60, and 70 ppm, and all combinations of these rates.

The study was a follow-up on an earlier experiment by Thompson (1965) and was conducted in the greenhouse using a modification of the sand-culture technique of Gauch and Wadleigh (1943). Responses were assessed in terms of various measures of growth and development as well as nutrient concentrations in plant tissues.

REVIEW OF LITERATURE

The nutrition of forest trees has been of interest to man since the era of Van Helmont's classical willow-twig experiment in the seventeenth century.[1/] Though his interest was purely academic, and the conclusions drawn were erroneous, his work may have been the first in a field that has since grown in tremendous proportions. Torsten Ingestad (1962), a present-day tree nutritionist, credits European workers of the late 1800's with the first serious interest in the field by the introduction of soil, litter, and plant tissue analyses.

Following these works, interest and experimentation in tree nutrition developed rather slowly for several decades. However, interest was renewed during the early part of the twentieth century. Two very thorough compilations of world literature stand as evidence of the geometric progression of research in the field. White and Leaf (1956) presented approximately 700 references directly related to tree nutrition and forest fertilization research conducted through 1956. According to Mustanoja and Leaf (1965), during the next seven years (1957 to 1964) nearly 1300 works were added to the stock of world literature concerning the nutrient relations of forest trees. Thus,

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[1/] Van Helmont lived during the period, 1577-1644. Although the exact date of his experiment is not known, its account was first published, posthumously, in 1648 by his son in Ortus Medicinae (Krikorian and Steward 1968).

from 1957 through 1964, available information almost doubled that which existed prior to 1957. Since 1964 no complete literature compilations have been published. However, the National Plant Food Institute, through its Forest Fertilization Clearing House Reports, has annually published information on research in progress as well as abstracts of papers published during the previous year.

Also indicative of the increasing interest in tree nutrition in the United States are the two symposia held in this country in recent years. In 1958 Duke University was host to a meeting of scientists interested in mineral nutrition and related problems (Ralston et al. 1959). And at the University of Florida in 1967 U.S. workers convened to discuss current tree nutrition-forest fertilization research (Bengtson et al. 1968).

Although much of the published information has concerned American conifers, relatively little work has been done with loblolly pine. Research in the United States with the genus Pinus has been conducted mainly in the Southeast and has, therefore, been concerned primarily with slash pine (Pinus elliottii Engelm.). Many of the studies have been field trials, with a lesser number being conducted under controlled nutritional and environmental regimes. The present review is concentrated on southern pine research, both field and greenhouse, with particular emphasis on the nitrogen and phosphorus relations of loblolly pine. However, some references relating to other conifers, both in the United States and elsewhere, have been included and are presented in the following pages by country or continent and species.

Research in Europe

European research in tree nutrition has included laboratory, greenhouse, and field studies. Several are reported here as examples of recent work with various coniferous species.

The nitrogen and phosphorus nutrition of Japanese larch, [Larix leptolepis (Sieb. and Zucc.) Gord.], was studied in soil-pot culture in Holland by Van Goor (1953). The experiment included three soils which were similar in physical properties but widely different in nitrogen and phosphorus status. One soil was "poor" in both N and P, one was "rich" in N and poor in P, and a third was rich in both elements. All combinations of four levels of nitrogen as NH_4NO_3 and four levels of phosphorus as H_3PO_4 were applied in solution at regular intervals from seeding in May until harvest in September. Each pot received a total of 1500 cc of nutrient solution resulting in total rates of application of 0, 37.5, 75, and 150 parts per million of N and 0, 54, 108, and 216 ppm of P. In the soil poor in nitrogen and phosphate, N in small quantities given in combination with P increased growth, but greater supply of N decreased growth. Additions of P clearly stimulated growth except in the absence of nitrogen. In this soil, therefore, a positive N x P interaction was demonstrated. Phosphorus stimulated growth considerably in the soil poor in phosphate and rich in nitrogen, but N applications decreased growth in this soil. In the soil rich in both nutrients, the N x P interaction was also negative. However, nitrogen did not decrease growth significantly. In terms of nutrient absorption, an antagonism between N and P was discovered, which, according to the author, was independent of differences in growth. In all three soils P absorption was decreased by an increase in nitrogen absorption and

vice versa. There also appeared to be a close correlation between N/P ratio of needles and dry weight of shoots. A distinct optimum in growth over a narrow range in N/P of about four to five was characteristic for all three soils. The author concluded that the poorer the soil is in phosphorus the more rapidly will Japanese larch growth decrease as nitrogen supply is increased.

Working in solution culture in the laboratory, Ingestad (1962) studied the nutrition of Scotch pine (Pinus sylvestris L.). Plants were grown under artificial light for 95 days in 1-liter glass beakers. Several levels and combinations of nutrients were compared. Data for nitrogen and phosphorus indicated an optimum supply of somewhat higher than 50 ppm N and somewhat lower than 20 ppm P. In addition to optimum supply levels, ranges in foliar nutrient content of plants exhibiting "optimum" growth response were reported. They were as follows: N -- 2.4 to 3.0%; P -- 0.15 to 0.40%; K -- 0.9 to 1.6%; Ca -- 0.04 to 0.3%; Mg -- 0.12 to 0.18%; Fe -- somewhat more than 0.005%; and S -- approximately 0.2%.

Tamm (1965) summarized experiences with fertilization of several species of the genera Picea, Pinus, and Betula in Sweden. On well-drained mineral soils strong responses to nitrogen fertilizer have been obtained. However, the effects of phosphorus, potassium, or lime have been small or nill, at least during the first five to ten years after application. The responses to nitrogen on these soils have been of rather short duration, lasting four to five years. Response to mineral fertilizer has been obtained on drained peatlands as well, but improved growth due to PK application depends on the nitrogen content. Peatlands with a low nitrogen level have been found to need NPK fertilization.

Shallow peatlands and poorly-drained mineral soils seem to respond to N alone or NPK. It is believed that fertilizer response is better on well-drained sites than on temporarily waterlogged sites. This has been found to be true also of slash pine in greenhouse and field studies in the United States (Schultz 1968, Walker 1962). Except for afforestation of abandoned fields on deep, drained peats where a moderate application of PK seems essential for survival and growth, results of fertilization at planting time have not been good in Sweden.

Research in Canada

Swan (1960) grew white spruce [Picea glauca (Moench) Voss], black spruce [P. mariana (Mill) B.S.P.], jack pine (Pinus banksiana Lamb), and western hemlock [Tsuga heterophylla (Raf.) Sarg.] for 15 weeks in sand culture using an automatic subirrigation system. Nitrogen levels were 0, 1.2, 11.2, and 140 ppm in one series, and levels of 0, 0.62, 6.2, and 62 ppm P were included in a second series of treatments. Based on the dry weight of the shoot portions of 20 seedlings, the optimum level of nitrogen was found to be 140 ppm; however, since this was the maximum rate tested, the true optimum of N was likely higher than 140 ppm. In the phosphorus series best growth occurred at the 6.2 ppm level of P. Seedling weight was found to be significantly less at the 62 ppm P rate. The author found the concentration of P in the shoot tissue to be highest at the 62 ppm level and concluded this to be an indication of excessive P absorption which had resulted in mild toxicity.

A secondary portion of this experiment (Swan 1960) tested the relative merit of nitrate and ammonium sources of nitrogen. Results gave some indication that NH_4^+- was superior to NO_3^--nitrogen. This

is in agreement with the findings of Pharis, Barnes, and Naylor (1964) who made a similar comparison for loblolly pine.

Research in Australia

Australia has long been a center of investigation into nutrition and fertilization of conifers including the American southern pines.

Kessell and Stoate (1936) were among the early workers on that continent, and they found that applying a dressing of soil taken from old pine stands or alternatively spreading fruiting bodies of Rhizopogon luteolus on the soil surface helped alleviate stunting of Monterey pine (Pinus radiata D. Don) and cluster pine (P. pinaster Ait.) seedlings. Although very few data were presented, the authors obtained what was said to be remarkable results with superphosphate. Including Ca, N, and K with superphosphate did not increase the response.

In an effort to correct phosphate deficiency in loblolly and slash pine, Young (1948) tested several rates and forms of phosphorus amendments. On a sandy podzolic soil the optimum total P_2O_5 "value" of the upper 4 inches of soil was found to be approximately 200 ppm. Rock phosphate was found to be as effective as superphosphate.

Also recognizing the importance of phosphorus in Australian soils, Baur (1959a) in 1946 began a series of experiments to investigate the phosphorus nutrition of loblolly and slash pine. Soil on which these studies were conducted were red and yellow podzolics with high clay content and derived from shales. Many swamps with heavy gley soils occurred in the low parts of the area. In the first study an application of 3 hundredweight (cwt) of superphosphate per acre was compared to no P_2O_5. Three-year diameter growth revealed a significant

response by both species. The data suggested that the response was greater by loblolly pine than slash pine. In a second phase of the same study one subplot in each species was given a second dressing of phosphate at the rate of 3 cwt per acre, resulting in a study composed of 0, 3, and 6 cwt superphosphate per acre. Results for the following growing season were highly significant and indicated all three rates to be significantly different.

In 1952 another study consisting of five treatments -- 0, 2, 4, 6, and 8 cwt superphosphate per acre -- was initiated by Baur (1959a). The results in 1955 indicated that all levels of phosphate were equally good and significantly better than controls. In all studies in this series improvement in tree vigor was more striking than the quantitative data indicated. The author concluded that loblolly can show P deficiency on sites which support good slash pine stands. Baur (1959b) also indicated that the lowest limits for a P response by slash pine in Queensland is 150 ppm total P (extractable with concentrated HCl) and 210 ppm P for loblolly pine.

The influence of addition of elements other than phosphorus has also been studied in Australia. The effect of N, P, S, and Mg on the growth of loblolly pine in a pot study involving a lateritic podzolic soil was conducted in 1959 (Queensland Forest Service 1959). A factorial combination of the following treatments was used:

(1) N as $NaNO_3$--nil, 3, 6 cwt per acre;

(2) P as NaH_2PO_4--0.215, 1.72, 3.44 cwt per acre;

(3) S as Na_2SO_4--nil, 1 cwt per acre;

(4) Mg as $MgCl_2$--nil, 1 cwt per acre.

Nitrogen and phosphorus increased dry matter production, with a highly

significant N x P interaction. Phosphorus increased yields at all N levels, but best growth was obtained in the presence of 6 cwt per acre of $NaNO_3$. However, no significant increase in yield was obtained by increasing P supply beyond 1.72 cwt per acre of NaH_2PO_4. There was no response to N at the lowest level of P, but when phosphorus was adequate, the yield increased as the N level increased.

The fertilizer requirements of loblolly pine have been studied rather intensively by B. N. Richards. He conducted a series of greenhouse and field experiments (Richards 1961a) and found deficiencies of both phosphorus and nitrogen to restrict growth of loblolly pine in sandy podzolic soil of the coastal lowlands of southern Queensland. A strong interaction was observed between these elements, maximum response being obtained only when both were added. Loblolly pine responded to phosphorus during the first year in the field only when grass competition was controlled by cultivation. A significant cultivation x phosphorus interaction was observed, and it was speculated that this could be another expression of the N x P interaction, since cultivation likely increased the rate of N mineralization. Lime-induced chlorosis was observed in two pot experiments which involved high rates of fertilizer phosphorus and $CaCO_3$ at the rate of 20 cwt per acre. Iron was found to accumulate in the stems at the expense of the foliage indicating that high pH had resulted in immobilization of iron within the plant. Adding an iron chelate caused redistribution of iron and disappearance of the chlorosis.

Investigating phosphate fertilization of slash pine, Richards (1961b) applied superphosphate (4 cwt per acre) and rock phosphate (2 cwt per acre) to a 6-year-old slash pine stand in 1940. The stand

was growing in a shallow lateritic podzolic soil. Fertilizer applied in 1940 was still effective after 17 years. A thinning yielding about 500 ft^3 per acre was possible in the fertilized plots at 20 years, whereas the author expressed doubt that unfertilized plots would reach merchantable size. By 1960 plots receiving superphosphate had produced 2300 ft^3 total merchantable volume per acre, rock phosphate plots had produced 2000 ft^3 per acre, and unfertilized controls about 450 ft^3 per acre. Under the conditions of this experiment 2 cwt per acre of rock phosphate was almost as effective as 4 cwt per acre of superphosphate.

Following the above experiment Richards and Bevege (1967) continued forest fertilization research in Australia with a series of experiments involving loblolly pine seedlings. The first of these studies was designed to test the effect of cultivation, $(NH_4)_2SO_4$, and NaH_2PO_4 on seedlings in the field. In a split-plot design with cultivation on major plots and fertilization on subplots, a total of 511 pounds of N per acre was applied over a four-year period in 12 increments with 36 pounds being given in the year of establishment. Over the same period the equivalent of 8 cwt of superphosphate per acre was applied in five split applications, one-half at planting. The data revealed (1) a height growth response to phosphorus only on cultivated plots and (2) the effect of P was enhanced by N. Nitrogen alone depressed height growth, but the trend was reversed in the presence of phosphorus. The same interactions were significant the second year, but N was not depressive in the absence of P. Several years earlier Richards (1961a) obtained somewhat similar results in that both cultivation and nitrogen enhanced the response to phosphorus.

The second study in this series (Richards and Bevege 1967) consisted of a 4 x 3 factorial of superphosphate and urea on a cultivated site. Superphosphate was applied at 0, 4, 8, and 16 cwt per acre over a four-year period, one-half of each rate being given at establishment. Urea was applied at 0, 1, and 2 cwt per acre four times each year for four years. Results indicated a significant N x P interaction. Without N, no P response was obtained, and adding N without P depressed growth. The best combination was found to be N at 4 cwt per acre and P at 2 cwt per acre.

The third study of Richards and Bevege (1967) examined the effect of urea applied in the following treatments: (1) four equal dressings of 50 pounds of N per acre each year for four years, (2) four equal dressings of 50 pounds of N per acre during the first year only, (3) one dressing of 200 pounds of N per acre each year for four years, and (4) one dressing of 200 pounds of N per acre at establishment only. Urea increased height growth during the first two seasons, a single application the first year producing the same effect as split applications during the first year. The addition of urea after the first season demonstrated no clear advantages.

In generalizing about the responses obtained in the above series of studies, Richards and Bevege (1967) stated that loblolly pine will respond rapidly to fertilization with phosphorus on cultivated sites, though nitrogen may be necessary to ensure a significant response. Presumably the magnitude of the nitrogen effect depends on the amount of soil nitrogen mobilized as a result of cultivation and how much of this N becomes available to the trees. If soil moisture conditions are favorable for mineralization, the effect of cultivation can be so

pronounced as to temporarily mask a response to fertilizer nitrogen. However, to ensure quick response to phosphorus, addition of nitrogen appears essential. According to the authors the major limiting nutrient for loblolly pine on lateritic podozolic soils of the coastal lowlands of subtropical Queenslands is phosphorus. Results of investigations by other Australians (Kessell and Stoate 1936, Young 1948, Baur 1959a, 1959b) seem to support this view.

The nutrition of Pinus pinaster has very recently received attention in Australia. Keay, Turton, and Campbell (1968) broadcast urea and superphosphate in a 13-year-old plantation on a lateritic gravelly soil in western Australia. Rates tested were 0 and 200 pounds of urea per acre and 0, 200, 800, 3200, and 12,800 pounds of superphosphate per acre and all combinations of these rates. As early as six months after treatment, significant increases in needle weight and N and P content of needles from the top whorl were observed. A significant N x P interaction was measured with greatest dry weight being produced at the two highest levels of phosphorus (designated P_3 and P_4) and the higher level of nitrogen (N_2). Concentration of phosphorus in the needles increased with increases in the rate of applied P but were unaffected by nitrogen application. Nitrogen concentration, however, was increased by both N and P. The combination of N_2 and P_3 approximately doubled the concentration of chlorophylls. The N_2P_3 treatment also significantly increased the rate of $^{14}CO_2$ fixation. It was observed that young needles were more active in $^{14}CO_2$ fixation in both treated and untreated plots than were mature needles. The N_2P_3 combination also doubled the rate of stem growth, and fertilized trees continued to grow during the hot, dry summer season while unfertilized trees ceased growth.

Research in the United States

Longleaf pine.--The nutrition of longleaf pine (Pinus palustris L.) has been almost completely ignored by those involved in tree nutrition research (Brendemuehl 1968). The earliest investigation on record, in fact one of the earlier tree nutrition studies in the United States, concerning this species was conducted by Pessin (1937). Studying the effect of a deficiency of several essential elements on the growth of longleaf pine in solution culture, the author transplanted 3-week-old seedlings to 2-quart mason jars containing the following solutions: complete, -N, -P, -Ca, -Mg, -S, and -Fe. The complete solution contained Ca, N, K, P, Mg, S, and Fe at levels thought to be adequate. Nitrogen and phosphorus were supplied at rates of 421 ppm and 140 ppm, respectively. After 222 days plants growing in the complete solution had the greatest dry weight, most lateral roots, longest needles, and the most healthy color. As would be expected, plants grown without nitrogen were pale green to brown and smaller than those in the complete medium. In view of results with other pines (Hobbs 1944, Swan 1960, Richards 1961a), the most surprising result was the response of plants in the minus phosphorus treatment. These plants were reported to have been only somewhat smaller in terms of dry mass. "Externally the absence of this element did not exhibit any evidence of injury." Seedlings possessed normal color and were described as "vigorous." Plants grown in the absence of iron exhibited the lowest dry weight and were yellow or almost white, weak and spindly.

In soil-pot culture in south Mississippi, Allen and Maki (1955) studied three fertilizer treatments, no fertilizer, notrogen, and complete NPK fertilizer. Fertilizer levels were 7.7 g NH_4NO_3, 80 g

20 percent superphosphate, and 2 g 50 percent muriate of potash per 2-gallon crock. In terms of survival and growth of transplanted seedlings, NPK was the superior treatment with no significant response to nitrogen alone. Applications of complete fertilizers by Bateman and Roark (1957) and Derr (1957) also stimulated growth of longleaf pine, although Derr measured a reduction in survival due to fertilization.

The work of Brendemuehl (1968) indicated total seedling growth to be due primarily to combinations of nitrogen and phosphorus. Greatest dry weight, however, was produced with a combination of 150 pounds of N per acre, 300 pounds of P per acre, and 75 pounds of K per acre. His experiment was conducted in the greenhouse using a sandy Florida soil.

Shortleaf pine.--Working with several northern pines and shortleaf pine (Pinus echinata Mill.), Hobbs (1944) studied symptoms of a deficiency of nitrogen, phosphorus, potassium, and magnesium. Plants were grown for 26 weeks in solution culture. Seedlings grown without potassium were stunted; needles were short and bluish-green. Copper-colored necrosis was common in meristematic tips. Moderately stunted plants with leader chlorosis and needles green at the base, chlorotic in the central region, and necrotic on the tip were characteristic of seedlings receiving no magnesium. Nitrogen-deficient plants were pale green. Upper portions of the stunted shortleaf remained green and free of chlorosis while the basal region become necrotic, with necrosis gradually progressing upward.

Fourteen years later Roth and Evans (1958) applied a complete fertilizer plus supplemental nitrate (2000 pounds of 3-9-6 per acre and 1000 pounds of $NaNO_3$ per acre) to several stands of shortleaf pine ranging in age from 15 to 35 years. Treatment was repeated every three

years over a period of 8 to 12 years depending on the stand. Total fertilizer nitrogen contained in the treatment was equivalent to 220 pounds per acre per application. At the end of the experiment (8 to 12 years) fertilizer had doubled diameter growth.

Curlin (1963) tested fertilizer response of natural stands of shortleaf pine by applying fertilizer treatments to thinned and unthinned stands in the Tennessee Valley. Three fertilizer treatments were applied in a randomized block design on uniformly thinned and unthinned portions of each stand in March soon after thinning. Treatments were (a) control, no fertilizer, (b) ammonium nitrate at the rate of 300 pounds of nitrogen per acre, (c) calcium metaphosphate at the rate of 131 pounds of phosphorus per acre, and (d) a combination of 300 pounds of N per acre and 131 pounds of P per acre. Diameter was measured yearly, and growth expressed in basal area increment per tree. Growth was increased as much as 300 percent over the unthinned check plots by thinning and nitrogen fertilization. Nitrogen alone applied to thinned plots produced 40 percent more basal-area growth per tree than the thinned check plots. Responses were still evident four years after treatment. Response to phosphorus was erratic and often adverse. The author indicated that the adverse effect may have been due to surface-applied, relatively immobile phosphorus stimulating growth of the competing vegetation.

Slash pine.--The nutrition of slash pine has received considerable attention in recent years, particularly in the southeastern region of the United States. Research with this species has been predominately fertilizer field trials, with relatively few pot-culture experiments on record.

Probably the most thorough sand culture investigation was that of McGee (1963) who studied N, P, and K requirements of slash pine seedlings. Nitrogen was applied at 0, 5, 25, 125, and 625 ppm; P at 0, 1, 5, 25, and 125 ppm; K at 0, 5, 25, 125, and 625 ppm. Thirty combinations of these rates were tested in an incomplete factorial by regression analysis. Response curves for both N and K reached maximums between 125 and 625 ppm. It was concluded, therefore, that the optimum levels lie between the two highest rates of N and K tested -- 125 and 625 ppm. The optimum level of phosphorus apparently was not reached since the response curve showed no tendency for flattening at 125 ppm, the highest level of applied P. Shoot/root ratio was the only variable influenced by an interaction but was found to be largely a function of N supply. As N increased, a greater percentage of the total dry weight of the plant was found in the shoot. The percentage of N, P, and K in the shoot and root tissue increased with each additional increment of nutrient supply. However, nitrogen was measured in greatest quantity in the shoot while P and K content was highest in root tissue.

In soil pot-culture Brendemuehl (1968) conducted a series of greenhouse studies using material from the 0- to 10-inch portion of a Lakeland profile. Of the various elements tested (N, P, K, Ca, Mg, S, and micronutrients) only N and P were found to influence growth. Phosphorus was found to be the element in shortest supply. While growth was increased by P alone, the greatest response occurred when N and P were applied together at about a 1:1 ratio. All other elements tested alone or with N or P produced no additional growth. Foliar N increased as the supply of N increased but decreased as the P supply increased. Foliar P increased as the amount of P applied increased

and decreased with each increase of N at all rates of P supply. Nitrogen applied without P increased foliar K, but foliar K decreased at all other levels of N and P. Calcium in the foliage was not affected by N or P. Foliar Mg decreased as the rate of N or P or combinations of N and P increased.

A recent pot study concerning the nutrition of slash pine was that of Schultz (1968). Using Bladen fine sandy loam in the greenhouse, the author studied the effects of fertilization and flooding on 1-year-old slash pine transplants. Seedlings were grown for nine months with and without nitrogen-phosphorus fertilization and flooding. The fertilizer consisted of the equivalent of 100 pounds of N per acre and 100 pounds of P per acre applied to the soil surface as a water solution of diammonium phosphate. Fertilization more than doubled seedling dry-weight production under well-drained conditions. Under the flooded regime, dry weight was increased by 40 to 50 percent by fertilization. European work (Tamm 1965) has also indicated poorer fertilizer efficiency on excessively wet soils.

One of the earliest field studies with this species was established in 1945 to test the effect of colloidal phosphate on height growth of slash pine (Barnes and Ralston 1953). Several levels were broadcast and applied in the planting hole, with and without plot cultivation, at two locations in Florida. Response to 1 ton of collodial phosphate per acre broadcast on the soil surface was detected at the 5-percent level of probability. Two tons per acre on the surface increased the significance to the 1-percent level. At one location the 0.5-ton-per-acre treatment was significant at the 5-percent level, and cultivation

of the same treatment increased the level of significance to 1 percent. Phosphate applied in the planting hole had no effect on growth.

Gilmore and Livingston (1958) studied pulpwood volume response 19 years after fertilizing slash pine with two levels of complete fertilizer. Treatments were (1) no fertilization, (2) 39, 30, and 24 pounds of N, P_2O_5, and K_2O per acre, and (3) 96, 108, and 63 pounds of the same amendments per acre. Nineteen years after treatment, plots fertilized at the higher rate yielded 21 percent more volume than unfertilized controls. These results were obtained on a sandy loam in Alabama.

Fertilization of slash pine in Florida has been studied in detail by W. L. Pritchett and his associates. On Leon fine sand Pritchett and Swinford (1961) measured a response to colloidal phosphate. Fifteen years after applying 0.5 ton per acre in alternate 4-foot strips, treated plots averaged 45 percent more cordwood than unfertilized plots.

Superphosphate was applied at rates of 0, 17.5, and 35 pounds of P per acre and rock phosphate at rates of 35, 70, 140, and 280 pounds of P per acre (Pritchett and Llewellyn 1966). Certain plots were also treated with 50 pounds of N per acre annually. Significant increases in height and diameter growth were observed in five of eight experiments as a result of added P. Response to P alone, however, was evident only on poorly drained sands. Nitrogen alone suppressed growth, but when applied with 35 pounds of P per acre as superphosphate, N resulted in additional response. After the third year, 140 pounds of P per acre from rock phosphate appeared to be as effective as 35 pounds of P as superphosphate. The optimum level of tissue P in current needles of 3- to 5-year-old trees was approximately 0.10 percent. In the two

experiments on deep, well-drained sands, no response to P alone was obtained. Only plots receiving 40 pounds of N per acre annually plus 35 pounds of P per acre showed significant growth increases.

Also in Florida, two rates, 20 and 40 pounds per acre, of 3-18-6 and 7-7-7 were applied to individual slash pine trees in a 21-year-old stand on a Plummer fine sand (Hoekstra and Asher 1962). Average radial growth per plot for the five years following treatment was subjected to covariance analysis, using the 5-year radial growth immediately preceding treatment as the covariant. The average effect of both levels of 7-7-7 was greater than the effect of both rates of 3-18-6. This may be an indication of a response to nitrogen. For both fertilizers the higher level was superior to the lower level. An increase from 20 to 40 pounds of 3-18-6 had a greater effect than the same increase of 7-7-7. The authors seemed inclined to believe that radial growth depended on the amount of N applied in the presence of P and K. These workers found covariance analysis satisfactory and postulated that failure to detect significant responses in previous stand fertilization studies may have been due to a failure to consider certain covariants.

In southern Georgia on Lynchburg loamy sand, Hughes and Jackson (1962) found somewhat different results with the same species. Seedlings were fertilized during the first and second growing seasons. Nitrogen and K_2O each at 100 pounds per acre with 0, 50, and 100 pounds of P_2O_5 per acre in most cases gave good height growth response after two growing seasons. Addition of K without N or N without K had a depressing effect on growth. However, phosphorus alone at the rate of 50 pounds P_2O_5 per acre was the best fertilizer tested.

A 9-year-old slash pine plantation in the Georgia coastal plain was treated with 200 pounds of N per acre, 44 pounds of P per acre, and a combination of N and P (Walker and Youngberg 1962). Diameter and basal area growth responded to N each of three years after fertilization. Maximum stimulation occurred the second year after treatment, however. Response to N for the 3-year period was 12.4 percent over controls. Phosphorus response for the same period was nonsignificant. Foliage content of N, P, K, and Ca was increased one year after treatment, but no differences were apparent after three years.

Testing the effect of flooding and fertilization, Walker (1962) grew slash and loblolly pine seedlings in Bladen clay on field plots with three water depths: -4 inches, $\pm$0, +4 inches, and check (subject to natural rainfall). The following fertilizer treatments were superimposed on the water-depth treatments: (1) check, no fertilizer; (2) 1000 pounds 8-8-8 per acre plus 100 pounds per acre of a mixture of trace elements broadcast in mid-April, 5 weeks before water treatment began; and (3) same as 2 plus 400 pounds of diammonium phosphate per acre applied in mid-July, 6 weeks after water treatments were begun. Survival, height growth, needle length, foliage color, and foliar N, P, and K were influenced by both water and fertility levels. The best water treatment was -4 inches. Growth of both species during the first two seasons was increased significantly by 1000 pounds of 8-8-8 plus 100 pounds of trace elements per acre. Holding water 4 inches deep on the plots was found to reduce the fertilizer response. Schultz (1968) also found this to be true in a greenhouse experiment involving fertilization and flooding of slash pine seedlings.

One of the few forest fertilization studies to consider economic as well as biological response was that of Malac (1966). Four levels of 14-7-7, 0, 420, 840, and 1680 pounds per acre, were applied to a 20-year-old slash pine stand in 1959. Additional treatments included split applications of the highest rate over two and four years. Five-year height, diameter, and volume growth were found to be relatively constant regardless of treatment. However, all fertilizer treatments were significantly better than the unfertilized control. Response was measured on individual trees and seemed to be independent of stand density within the range of stocking encountered in this study. Assuming the physiological response to be constant, the author theorized that response on an area basis is then a function of stocking. The greatest physiological response in terms of cubic feet per tree was from split applications of the highest rate. The greatest net monetary yield was obtained from the lowest rate, 420 pounds per acre. Pursuing the economic aspect further, the author discussed two hypothetical slash pine stands with densities of 200 and 300 stems per acre. If 420 pounds of 14-7-7 per acre were applied to 200 stems per acre, the investment for fertilizer would return 5 percent, while the same rate on 300 stems per acre (assuming equal physiological response per tree) would yield 10 percent on the investment. Though much of the economic and stand density aspects were theoretical, the paper did point up the need for considering stand density in forest fertilization.

Working with sands classified as poorly to moderately drained, Broerman (1967) established an N x P study with slash pine. The soils on which the study was established were strongly acid and low in nutrient content. Total phosphorus averaged 58 ppm, 6 ppm "available" P, less

than 40 ppm K^+ and Mg^{++}. Four levels of each and all combinations of N and P were applied as NH_4NO_3 and superphosphate. Levels used were 0, 33, 67, and 100 pounds of N per acre and 0, 68, 115, and 162 pounds of P_2O_5 per acre. Nitrogen produced a highly significant response in terms of cubic-foot volume increases per tree. Contrary to the findings of Pritchett and Llewellyn (1966), the response to P or the N x P interaction did not approach significance. A comparison of the highest N level with controls indicated an 18 percent increase in volume growth over a 3-year period.

Loblolly pine.--Probably the first scientist in the United States to use the sand-culture technique with forest trees and also the first to study the nutrition of loblolly pine was Addoms (1937). She grew seedlings in 3-gallon crocks and applied nutrient solutions daily by the drip method. Although varying nutrient levels were not compared in this study, good growth was obtained at levels of 130 to 150 ppm N and 150 to 200 ppm P. However, since some foliage yellowing was noted, the author speculated that the N level may have been suboptimum.

Using subirrigated sand cultures Woodwell (1958) grew loblolly and pond pine (Pinus serotina Michx.) seedlings for 120 days under varying nutrient regimes. For loblolly pine the following optimum ranges were reported: N -- 75 to 600 ppm; P -- 40 to 600 ppm; K -- 25 to 300 ppm; S -- 12 to 100 ppm; Ca -- 20 to 100 ppm; and Mg -- 25 to 100 ppm.

The most complete nitrogen-phosphorus nutrition study concerning loblolly pine in sand culture was that of Fowells and Krauss (1959). One-year-old loblolly and Virginia pine (Pinus virginiana Mill.) seedlings were transplanted from the nursery to 5-gallon glazed earthenware crocks filled with quartz sand. The culture method was

that of Gauch and Wadleigh (1943) in a randomized block with three replications. Nutrient levels included were 0, 1, 5, 25, 100, 200, and 400 ppm N and 0, 0.1, 0.5, 1, 5, 25, 100, 200, and 400 ppm P. For all treatments in the P series the level of N was 100 ppm and in the N series P was held constant at 100 ppm. KH_2PO_4 and NaH_2PO_4 were used as sources of phosphorus, the former being used through the 100 ppm rate and the latter used in the higher rates. NH_4NO_3 was the source of nitrogen in all treatments. Micronutrients were supplied at levels considered to be adequate for the species. Pots were irrigated hourly with 0.5 gal of solution and replaced with fresh solutions every 3 weeks. To prevent dormancy day length was extended to 15 hours with artificial lighting.

Growth data from this experiment indicated optimum nitrogen levels for certain variables to be as follows: height -- 25 to 100 ppm; total plant weight (oven-dry) -- 100 ppm; needle weight -- 100 ppm; root weight -- 100 ppm; shoot to root ratio--increased as nitrogen level increased. Mycorrhizae were found on roots grown in a medium of low nitrogen. In the 100 ppm N solution lateral roots were long and fleshy. In the phosphorus series the 1-ppm-P treatment was as good or better than the other rates in terms of height growth and total plant weight. The classical symptoms of phosphorus deficiency were not evident, the only symptom being early defoliation. Pessin (1937) also failed to observe typical symptoms of phosphorus deficiency in longleaf pine.

Significant responses were also observed in terms of nutrient uptake (Fowells and Krauss 1959). The content of N in the needles was directly related to the supply of N in the growth medium. In the upper needles 1 ppm N resulted in 0.88 percent N while 400 ppm N yielded

a needle content of 3.06 percent N. In the phosphorus series in which N was held at 100 ppm, needle N content was about the same except in the 1 ppm P treatment, which showed a much lower N content. The authors suggested two possibilities for this: (1) low P resulted in less available energy for active uptake of NO_3^- and possibly NH_4^+; (2) low P supply reduced synthesis of chloroplastic, cytoplasmic, and nuclear proteins in the foliage. Needle phosphorus content for the 1 ppm P treatment was found to be 0.16 percent and 0.18 percent for the 400 ppm level of this element. The percentage of P in the needles at the 1 ppm level of N was significantly greater than at higher concentrations of N. Two possibilities were offered to explain this result. (1) There could have been a decrease in competition between NO_3^- and PO_4^- ions. Van Goor (1953) suggested an antagonism between N and P. (2) The higher P concentration was the result of phosphorus being concentrated in less dry matter because of poor growth in the 1 ppm N treatment. The highest concentration of potassium was found in plants treated with 1 and 5 ppm N. This may also have been due to the lesser growth associated with low supply of N. The concentration of calcium was found to be highest in the low N treatments, but total calcium uptake was less. In the P series calcium level in the needles was fairly constant. Best growth occurred when the nitrogen content in the foliage was in the range of 1.7 to 2.3 percent and phosphorus in the range of 0.14 to 0.16 percent. A deficiency of phosphorus was observed at 0.10 percent P. The authors concluded that the optimum supply of N for loblolly and Virginia pine lies in the range of 25 to 100 ppm N. For phosphorus 1 ppm appeared to be adequate for good growth.

In another nutrition study, loblolly pine seedlings were grown in automatically irrigated sand cultures supplied with various levels of K, Mg, and Ca from deficiency to surplus (Sucoff 1960). The purpose of the experiment was to examine distribution and redistribution of these elements within the seedlings. After seven months when seedlings ranged in height from 5 to 80 cm, some of the plants were harvested. Then the supply of Ca and Mg was withheld and the remaining plants were allowed to grow another two to three months. Potassium was found to be highest in needles from the uppermost portion of the stem. The concentration of K decreased as needles matured. If the supply of K was too low to support maximum growth, the concentration of this element in mature needles was uniform at all locations on the stem. Magnesium concentration generally was uniform throughout the plant. When K was deficient, the highest concentration of Mg was in the lower needles. When the supply of Mg was suddenly withheld, Mg was redistributed, moving from the older needles to support new growth. The calcium concentration was highest in the lower needles except when calcium limited growth. Then the Ca concentration was the same throughout the plant. Movement of Ca from older to newer needles in response to sudden withholding of Ca was not detected in this study.

Sucoff (1961) also studied potassium and magnesium deficiency symptoms in loblolly and Virginia pine seedlings in sand culture. Magnesium was supplied at concentrations of 0.013, 2, and 20 milliequivalents per liter, calcium at 0.01, 0.1, 1, 4, 6, and 15 meq per liter, and potassium at levels of 0.01, 01, 1, 4, 6, and 15 meq per liter. Results indicated potassium deficiency symptoms at 0 and 0.01 meq per liter for both species. Magnesium deficiency in both loblolly

and Virginia pine was induced at 0.013 meq per liter of Mg. Calcium deficiencies appeared only in the absence of this nutrient.

Attempting to define the relationship between nitrogen supply and drought resistance, Pharis and Kramer (1964) subjected loblolly pine seedlings to several levels of nitrogen and various drought regimes. Nitrogen as NH_4NO_3 was applied at 10, 50, 125, and 300 ppm N in nutrient solutions to plants growing in quartz sand in glazed crocks. All culture units were irrigated once daily for six months, except those subjected to drought treatment. In terms of height growth the 50 ppm level of N was found to be nearest to optimum. Nitrogen deficiency symptoms were observed at the 10 ppm level. Greatest dry weight occurred at 300 ppm; however, no measure of growth revealed statistical differences between the 50, 125, and 300 ppm rates. The authors concluded from plant height and general plant appearance that the optimum level of N is probably between 50 and 125 ppm. Plants grown at 50 ppm N were most resistant to drought. At higher levels drought resistance decreased.

The effect of nitrogen level, calcium level, and nitrogen source on loblolly pine growth was studied in a sand culture experiment at Duke University (Pharis, Barnes, and Naylor 1964). Plants were started from germinated seed and grown for 4-1/2 months, being daily irrigated with freshly prepared nutrient solutions. The treatments consisted of three N sources ($NaNO_3$, NH_4Cl, and urea) applied at two rates -- 10 and 75 ppm N. Calcium was supplied as $CaCl_2$ at levels of 0 and 200 ppm Ca. Results indicated that urea at 75 ppm N produced the greatest height growth, largest diameter, highest fresh and dry weights, and the lowest root/shoot ratio. Urea was also associated with the highest total N in the foliage while nitrate-treated plants contained the lowest level

of foliar N. Ammonium-N produced the greatest quantity of amino acids, nitrate-N the least. Nitrogen deficiency symptoms were noted for all 10 ppm N treatments, while calcium deficiency was not evident even at the zero calcium level. However, 200 ppm Ca resulted in slight increases in growth. Nitrate was associated with greatest quantity of foliar Ca at both levels of N.

Thompson (1965), also working with sand cultures of loblolly pine, tested various levels of N and P and found that maximum length of second internode occurred at 95 ppm N. The greatest number of lateral roots originating from the first 5-cm segment of the taproot was produced at 220 ppm N. Dry weight of mature needles and of the entire shoot was found to be maximum at 40 ppm P.

Switzer and Nelson (1956) reported results of a study of N, P, and K response of loblolly pine seedlings in the nursery. Three levels of N -- 0, 150, and 300 pounds per acre; two levels of P_2O_5 -- 0 and 300 pounds per acre; and two levels of K_2O -- 0 and 300 pounds per acre were tested. Dry weight of seedlings was affected only by nitrogen.

In a field trial in southern Arkansas, Zahner (1959) fertilized loblolly pine plantations four, five, and eight years old. Six treatments -- 100 pounds of N per acre, 300 pounds of N per acre, 300 pounds of N per acre plus PK, 300 pounds of N per acre plus micronutrients, 300 pounds of N per acre plus PK plus micronutrients, and no fertilization -- were tested. There was no height growth response; however, during the first year all fertilized plots were significantly better in terms of stem diameter than control plots. There was no difference between 100 and 300 pounds N per acre. During the second year, however, significant differences developed between 100

and 300 pounds N per acre, diameter growth being 12 and 23 percent, respectively, more than controls. The effect of fertilizer had largely disappeared by the third growing season. The average diameter growth superiority of fertilized trees over controls was 10 to 15 percent from 1953 through 1958. At no time during the study did micronutrient or PK treatments produce a significant response. The author stated that smaller applications repeated periodically over the five years would have maintained growth at an accelerated rate. In offering a possible explanation for the lack of height growth differences, Zahner theorized that, because of loblolly pine's strong apical dominance, the stem tip received the materials necessary for good height growth even on the unfertilized control plots.

Maki (1960), studying fertilization of loblolly pine in the lower Piedmont of North Carolina, applied nitrogen (as NH_4NO_3) at 0, 80, and 160 pounds N per acre and phosphorus (as superphosphate) at rates of 0, 40, and 80 pounds of P_2O_5 per acre. Two plantations 5 and 10 years old were treated. During the second, third, and fourth growing season after initial treatment, 40 pounds of K_2O per acre were applied to all plots. Dry weights of needles collected from the top of the trees were significantly greater than controls in all nitrogen-treated plots. The heaviest rate of N appeared to increase needle length by an inch or more, and the proportion of fasicles with more than three needles also increased. Nitrogen and P percentages were increased by fertilization, but K content was not affected. In spite of increases in foliage weight and composition, height and diameter growth were not outstanding. Treatments supplying higher N resulted in more vigor and 20 percent greater diameter growth compared to controls, but initial indications of

better height growth had begun to fade by the end of the ninth season after first fertilizer application. Maximum height response was only 10 percent to the highest rate of nitrogen. With respect to height growth response, these results are similar to those of Zahner (1959) in Arkansas.

In Louisiana Linnartz (1961) applied urea, treble superphosphate, and muriate of potash to individual trees in loblolly pine plantations on (1) Shubuta sandy loam in northern Louisiana, (2) a complex of Bowie fine sandy loam, Ruston loam, and Beauregard loam in central Louisiana, and (3) Ruston sandy loam in the southeastern region of the state. Rates tested were 0, 100, and 200 pounds of N, P_2O_5, and K_2O per acre applied singly and in all combinations. Nitrogen alone depressed height growth on the Shubuta soil, while phosphorus alone increased growth. Superphosphate at 100 pounds P_2O_5 per acre resulted in best growth on this site. On the Bowie-Ruston-Beauregard complex nitrogen alone also depressed growth and phosphorus alone increased growth, but a combination of 100 pounds N plus 100 pounds P_2O_5 per acre yielded the best height growth. On the third soil, Ruston sandy loam, only a response to nitrogen alone was observed. Nitrogen at 100 pounds per acre produced greatest height growth; however, available P in the soil was relatively high so this response may have been an N x P interaction.

Moehring (1964) studied the effects of irrigation and fertilization on the growth of loblolly pine seedlings. Plots of 1-year-old seedlings on a Grenada silt loam were treated as follows: (1) water -- rainfall supplemented to a level of 2 acre-inches per week by sprinkler, June through October, (2) fertilizer -- 10-20-10 applied in April, NH_4NO_3 applied in June, both at the rate of 100 pounds per acre, (3) a

combination of the above treatments. After six consecutive years of treatment, watered and fertilized trees averaged 5.1 feet taller and fertilized trees averaged 1.5 feet taller than the controls. In terms of diameter, a combination of water and fertilizer increased growth by 34 percent, while fertilizer alone produced a 25-percent increase. With average volume of the 20 tallest trees in each plot as a measure of response, water alone was found to increase growth by 56 percent; fertilizer alone resulted in 111 percent more volume, and the two combined produced 155 percent more wood volume than untreated controls. After eight years of growth, 8, 12, 17, and 20 cords per acre were found on the control, watered, fertilized and watered+fertilized plots, respectively. Wood specific gravity was reduced only slightly by water and water+fertilizer, but it was significantly reduced by fertilizer alone. In terms of dry weight, however, fertilizer produced more wood because of the additional volume.

Carter and Lyle (1966) conducted an experiment on two Alabama soils to test the effect of fertilizer on 2-year-old loblolly pine in the field. A randomized block design with a 2^3 factorial arrangement of treatments was used on two sites -- a relatively fertile Piedmont soil and an infertile Coastal Plain soil. Nitrogen was applied at the rate of 150 pounds per acre the first year and 300 pounds per acre the second and third years. Phosphorus was applied the first year only at 750 pounds of superphosphate per acre. Potassium was applied all three years at 125 pounds of muriate of potash per acre per year. Only nitrogen showed a significant growth response. On the Coastal Plain soil N produced an increase in height growth while diameter growth responded to N on both sites.

On Sawyer sandy loam in southern Arkansas, Moehring (1966) conducted a field study with 8-year-old loblolly pine. The following treatments were tested: (1) a single broadcast application of 100 pounds of N per acre as NH_4NO_3 in April of 1958, (2) two successive broadcast applications of 100 pounds N per acre in April 1958 and April 1959, (3) untreated controls. Basal area growth of fertilized trees surpassed controls in 1958 and 1959; however, the effect had disappeared two years after application. The decrease in growth rate corresponded to a rapid reduction of the foliar-N advantage of fertilized over unfertilized trees.

On the upper Coastal Plain of Louisiana, Merrifield and Foil (1967) failed to measure a fertilizer response by this species. Applying NH_4NO_3, superphosphate, and KCl singly or in various combinations on moderately well-drained, acid, sandy loams and loamy fine sands had no significant effect on the height or diameter growth of seedlings. NH_4NO_3 at 200 pounds of N per acre significantly reduced tree height unless an equal amount of P_2O_5 was added.

In southeast Louisiana, however, Box (1968) demonstrated a growth response of loblolly pine to intensive culture including fertilization. Treatments included a slow-release fertilizer, ferrous ammonium phosphate, applied at a rate of 8 ounces per tree at planting, irrigation, and weed and insect control. An additional application of NH_4NO_3 was given four years later. Results after five years revealed that fertilizer alone increased heights by 3 feet and diameters by 1.2 inches. Complete control of vegetation was more effective than fertilizer alone, however.

Although the effects of fertilization have been evaluated largely in terms of growth responses and changes in nutrient content of plant tissues, some work has been conducted to test other effects such as seed production and changes in wood properties. For example, Wenger (1953) applied 25 and 50 pounds of 7-7-7 per acre to 25- and 40-year-old loblolly pines in southeast Virginia. In the 25-year-old stand fertilized trees produced a significantly greater number of cones than unfertilized trees. There was no significant difference between the two rates of fertilization, however. No response was measured in the 40-year-old stand.

Several years later (Texas Forest Service 1960) fertilization of 7-year-old grafts was found to increase conelet numbers. Application of 300, 500, and 500 pounds of N, P, and K per acre, respectively, produced 17.5 conelets per graft. Eleven conelets per graft were produced by plants treated with 100-200-200 pounds of N, P, and K per acre. Unfertilized plots produced an average of only 1.9 conelets per graft.

Studying the effects of fertilization on wood properties of loblolly pine, Zobel et al. (1961) applied three fertilizer treatments to 16-year-old trees in the middle Piedmont of North Carolina. The treatments included 160-80-80 (heavy), 80-40-40 (moderate), and none (check). Specific gravity was significantly decreased (up to 16%) by both rates of application. Tracheid length and cellulose yields decreased but not significantly. Slight but nonsignificant increases in diameter were also measured. The study included only 24 trees, and a great deal of variability between trees receiving like treatment was observed. All trees did not show the trends reported above, which may

indicate the importance of considering individual-tree responses in experiments of this sort. Such information could be of significance in the development of improved strains.

Moehring (1964) measured a significant reduction in wood specific gravity by fertilizer. However, due to increases in volume, fertilization produced a greater quantity of wood mass than the unfertilized controls.

Other Species

Bensend (1943) investigated the nitrogen nutrition of jack pine (Pinus banksiana Lamb.) in sand culture. Seedlings were grown for 83 days and supplied with nutrient solutions containing 0, 48, 95, 145, 230, 275, 336, 537, 702, and 855 ppm nitrogen. Total seedling weight, height, and stem weight increased rapidly with increases in N supply up to 230 ppm. Root mass was found to reach a maximum at 200 ppm N. Increases in nitrogen supply caused a decrease in root/shoot ratio up to 145 ppm N. In all cases N content of seedlings increased as the rate of applied N was increased.

After growing loblolly and pond pine in sand cultures at various levels of nutrition for 120 days, Woodwell (1958) reported the following optimum ranges for pond pine: 25 to 600 ppm N; 20 to 600 ppm P; 20 to 125 ppm K; 12 to 100 ppm S; 20 to 100 ppm Ca; and 25 to 100 ppm Mg.

The work of Brendemuehl (1968) with slash pine is reported in a previous section. Sand pine [Pinus clausa (Chapm.) Vasey] was also included in that soil pot-culture experiment, and the results were very similar to those for slash pine. Phosphorus was found to be the element in shortest supply. P alone increased growth while N+P combinations

resulted in further increases. All other elements failed to yield significant responses.

Earlier in the Pacific Northwest, Viamis, Biswell, and Schultz (1951) applied fertilizer at rates of 200 pounds of N per acre, 300 pounds of P_2O_5 per acre, and 200 pounds of K_2O per acre to ponderosa pine (Pinus ponderosa Laws.) seedlings in soil pot-culture using a residual sandy loam. Other treatments were without N, without P and without K. Omitting P and K had little effect, but omitting N significantly reduced seedling growth.

In the Northeast, Heiberg, Madgwick, and Leaf (1964) remeasured fertilized and unfertilized plots of 30- to 35-year-old plantations of red pine (Pinus resinosa Ait.) on potassium-deficient outwash sands on the Pack Forest in New York. Compositing the data from several plantations, the authors found very highly significant responses in total height, internodal growth, increased basal area, and decreased number of live whorls from potassium fertilizers. Maximum height growth was measured in the fifth or sixth year after treatment. Twenty years after treatment fertilized trees had a 45 percent height advantage over unfertilized trees. The duration of the response was thought to be due to a combination of a site inherently low in productivity and previous degradation by exploitive agriculture. The paper did not clearly present an optimum level of potassium; however, the response curve appeared to be steep up to 50 pounds per acre. Beyond 50 pounds per acre the slope decreased somewhat, reaching a plateau at 100 pounds per acre.

Studying mineral element relations of black spruce, Watt (1966) found a significant correlation between foliar content of nitrogen and

phosphorus and site quality. Both elements were found deficient on poor quality muskegs in Minnesota. These sites were treated with 300 pounds of N per acre as NH_4NO_3 and 300 pounds of P per acre as treble superphosphate applied each of two growing seasons. Height growth was increased by two and one-half times. In a second study three levels of N -- 50, 100, and 300 pounds per acre -- and two levels of P -- 100 and 250 pounds per acre -- were tested. First season results showed that 100 and 300 pounds of N per acre and 100 and 250 pounds of P per acre were equally effective. Fertilization treatments increased foliar nitrogen and phosphorus in both experiments.

Ryker and Pfister (1967) applied fertilizer to plots of white pine (Pinus strobus L.) thinned to three levels of tree spacing: 9 x 9, 20 x 20, and 30 ft x 30 ft. Fertilizer treatments consisted of (1) check; (2) NH_4NO_3 at a rate equal to 300 pounds of N per acre applied in 1960, 1961, and 1962; (3) 13-13-13 at a rate equal to 312, 136, and 259 pounds of N, P, and K per acre. Fertilizer was applied immediately preceding fall precipitation. Diameter and height were measured at the beginning and end of the 4-year period, 1961-64. Results indicated that during this period thinning increased average annual diameter growth by 39 percent. Neither N nor NPK had a significant effect in unthinned plots. However, fertilizer caused an additional 36 percent increase in diameter growth on the thinned plots. There was no difference between the 20 x 20 and the 30 ft x 30 ft spacings. Nitrogen alone was as effective as NPK, but both were significantly better than no fertilizer on the thinned plots. The authors concluded that in unthinned plots the limiting factor was probably soil moisture deficiency due to intense competition.

Apparently thinning reduced competition for moisture sufficiently to allow a response to fertilization.

Summary

Willis (1960) stated that "Even a casual examination of the literature on the response of forests to fertilizers will reveal a variety of conflicting results. Some studies show no increased beneficial growth from the use of fertilizers; others produce increases of a magnitude that would appear to justify fully the use of fertilizers on tree plantings." Nine years later this statement is still largely true. Perhaps this should not be surprising since an array of species, experimental techniques, and environments are encountered in a study of the literature on this subject.

In spite of the variation existing in published reports on nutrition of conifers, a few trends should be noted from the works reviewed in this paper. Probably the most consistent results have been obtained in Australia, where phosphorus seems to be generally in short supply. Experiments there have demonstrated responses to phosphorus applied alone (Kessel and Stoate 1936, Young 1948, Baur 1959a, Richards 1961b), and others have shown significant responses to phosphorus when applied with nitrogen. Studies by Richards (1961a), Queensland Forest Service (1959), Richards and Bevege (1967), and Keay et al. (1968) have clearly demonstrated a nitrogen-phosphorus interaction.

Research in North America (Canada and the United States) and Europe has produced much more variable data. This may, however, be due to the fact that studies on these continents have included laboratory, greenhouse, and field experiments, whereas Australian work has been

limited to field trials entirely. Most sand culture and soil pot studies have attempted to establish nutrient concentrations or ranges of concentrations producing maximum growth. These data are summarized in Table 1.

Field responses by conifers in the United States have resulted from nitrogen alone (Walker and Youngberg 1962, Hoekstra and Asher 1962, Curlin 1963, Broerman 1967, Switzer and Nelson 1956, Zahner 1959, Maki 1960, Linnartz 1961, Carter and Lyle 1966, Moehring 1966), nitrogen and phosphorus (Linnartz 1961, Watt 1966, Schultz 1968), and complete fertilizer (Allen and Maki 1955, Bateman and Roark 1957, Derr 1957, Roth and Evans 1958, Walker 1962, Malac 1966, Gilmore and Livingston 1958, Brendemuehl 1968, Moehring 1964, Wenger 1953, Texas Forest Service 1960, Ryker and Pfister 1967). The most outstanding responses to phosphorus have been by slash pine in the southeastern United States (Barnes and Ralston 1953, Hughes and Jackson 1962, Pritchett and Swinford 1961, Pritchett and Llewellyn 1966). These have been most pronounced on poorly drained soils extremely low in phosphorus (Pritchett and Llewellyn 1966).

Response to potassium alone apparently has been limited to glacial outwash soils of the northeastern USA (Heiberg et al. 1964).

In Europe, Van Goor (1953) reported an N x P interaction and Tamm (1965) discussed responses to nitrogen on well-drained soils and to phosphorus and potassium on poorly drained sites if nitrogen is present.

Table 1. Summary of laboratory and greenhouse experiments on pine nutrition

Reference	Species	Technique	Optimum concentration					
			N	P	K	Ca	Mg	S
			Parts per million					
Ingestad (1962)	Scotch pine	solution culture	50-150	20	50	40	15	20
Swan (1960)	jack pine	sand culture	140	6.2	--	--	--	--
McGee (1963)	slash pine	sand culture	125-625	125	125-625	--	--	--
Addoms (1937)	loblolly pine	sand culture	130-150	150-200	--	--	--	--
Woodwell (1958)	loblolly pine	sand culture	75-600	40-600	25-300	20-100	25-100	12-100
Fowells and Krauss (1959)	loblolly pine	sand culture	100	1	--	--	--	--
Pharis and Kramer (1964)	loblolly pine	sand culture	50	--	--	--	--	--
Pharis et al. (1964)	loblolly pine	sand culture	75	--	--	--	--	--
Thompson (1965)	loblolly pine	sand culture	95-220	40	--	--	--	--
Bensend (1943)	jack pine	sand culture	200+	--	--	--	--	--
Woodwell (1958)	pond pine	sand culture	25-600	20-600	20-125	20-100	25-100	12-100

METHODOLOGY

This study was conducted in a greenhouse of the School of Forestry and Wildlife Management, Louisiana State University, Baton Rouge. A modification (described below) of the nutrient-solution, sand-culture technique of Gauch and Wadleigh (1943) was employed.

Treatments

Four levels of nitrogen and eight levels of phosphorus were supplied singly and in all combinations, resulting in 32 different treatments. Levels in parts per million were as follows: N (as NH_4NO_3)[2/] -- 0, 100, 200, and 300; and P (as NaH_2PO_4) -- 0, 10, 20, 30, 40, 50, 60, and 70. Nutrient solutions were prepared by diluting portions of concentrated stock solutions in distilled water. Illustrated in Table 2 are the 32 treatments and the volume of stock used in preparing the solution for each treatment. Stock solutions were prepared with reagent grade chemicals.

The levels of the other essential elements not tested were held constant as shown in Table 2. Sources and concentrations of these elements are given in Table 3.

[2/] Initially urea was the source of nitrogen. However very rapid increases in pH were noted early in the experiment and were suspected to be due to urea hydrolysis. Substitution of NH_4NO_3 in the solutions eliminated the problem.

Table 2. Treatments and stock solutions used in preparation of nutrient solutions

Treatment			Volume of stock solutions[1/] per 10 liters of nutrient solution						
No.	N	P	N	P	K	Ca	Mg	Fe	Micro
	- ppm -		- - - - - - - - - - Milliliters - - - - - - - - - -						
1	0	0	-	-	25	25	25	25	25
2	0	10	-	25	25	25	25	25	25
3	0	20	-	50	25	25	25	25	25
4	0	30	-	75	25	25	25	25	25
5	0	40	-	100	25	25	25	25	25
6	0	50	-	125	25	25	25	25	25
7	0	60	-	150	25	25	25	25	25
8	0	70	-	175	25	25	25	25	25
9	100	0	25	-	25	25	25	25	25
10	100	10	25	25	25	25	25	25	25
11	100	20	25	50	25	25	25	25	25
12	100	30	25	75	25	25	25	25	25
13	100	40	25	100	25	25	25	25	25
14	100	50	25	125	25	25	25	25	25
15	100	60	25	150	25	25	25	25	25
16	100	70	25	175	25	25	25	25	25
17	200	0	50	-	25	25	25	25	25
18	200	10	50	25	25	25	25	25	25
19	200	20	50	50	25	25	25	25	25
20	200	30	50	75	25	25	25	25	25
21	200	40	50	100	25	25	25	25	25
22	200	50	50	125	25	25	25	25	25
23	200	60	50	150	25	25	25	25	25
24	200	70	50	175	25	25	25	25	25
25	300	0	75	-	25	25	25	25	25
26	300	10	75	25	25	25	25	25	25
27	300	20	75	50	25	25	25	25	25
28	300	30	75	75	25	25	25	25	25
29	300	40	75	100	25	25	25	25	25
30	300	50	75	125	25	25	25	25	25
31	300	60	75	150	25	25	25	25	25
32	300	70	75	175	25	25	25	25	25

[1/] Concentrations of stock solutions were: N--40,000 ppm, P--4,000 ppm, K--40,000 ppm, Mg--20,000 ppm, Fe--400 ppm, and Micro--20 ppm Mn; 20 ppm B; 20 ppm Zn; 8 ppm Cu; 8 ppm Mo.

Table 3. Concentrations and sources of elements in nutrient solutions

Element	Source	Concentration	
		Source	Element
		- - mmol/l - -	- - ppm - -
N	NH_4NO_3	0 - 10.65	0 - 300
P	$NaH_2PO_4 \cdot H_2O$	0 - 2.25	0 - 70
K	KCl	2.56	100
Ca	$CaCl_2 \cdot 2H_2O$	2.52	100
Mg	$MgSO_4 \cdot 7H_2O$	2.06[1/]	50
S	$MgSO_4 \cdot 7H_2O$		65
Fe	$Na_2Fe(EDTA)$	.09850	1
Mn	$MnCl_2 \cdot H_2O$	.00901	.5
B	H_3BO_3	.00280	.05
Zn	$ZnSO_4 \cdot H_2O$	.00077	.05
Cu	$CuSO_4 \cdot 5H_2O$	.00023	.02
Mo	$H_2MoO_4 \cdot H_2O$	.00019	.02

[1/] The 2.06 mmol $MgSO_4 \cdot 7H_2O$ per liter supplied 50 and 65 ppm of Mg and S, respectively.

In addition to the above treatments, six culture units were set up to test the effect of N and P levels not included in the main study. These "supplementary treatments" included two levels of nitrogen -- 25 and 75 ppm, and four levels of phosphorus -- 0.5, 5, 150, and 200 ppm. In the nitrogen treatments P was held constant at 30 ppm, and in the phosphorus series nitrogen was supplied at 100 ppm.

Experimental Design and Physical Layout

A randomized block design with three replications was utilized, and within each block treatments were randomly assigned in a complete 4 x 8 factorial. The result was a total of 96 culture units arranged as shown in Figure 1. An overall view of the experiment, which occupied the bench space in the north one-half of the greenhouse, is shown in Plate 1. The three replications or blocks were arranged parallel to the length of the greenhouse, which is directionally oriented north and south. The replications were on either side of the greenhouse aisles.

Culture Unit and Irrigation Technique

Seedlings were irrigated with a semi-automatic technique similar to the one developed by Gauch and Wadleigh (1943). The apparatus is diagrammed in Figure 2. Each unit consisted of a 5-gal glazed crock (1)[3/] filled with quartz sand (2) in which the plants were grown. On the floor beneath the crocks with seedlings was a 10-liter glass carboy (7) containing the nutrient solution (8). The solution delivery unit also included a glass check valve (9) to regulate filling and emptying

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[3/] Numbers in parentheses refer to numbers in Figure 2.

Rep C		Rep B		Rep A	
5	15	25	18	24	10
17	2	28	11	22	19
25	24	2	32	26	9
28	3	9	3	15	14
19	9	26	21	13	3
31	6	22	6	21	6
29	22	19	1	8	25
11	4	13	12	31	17
21	16	24	14	4	30
20	7	7	27	29	27
18	12	16	23	23	12
8	26	15	17	11	18
13	30	10	30	32	1
32	1	5	20	5	28
10	14	31	8	2	20
27	23	4	29	7	16

Figure 1. Greenhouse setup. Numbers refer to treatments listed in Table 2.

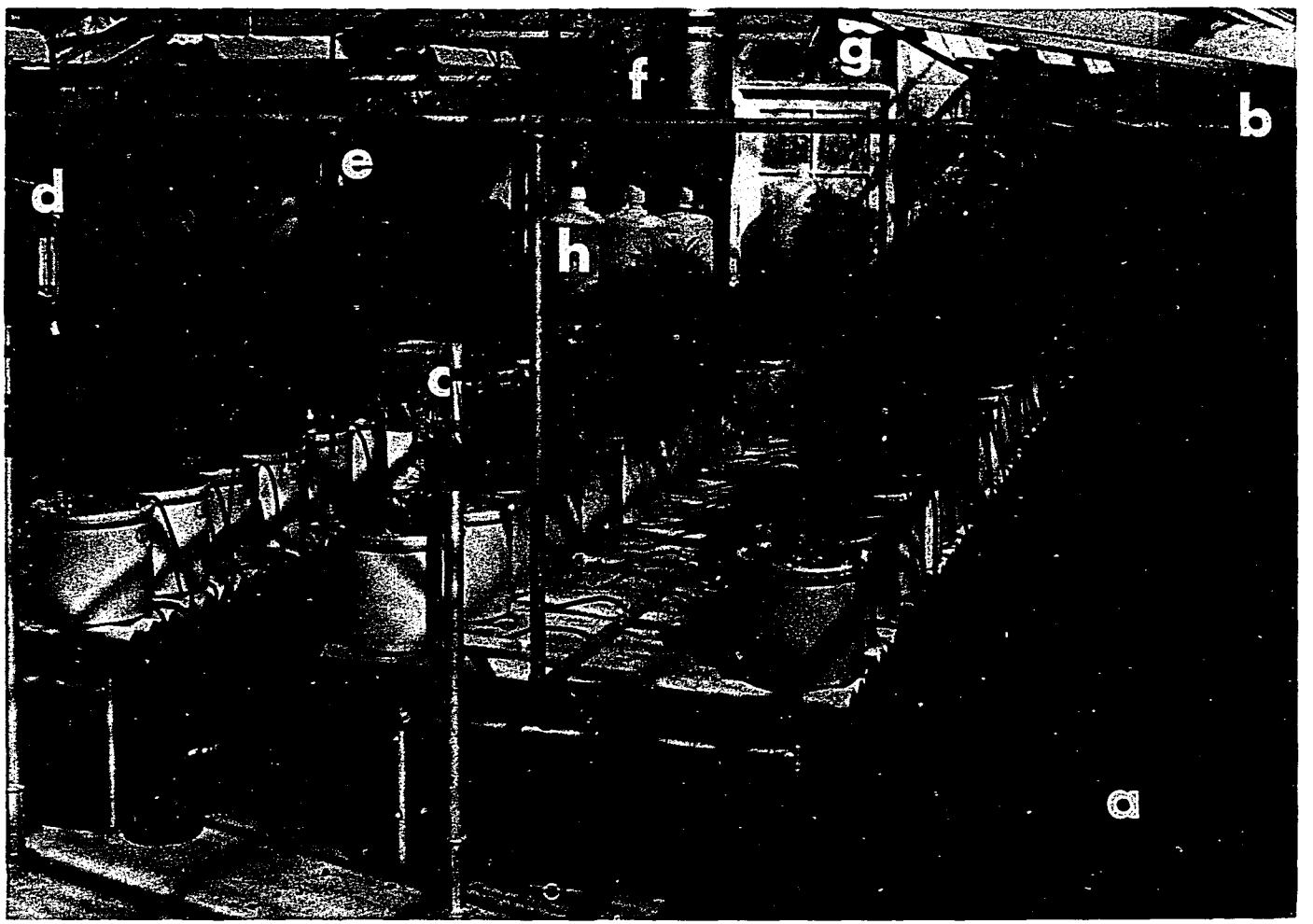

Plate 1. Overall view of experiment, photographed from the south end and slightly to the right. Note the air compressor (a), time switch (b), roof vent control (c), thermometer (d), furnace (e), water still and tank (f), flourescent light units (g), polyethylene storage bottles (h).

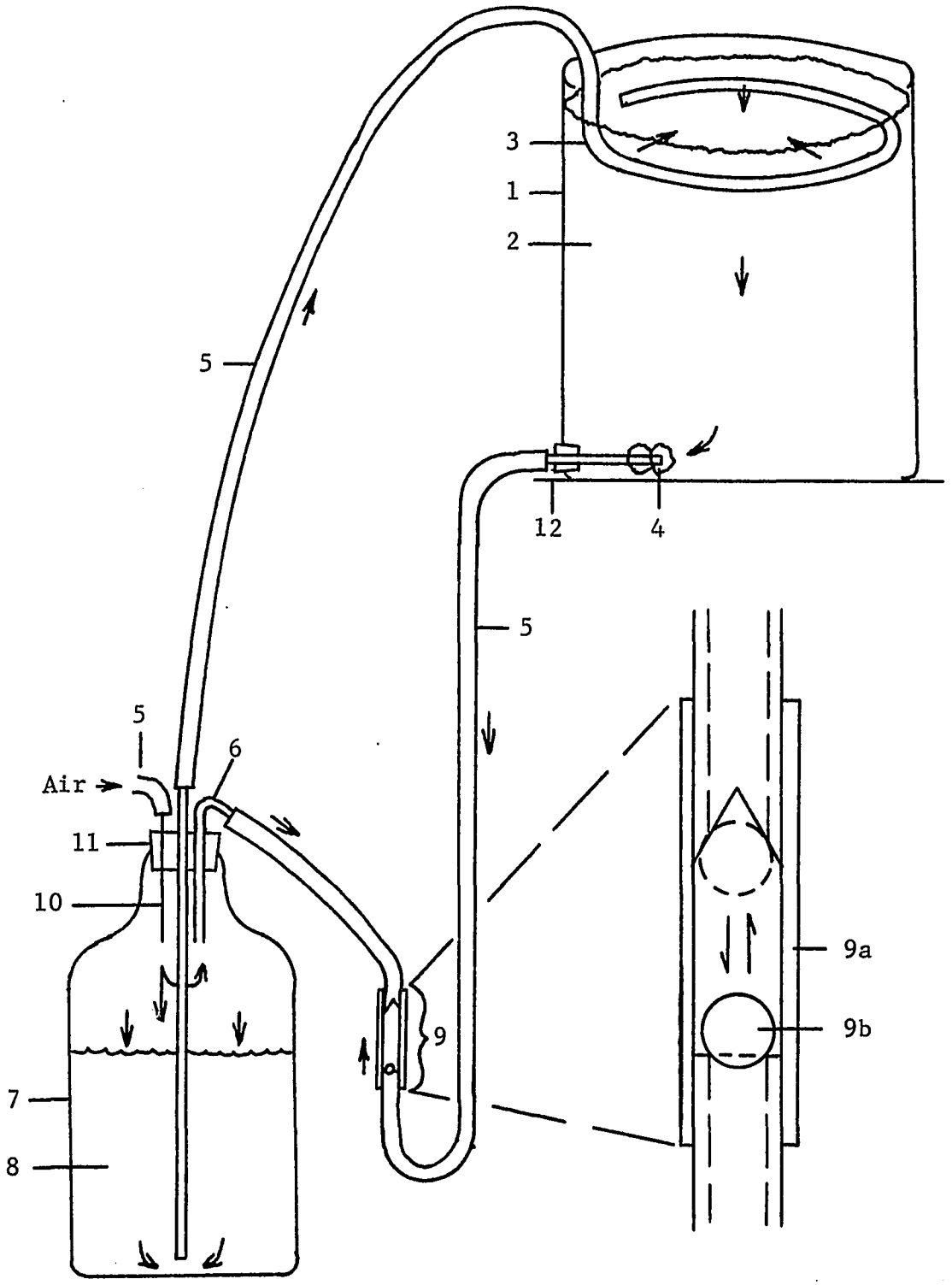

Figure 2. Cross-sectional view of sand-culture apparatus. Numbers are referred to in the text.

of the glazed crock. The carboy and check valve are also shown in Plate 2.

At daily intervals an electrically operating air compressor (Plate 3a) was manually activated forcing air into a network of galvanized iron pipe and rubber tubing (Plate 4). The air passed through a 1/2-mm capillary tube into the space above the nutrient solution in the carboy. As the pressure increased in the carboy, the glass bead (9b) in the check valve (9) was forced downward, closing the valve. This in turn caused pressure to build up in the carboy resulting in solution being forced through the delivery tube to the top of the crock above. At the upper edge of each crock the delivery tube from the carboy was connected to a tubular polyethylene ring which was perforated toward the center and buried 1 inch below the surface of the sand. This permitted an even distribution of the nutrient solution. Approximately 3 liters were delivered to the crock during each flushing cycle.

Preliminary trials indicated that approximately 11 minutes were required to fill the crock to a level slightly above the surface of the sand. A time switch (Plate 3b) was installed and adjusted to break the electrical circuit to the air compressor after 11 minutes. An orfice in the end of the pipe shown in Plate 4 allowed the pressure to be released from the solution carboys. Enough pressure was generated by the compressor to operate the system even with air constantly escaping through the opening. Within 4 to 5 minutes after the compressor had stopped, the pressure in the carboy had decreased sufficiently so that the pressure head of the solution in the crock could lift the glass bead in the check valve from its closed position, allowing the solution to

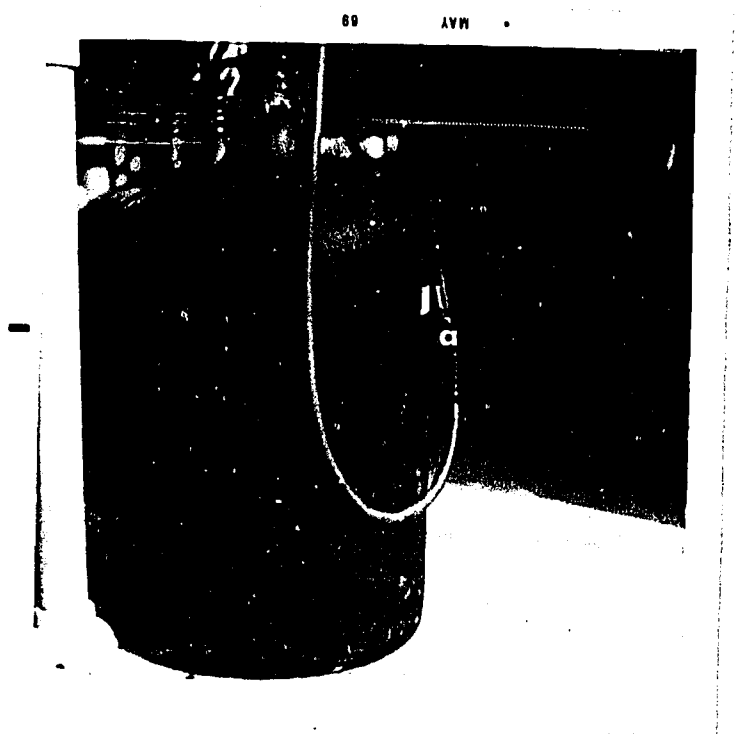

Plate 2. Solution carboy and check valve (a).

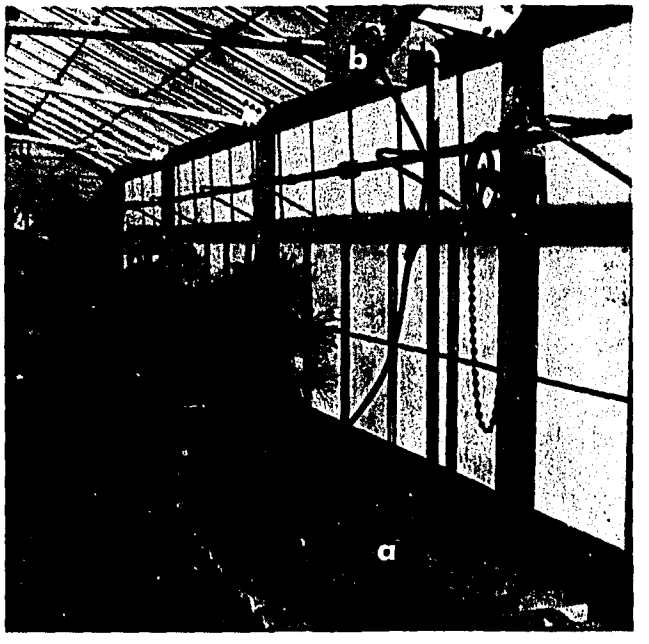

Plate 3. Air compressor (a) and time switch (b).

Plate 4. Part of the air distribution system. Galvanized pipe shown supplied air to one-third of the study.

return to the carboy. A notch in the rubber tube at the upper end of the valve (Figure 2) prevented the glass bead from sealing the opening and halting crock drainage. All glass tubing and fittings exposed to sunlight were covered with black electrical tape to retard the growth of algae, and the glass carboys were painted black.

The following is a list and description of materials used in constructing the culture unit and irrigation apparatus shown in Figure 2. The numbers correspond to the numbers shown in the figure.

1. 5-gallon earthenware glazed crock
2. Quartz sand, 20 mesh
3. Polyethylene distribution tube
4. Glass-wool filter covering drain tube
5. Rubber tubing, 3/8" I.D.
6. Glass tubing, 5 mm O.D.
7. Glass carboy, painted black, 10 liter capacity
8. Nutrient solution
9. Check valve

9a. Glass tube, 7 mm I.D. x 2-1/2 inches long

9b. Glass bead, 5 mm diameter

10. Capillary tube, 1/2 mm I.D., 5 mm O.D. by 2 inches long to serve as a modulator of the air supply and ensure uniform air pressure to all units
11. Rubber stopper, No. 6, with 3 holes
12. Greenhouse bench.

Study Establishment and Culture

During the first week of April 1966, 102 glazed earthenware crocks of 5-gal capacity were filled with pure quartz sand[4/] to a point 1-1/2 inches from the upper edge of the crock. Each crock was then flushed with 0.5N HCl to dissolve and remove minute quantities of minerals. Following acid leaching, the sand was flushed repeatedly with tap water until the reaction of the solution draining from the crock reached pH 6 or higher as measured with pH indicator paper. At this point each crock was flushed twice with distilled water to remove tap water held in the sand.

On April 11, 1966, all the crocks were covered by a single sheet of polyethylene and prepared for fumigation. Edges of the sheet were sealed to the greenhouse floor with soil. Two 1-pound pressurized cans of methyl bromide were then released under the sheet. Twenty-four hours later the sheet was removed, and the crocks were transferred to their assigned places on the benches.

On April 16, 1966, thirteen stratified loblolly pine seeds were evenly distributed on the sand surface in each pot. All seeds were collected from a single parent tree in Livingston Parish, Louisiana. Seeds were pressed into the sand surface but were not completely covered. The sand was moistened twice daily with a fine spray of distilled water until germination was complete.

By April 23, 1966, 90 to 100 percent of the seeds in each crock had germinated. The plants were watered by hand until approximately

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4/ Purchased from Ottawa Silica Co., Ottawa, Illinois.

two weeks following germination. On May 7, 1966, the carboys were filled with distilled water, and for the 20 days following the plants were irrigated with the semi-automatic apparatus previously described. This enabled a check of the system and a determination of the time required to irrigate the crocks.

Nutrient solutions were prepared on May 26, 1966, and on May 27 plants began receiving their assigned treatments. By June 1 green algae had begun to grow on the surface of the sand, particularly in crocks being irrigated with high nutrient levels. Rock gravel that had been washed with 1N HCl and sterilized at 110°C for 48 hours was applied in a 3/4-inch layer to the sand surface. This controlled algae growth effectively since the gravel dried rapidly after solution had drained from the surface. Thompson (1965) also found this to be a satisfactory control for algae.

Reaction of the nutrient solutions was checked initially and at frequent intervals with a glass-electrode pH meter. In some crocks values in the range of pH 7.0 to 8.5 were found after two days' use. Nutrient solutions were discarded every three weeks and replaced with freshly prepared solutions.

Approximately eight days after first treatment many plants had severely chlorotic or necrotic meristematic stem tips. A deficiency of iron resulting from high pH was suspected, and an emulsified $Na_2FeEDTA$ solution (1.15 grams Sequestrene 330[5/] per liter) was applied to the chlorotic tips of some plants. The seedlings, however, failed to regain normal color.

5/ Geigy Chemical Company

Attempts were made to maintain a lower solution pH level by adding 1N HCl, but the acidifying effect of HCl was found to be too temporary to be practicable. It was soon suspected that urea hydrolysis was responsible for the high pH. Ammonium nitrate, therefore, was substituted for urea as the source of nitrogen on June 28, 1966. This problem will be discussed more fully in the next section.

On July 27, 1966, the number of plants per crock was reduced to five. An attempt was made to leave five plants of similar size and uniformly spaced in the crock.

Occasionally during the course of the experiment it was necessary to spray with DDT (1-1/2 teaspoons concentrated material per liter) to control cutworms and aphids. To assure like treatment, DDT was applied to the entire study, even though only a few plants were infested. Also periodically during the summer of 1966 the greenhouse exterior had to be sprayed with a white lead-gasoline mixture to reduce sunlight intensity and resulting excessive heat inside the building. This mixture consisted of approximately 2-3/4 lb. of white lead per 2 gal of gasoline.

On November 11, 1966, fluorescent lights were installed to lengthen the light period by 4 hours and prevent normal autumn dormancy. Automatic time switches turned the lights on at 5:00 P.M. and off at 9:00 P.M. Six light units were suspended 4 feet above the top of the crocks. Each unit was 3 feet long and held three 40-watt Sylvania Gro-Lux bulbs backed by a white enamel reflector. Light intensity at the rim of the crocks averaged 60 foot-candles.

Harvesting

On February 21, 1967, ten months from germination and nine months from first treatment, harvesting was begun by tilting the crock on its side and gently running a stream of tap water around the base of each plant to free it from the sand. Extreme care was taken to minimize secondary root breakage and loss. As soon as all sand was washed from the crock and plant roots, the plants were removed and given a final rinsing in distilled water. Plants from a single crock were immediately placed in a large plastic bag which was then tightly closed with a rubber band. Bags were transported to the Louisiana State University Horticulture Department where they were stored in a "walk-in" refrigerator at 2°C. The harvesting operation was completed on February 24, 1967.

Measurements

With the assistance of several student workers, the green plants were removed from cold storage and measured. The following is a list of the variables measured with a brief description of procedures involved:

1. Root volume, measured to the nearest 0.1 cc by water displacement. Roots were blotted free of water before being immersed in water for this measurement.
2. Taproot length, measured to the nearest 0.1 cm
3. Total length, measured to the nearest 0.1 cm
4. Length of each internode, measured to the nearest 0.1 cm. The first internode was actually the hypocotyl measured from the root collar to the primary needle scars.

5. Shoot length, measured to the nearest 0.1 cm
6. Needle length, two mature needles picked randomly from each plant and measured to the nearest 0.1 cm
7. Number of branches per whorl
8. Total number of branches
9. Number of primary lateral roots per 5-cm segment of the taproot
10. Total number of primary lateral roots.

After the above measurements were made on the green plants, each was dissected into the following components: mature needles, immature needles, mature stem, immature stem, branches, taproot, and lateral roots. Judgment of maturity of stem and needle tissue was purely subjective. In the case of needles, the distinction was based on color, size, and location on the plant. Mature needles were a dark green, fully developed, and located on the basal region of the main stem and/or branches. The portion of the stem supporting immature needles was usually designated as immature stem. Though subjective, these separations are believed to be reasonably accurate.

These various components were placed in small paper bags and dried in a draft oven at 70°C for 48 hours. The following variables were then obtained (measured to the nearest 0.01 gram):

1. Weight of mature needles
2. Weight of immature needles
3. Weight of mature stem
4. Weight of immature stem
5. Weight of branches
6. Total shoot weight

7. Weight of taproot
8. Weight of lateral roots found on each 5-cm segment of the taproot
9. Total weight of root system
10. Root/shoot ratio (weight)
11. Ratio of mass of immature needle tissue to mass of mature needles, designated "maturity index."

All measurements were made on each of the five plants per crock. Raw data were averaged by computer, and treatment means were used in the statistical analyses.

It should be noted that some of the above variables could not be measured for the very small plants. As an example, plants receiving no phosphorus did not grow enough to make possible a distinction between mature and immature needles and stems.

Chemical Analyses

Mature needles, immature needles, mature stems, immature stems and branches, taproots, and lateral roots composited from the five plants per crock were ground separately in a Wiley mill to pass a 40-mesh screen. Components were analyzed for nitrogen, phosphorus, calcium, potassium, and magnesium by using the facilities of the Feed and Fertilizer Laboratory at Louisiana State University. Because of the shortage of tissue from some very small plants, a composite of the entire plant had to be analyzed rather than each component being analyzed separately. The improved boric acid Kjeldahl method (Horwitz et al. 1960) was used in determining the nitrogen content of plant tissues. Phosphorus, potassium, calcium, and magnesium were

extracted by methods presented in Jackson (1958). Phosphorus was analyzed by absorption spectrophotometry with a Bausch and Lomb colorimeter, potassium by flame emission spectrophotometry on the Beckman DU, calcium and magnesium by atomic absorption spectrophotometry with a Jerrell-Ash atomic absorption analyzer. Details of the chemical analyses are given in Appendix A.

Statistical Analysis

All variables studied were tested statistically with the IBM-1620 computer and programs of the Louisiana State University Computer Research Center. Sources of variation and degrees of freedom were partitioned as follows:

Source of variation	Degrees of freedom
Blocks	2
Nitrogen	3
0 N vs 100-300 N	1
100 N vs 200-300 N	1
200 N vs 300 N	1
Phosphorus	7
0 P vs 10-70 P	1
10 P vs 20-70 P	1
10-20 P vs 30-70 P	1
10-30 P vs 40-70 P	1
10-40 P vs 50-70 P	1
10-50 P vs 60-70 P	1
10-60 P vs 70 P	1
Nitrogen x Phosphorus	21
(0 N vs 100-300 N)(0 P vs 10-70 P)	1
(0 N vs 100-300 N)(10 P vs 20-70 P)	1
(0 N vs 100-300 N)(10-20 P vs 30-70 P)	1
(0 N vs 100-300 N)(10-30 P vs 40-70 P)	1
(0 N vs 100-300 N)(10-40 P vs 50-70 P)	1
(0 N vs 100-300 N)(10-50 P vs 60-70 P)	1
(0 N vs 100-300 N)(10-60 P vs 70 P)	1

Source of variation	Degrees of freedom
(100 N vs 200-300 N)(0 P vs 10-70 P)	1
(100 N vs 200-300 N)(10 P vs 20-70 P)	1
(100 N vs 200-300 N)(10-20 P vs 30-70 P)	1
(100 N vs 200-300 N)(10-30 P vs 40-70 P)	1
(100 N vs 200-300 N)(10-40 P vs 50-70 P)	1
(100 N vs 200-300 N)(10-50 P vs 60-70 P)	1
(100 N vs 200-300 N)(10-60 P vs 70 P)	1
(200 N vs 300 N)(0 P vs 10-70 P)	1
(200 N vs 300 N)(10 P vs 20-70 P)	1
(200 N vs 300 N)(10-20 P vs 30-70 P)	1
(200 N vs 300 N)(10-30 P vs 40-70 P)	1
(200 N vs 300 N)(10-40 P vs 50-70 P)	1
(200 N vs 300 N)(10-50 P vs 60-70 P)	1
(200 N vs 300 N)(10-60 P vs 70 P)	1
Error	62
Total	95

Computations were made beginning with the first orthogonal comparison in each of the above sets. However, no further comparisons were made if all except an insignificant portion of the sums of squares were accounted for by the comparisons already made.

RESULTS AND DISCUSSION

Loblolly pine seedlings displayed a marked response to the levels and combinations of levels of nitrogen and phosphorus supplied in nutrient solutions. These responses were evident in shoot growth and development, root growth and morphology, and nutrient uptake. Before these results are considered, however, the problem of shoot chlorosis encountered early in the study should be discussed.

As mentioned in the previous chapter, a severe chlorosis of the meristematic tips of most the seedlings developed within one week after treatment was begun. The upper one-half of the seedlings was characterized by a pale yellow, almost white coloration while the basal regions appeared pale green (Plate 5). The most severely affected plants suffered tip necrosis, typical of the condition of the seedling on the right in Plate 5. The symptoms were characteristic of deficiencies of either calcium or iron. Analysis of a few whole plants failed to show appreciably lower iron and calcium contents than healthy plants. However, had only chlorotic tissue been analyzed, the results might have been different.

A check of solution reactions revealed pH values in the range of pH 6.7 to 7.9 for solutions containing nitrogen. Some values ran as high as 8.5. Median pH values of the three replications of each treatment were as follows:

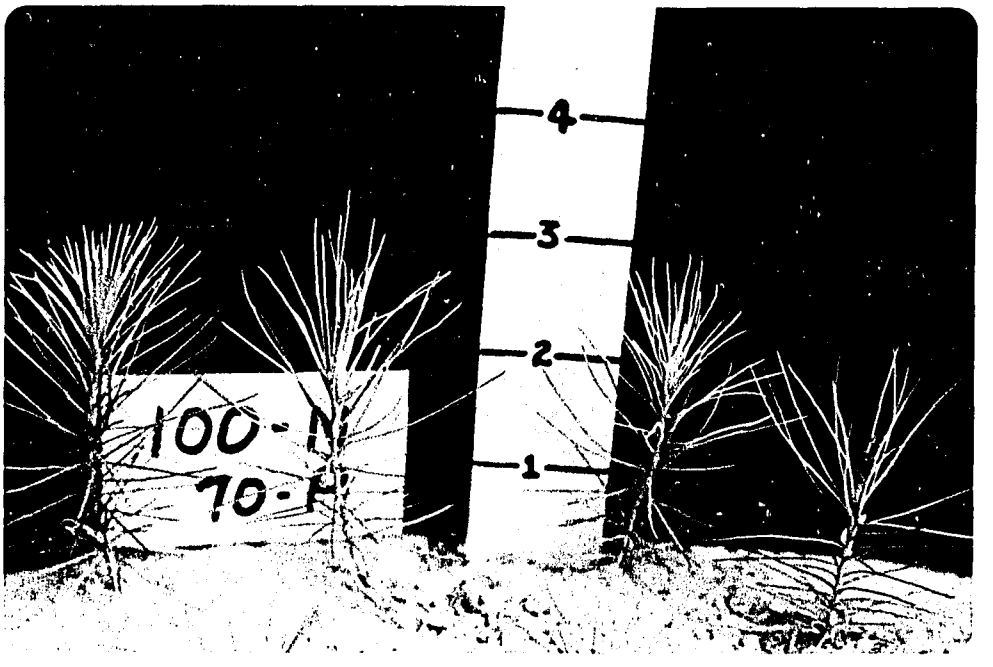


Plate 5. A typical case of severe chlorosis photographed in July approximately one month after initial treatment. Note the necrotic tip of the plant at right.

Levels of N	P (ppm)	Reaction (pH)	Levels of N	P (ppm)	Reaction (pH)
0	0	5.2	200	0	7.7
0	10	5.4	200	10	8.0
0	20	4.0	200	20	6.1
0	30	4.0	200	30	7.6
0	40	5.5	200	40	7.6
0	50	4.2	200	50	7.4
0	60	5.2	200	60	7.5
0	70	5.4	200	70	7.0
100	0	7.4	300	0	7.6
100	10	7.8	300	10	7.8
100	20	7.5	300	20	8.0
100	30	7.6	300	30	7.8
100	40	7.6	300	40	7.5
100	50	7.1	300	50	6.6
100	60	7.2	300	60	7.3
100	70	7.0	300	70	7.7

The chlorotic condition was, therefore, thought to be induced by a deficiency of iron and possibly calcium. Either of these elements, according to Hewitt (1966), can become unavailable in nutrient solutions with reactions in excess of pH 7.0.

The author soon suspected that high pH levels were related to nitrogen in the nutrient solutions. The most obvious evidence for this supposition was the lack of chlorosis in plants receiving no nitrogen. Secondly, the reaction of nitrogen-free solutions remained below pH 6.0. As stated previously, urea was being used as the source of nitrogen at the time this problem developed. According to Alexander (1961), urease-producing microorganisms effect the hydrolysis of urea to

ammonium carbamate in soils. This consequently results in an increase in pH. Since the buffering capacity of pure sand is virtually nil, the effect would be greater in sand than in soil. Hydrolysis of urea is therefore thought to be responsible for the increase in pH and resulting chlorosis. This hypothesis is supported by the fact that after the nitrogen source was changed to ammonium nitrate, pH of the solutions remained in the range of 5.5 to 6.5, and chlorotic plants regained normal coloration and resumed growth (Plate 6).

Growth resumption was much slower by those plants having terminal necrosis. In these cases a lateral bud became active and assumed the role of leader. The result was considerable variation in growth and plant heights early in the experiment. By the time the study was terminated, however, these differences were not obvious, although some of the variation in the data may be partially due to the early variation in growth.

Influence of N and P on Shoot Growth and Development

Virtually every measure of shoot growth and development was significantly affected by nutrient supply. Analyses of variance tests revealed, in most instances, significant interactions as well as significance of the main effects of nitrogen and phosphorus.

Total shoot elongation was influenced by nitrogen and phosphorus supply (Plates 7 and 8 and Figure 3). Maximum shoot elongation occurred at 100 ppm N combined with 50 and 60 ppm P. However, orthogonal tests (Appendix B, Table 14) indicated no significant difference between 10 ppm P and the higher rates of this element. The difference between 0 and 10 ppm P was highly significant, however. Thompson (1965) found

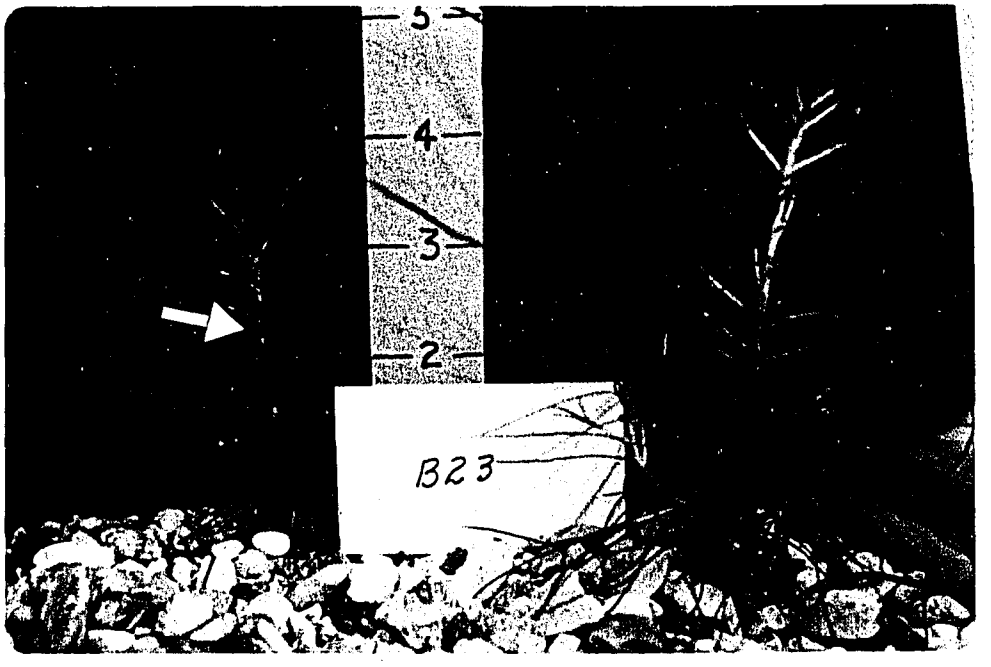


Plate 6. Formerly chlorotic plants photographed approximately two weeks after changing nitrogen source. Arrow indicates base of new growth.

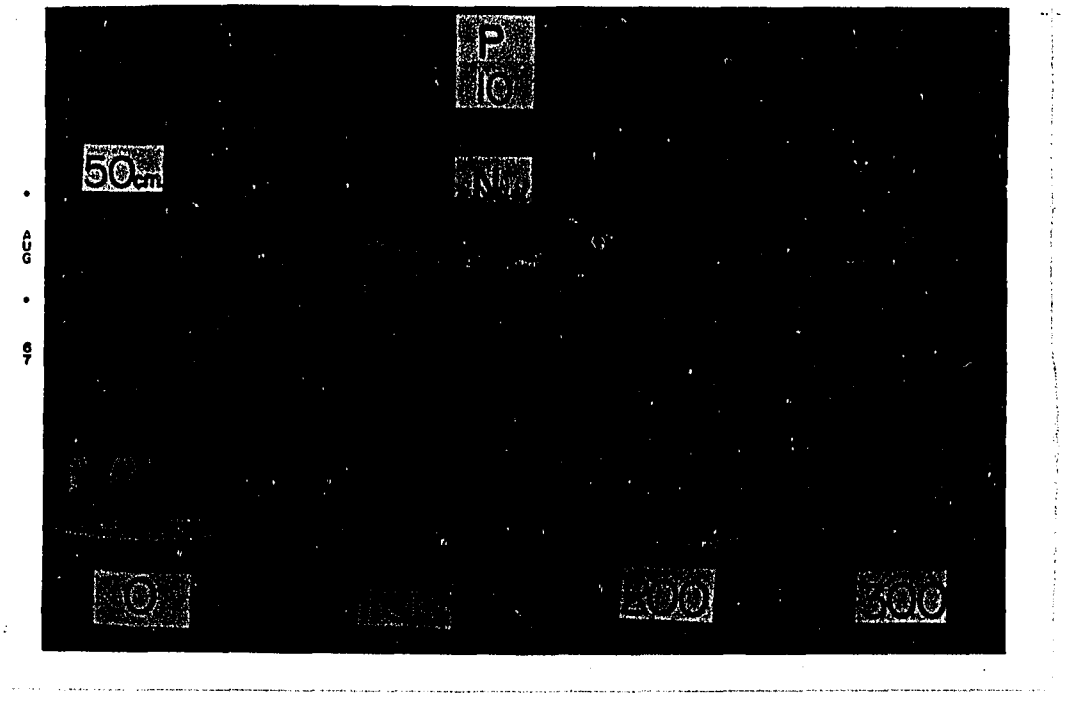


Plate 7. Response in shoot growth with increasing increments of nitrogen at 10 ppm of P.

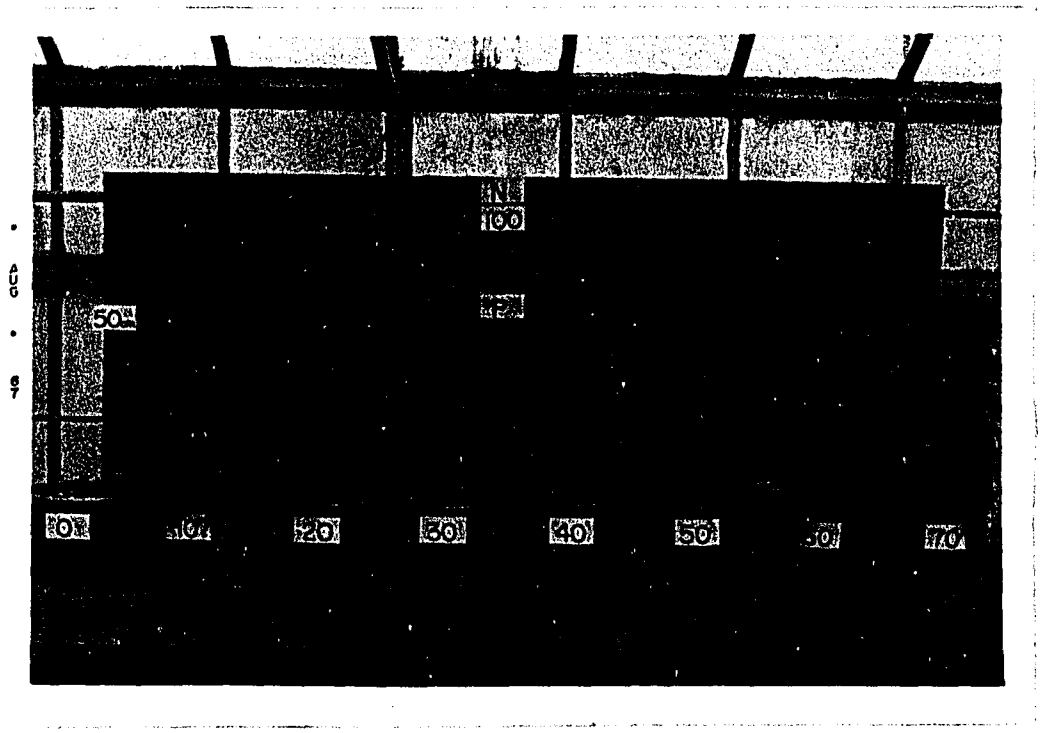


Plate 8. Response in shoot growth with increasing increments of phosphorus at 100 ppm N.

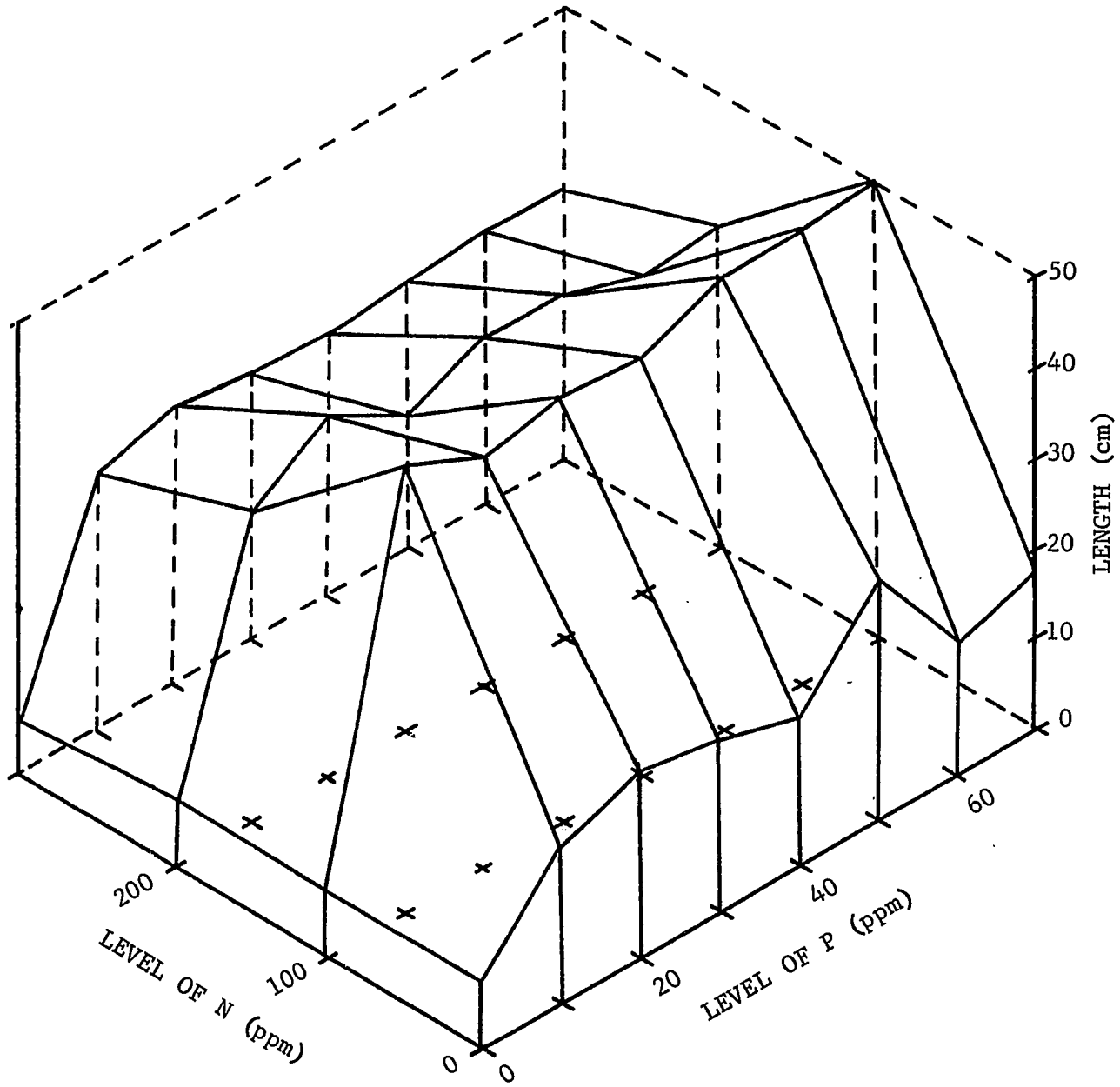


Figure 3. Shoot length as affected by nitrogen and phosphorus supply.

total shoot elongation to be independent of variations in nutrient supply but elongation of the second internode to be significantly influenced by nitrogen, reaching a maximum at 95 ppm. In the present study both total shoot length (Plate 7) and elongation of the second internode (Table 4) reached a maximum at 100 ppm nitrogen. Orthogonal comparisons clearly indicate 100 ppm to be the optimum level of applied nitrogen. Increasing the nitrogen concentration to 200 and 300 ppm resulted in significantly less growth. Statistical tests also revealed 300 ppm N to further reduce shoot growth below that of the 200 ppm rate of this element (Figure 3). However, the differences in growth between 200 and 300 ppm N were not as great as between 100 and 200 ppm N. The results of the present study agree with those of Fowells and Krauss (1959) who found maximum shoot growth between 25 and 100 ppm N. Working with slash pine, McGee (1963) found 125 ppm N to be optimum, with the response curve decreasing beyond this point.

Responses to phosphorus (Plate 8) and the effects of the nitrogen-phosphorus interaction (Figure 3) are somewhat more obscure than the nitrogen response. As mentioned above, maximum shoot elongation occurred at 50 and 60 ppm phosphorus when supplied with the optimum level of nitrogen, 100 ppm. Shoot-growth responses at intermediate levels of P are quite variable. According to the statistical analysis (Appendix B, Table 14) for shoot length, 87 percent of the variation resulting from the different levels of phosphorus was explained by the difference in shoot growth at 10 ppm P and the zero level of this element. This seems to indicate that the variation between 10 ppm P and 70 ppm P was due to chance, with no real difference

Table 4. Average[1/] effect of nitrogen and phosphorus on total shoot length, internode lengths, and total shoot weight

Levels of		Total shoot	Length of successive internodes						Total shoot
N	P	length	1	2	3	4	5	6	weight
- ppm -		- - - - - - - - - - Centimeters - - - - - - - - -							Grams
0	0	7.4	4.00	3.45	0	0	0	0	0.18
0	10	17.1	4.16	5.58	6.14	1.23	0	0	.98
0	20	21.4	4.03	8.26	8.60	.55	0	0	1.69
0	30	18.7	6.89	6.13	5.64	0	0	0	.77
0	40	15.8	6.02	6.33	3.47	0	0	0	.71
0	50	26.7	4.69	10.71	7.88	3.49	0	0	3.06
0	60	13.9	3.68	4.65	5.59	0	0	0	.67
0	70	17.5	4.32	6.64	6.43	.08	0	0	.69
100	0	7.4	4.20	3.12	.08	0	0	0	.15
100	10	48.6	3.92	15.32	11.67	13.41	4.33	0	19.33
100	20	45.4	4.24	13.70	10.55	15.43	1.47	0	17.63
100	30	47.2	3.35	15.04	8.86	12.72	7.19	0	21.11
100	40	45.9	3.81	14.83	9.56	12.84	4.88	0	20.92
100	50	50.4	3.82	20.05	10.58	10.17	5.73	0	23.48
100	60	50.5	4.85	11.94	11.84	14.15	7.31	1.39	23.60
100	70	47.8	3.51	14.03	10.14	16.37	3.51	0	22.36
200	0	7.1	3.94	3.13	0	0	0	0	.19
200	10	34.5	3.29	12.21	15.11	3.45	.4	0	8.24
200	20	38.8	3.90	9.06	8.30	8.19	8.27	1.11	14.86
200	30	34.4	3.69	9.72	12.99	7.20	8.20	0	12.35
200	40	38.3	3.50	9.81	14.48	9.61	.88	0	11.88
200	50	38.1	4.42	12.17	10.31	10.10	1.09	0	13.06
200	60	34.9	4.29	10.28	11.98	8.09	.25	0	11.31
200	70	36.1	4.18	11.29	11.57	7.62	1.46	0	12.95

Table 4. Continued

Levels of		Total shoot	Length of successive internodes						Total shoot
N	P	length	1	2	3	4	5	6	weight
- ppm -		- - - - - - - - - - Centimeters - - - - - - - - -							Grams
300	0	6.5	3.67	27.87	0	0	0	0	12.33
300	10	28.5	3.85	11.59	11.49	1.52	0	0	6.40
300	20	32.5	4.47	13.71	9.73	4.00	.56	0	7.81
300	30	28.5	4.42	9.22	10.79	3.53	.55	0	7.49
300	40	28.0	4.70	14.02	6.19	3.07	0	0	8.11
300	50	29.3	4.32	8.89	10.88	3.53	1.41	.24	9.93
300	60	30.8	3.88	10.30	11.83	4.13	.65	0	8.86
300	70	29.8	3.77	9.12	8.98	7.47	.44	0	7.99
	$\bar{X}$	29.93	4.18	9.91	8.46	5.69	1.60	.09	9.72
Treatment effect[2/]									
	N	**	*	**	**	**	**	ns	**
	P	**	ns	**	**	**	ns	ns	**
	NP	*	ns	ns	ns	**	*	ns	**

1/ Each value represents the mean of three replications.

2/ *; **; ns = significant at the 5-percent level of probability; significant at the 1-percent level of probability; and nonsignificant, respectively.

between these points on the response surface. These results are similar to those of Fowells and Krauss (1959). They found that loblolly and Virginia pine grew well at low levels of phosphorus; in fact, 1 ppm P was superior or equal to the higher levels of this element. The highest level of P used, 400 ppm, significantly reduced seedling heights from those at the 5 and 25 ppm rates. However, Thompson (1965) found 10 ppm of phosphorus to produce significantly less shoot mass than 40 ppm P. Beyond 40 ppm the phosphorus response curve decreased sharply, reaching a minimum at 160 ppm, the highest level of applied phosphorus. In Thompson's study, however, the different rates of P were applied at a constant level of nitrogen, whereas in the present study both elements were varied simultaneously.

The analysis of variance for shoot length revealed a highly significant N x P interaction. When tested by orthogonal comparisons (Appendix B, Table 14), however, most of the significance was due to interaction involving the zero rates of both elements. This indicates that had zero levels been excluded from the study, there would have been no significant interaction effect on shoot length. Therefore, phosphorus concentrations of 10 ppm and greater produced shoot growth responses which were independent of the level of applied nitrogen. The P response curves, then, are not significantly different in shape regardless of the rate of nitrogen if at least 100 ppm N is present in the growth medium. Likewise, at nitrogen concentrations of 100 ppm and greater the shoot growth response to nitrogen is independent of the levels of phosphorus, provided P is given at a minimum concentration of 10 ppm. These results are in fair agreement with those of McGee (1963)

who tested various combinations of N, P, and K. He measured a significant shoot-elongation response to these elements but found no interactions related to shoot growth.

In terms of oven-dry weight of the shoot, the responses were almost identical to those for shoot length (Figure 4). Maximum shoot material was found to be produced at 100 ppm N with significant decreases at the two higher rates of N. Again 50 and 60 ppm P when combined with 100 ppm N produced the greatest growth response. However, statistical tests (Appendix B, Table 15) revealed no significant variation in phosphorus response curves beyond the 10 ppm rate. In fact, 91 percent of the variation in phosphorus response was accounted for in the difference between 0 and 10 ppm P. Even though the N x P interaction was significant, all the significant variation was accounted for by the orthogonal comparison of 0 versus all other rates. Therefore, no meaningful interaction exists beyond the minimum applied levels of each element.

Shoot weight data in the present study agree to some extent with those of Thompson (1965) who found maximum shoot weights at 40 ppm P. However, he demonstrated a sharp peak in the P response curve, whereas in the present study 10 ppm P was as effective as the higher levels including 40 ppm. Thompson (1965), however, found shoot weight independent of variation in N supply. The shoot weight results of Fowells and Krauss (1959) and McGee (1963) were basically the same as previously mentioned for shoot length. Both those studies, as well as the present one, demonstrated approximately 100 ppm N to produce greatest shoot weight. Both showed fairly wide phosphorus ranges to

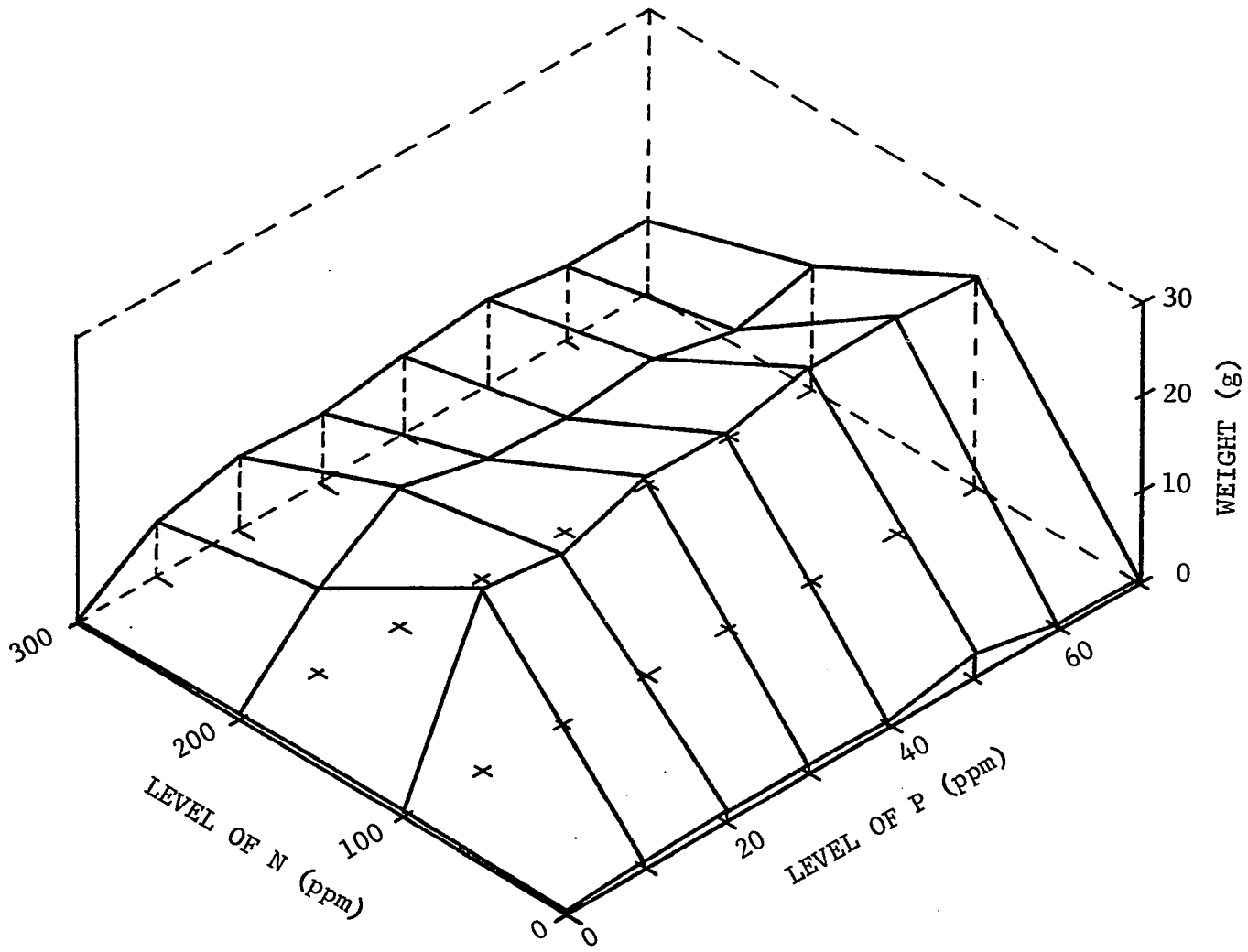


Figure 4. Shoot weight as affected by nitrogen and phosphorus supply.

produce maximum dry weight. However, McGee (1963) did not measure a decrease at the highest rate of phosphorus, 125 ppm, whereas Fowells and Krauss (1959) observed a decrease in shoot weight between 100 and 200 ppm P. These workers, however, found 1 ppm P to be as effective as 100 ppm P.

Since the major portion of photosythetic activity occurs in the leaves, it seems only logical to consider some needle weight and length relationships. Both mature needle weight (Figure 5) and length (Table 5) were highly influenced by nitrogen variation. Both reached maximum values at 100 ppm N and were significantly decreased by more concentrated N levels. However, no statistical difference (Appendix B, Table 16) was found between 200 and 300 N for the length variable. Mature needle weight was further reduced by increasing the nitrogen rate from 200 to 300 ppm. Fowells and Krauss (1959) also found that the weight of needles was greater in the 100 ppm N treatment than in the lower or higher nitrogen treatments. However, Thompson (1965) found no significant relationship between mature needle weights and nitrogen supply. He did, however, find a significant relationship between phosphorus supply and mature needle weight, with a significant difference between 10 and 40 ppm P. In the present study, phosphorus applied at 10 ppm was as effective as at the higher rates. Most (88 percent) of the variation in phosphorus response was accounted for by the difference between zero and the other rates of this element. The test for N x P interaction for mature needle weight again revealed most of the variation to be due to the inclusion of zero rates of N and P. However, sufficient variation remained after this comparison to lead

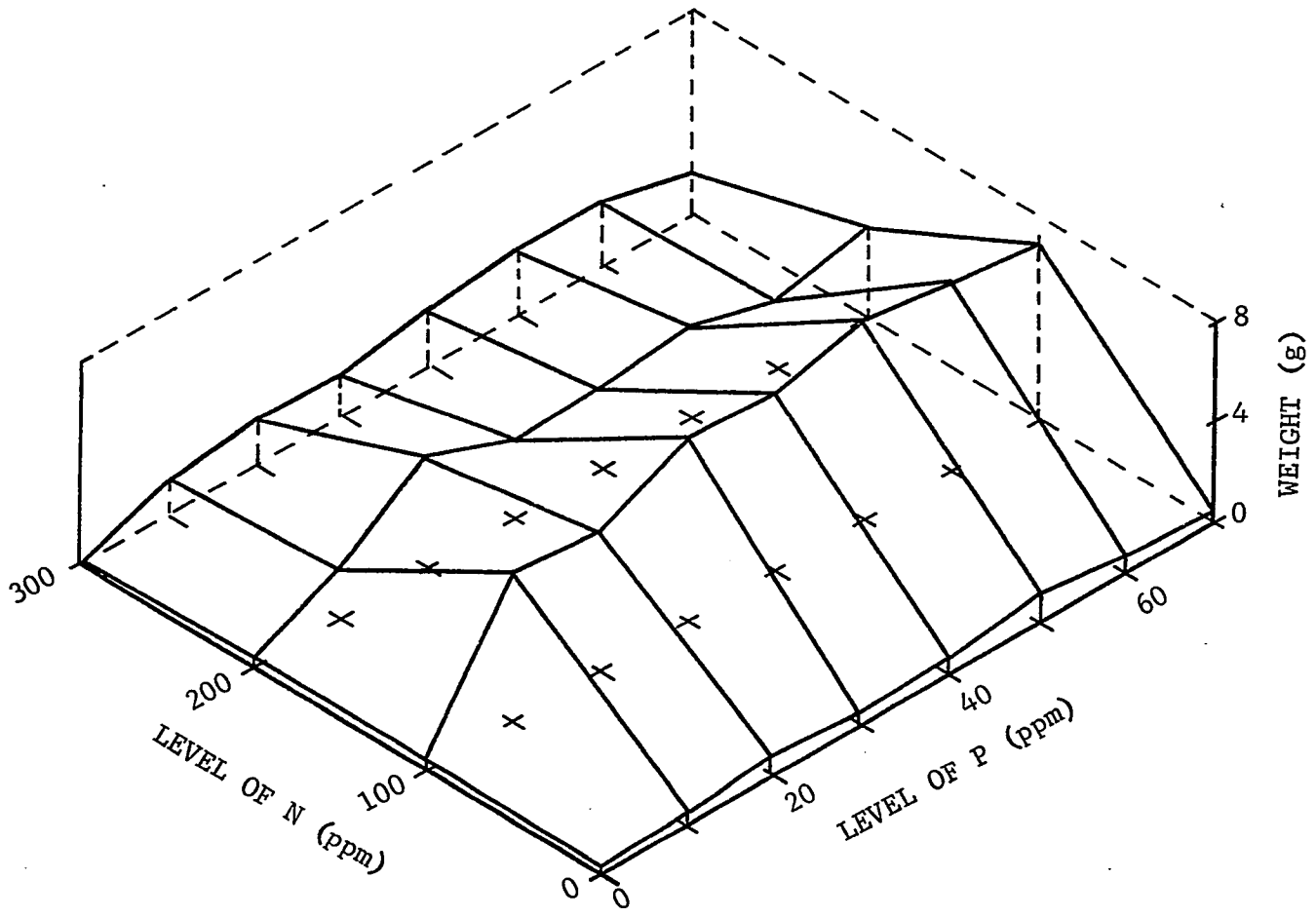


Figure 5. Weight of mature needles as affected by nitrogen and phosphorus supply.

Table 5. Average[1/] effect of nitrogen and phosphorus on individual shoot weight variables, needle length, and maturity index

Levels of N	Levels of P	Mature needle weight	Mature needle length	Immature needle weight	Mature stem weight	Immature stem weight	Branch weight	Maturity index[2/]
- ppm -		Grams	- cm -	- - - - - - - - Grams - - - - - - - -				
0	0	0.12	2.6	0.01	0.04	0.01	0	0.12
0	10	.45	8.9	.13	.28	.10	.030	.29
0	20	.71	10.5	.28	.49	.14	.060	.39
0	30	.39	9.6	.11	.19	.08	.004	.27
0	40	.41	9.2	.06	.18	.06	.002	.13
0	50	1.33	12.5	.33	.11	.16	.177	.25
0	60	.36	9.4	.10	.15	.06	0	.27
0	70	.38	8.7	.05	.18	.08	.009	.14
100	0	.10	2.7	0	.04	0	0	0
100	10	5.92	19.6	6.09	5.37	.55	1.404	1.03
100	20	5.42	20.3	6.10	4.06	.71	1.331	1.12
100	30	7.61	20.0	5.76	5.78	.60	1.362	.75
100	40	7.10	17.7	6.60	4.99	.61	1.621	.93
100	50	8.08	20.1	6.88	6.03	.84	1.649	.85
100	60	7.52	20.8	8.05	5.47	.86	1.700	1.08
100	70	6.93	20.5	7.37	5.61	.71	1.740	1.06
200	0	.12	1.2	0	.06	0	0	0
200	10	1.97	18.6	3.63	1.55	.68	.399	1.85
200	20	4.65	17.1	5.17	3.21	.62	1.206	1.12
200	30	3.19	19.5	5.42	2.46	.48	.799	1.72
200	40	3.20	18.5	4.71	2.46	.69	.816	1.47
200	50	3.88	18.2	4.86	2.91	.57	.839	1.27
200	60	2.64	18.7	5.24	2.09	.58	.767	2.00
200	70	3.71	18.1	5.25	2.55	.54	.921	1.41

Table 5. Continued

Levels of N	Levels of P	Mature needle weight	Mature needle length	Immature needle weight	Mature stem weight	Immature stem weight	Branch weight	Maturity index[2/]
- ppm -		Grams	- cm -	- - - - - - - - Grams - - - - - - - -				
300	0	.09	4.2	0	.03	0	0	0
300	10	1.47	17.4	2.96	1.16	.51	.303	2.04
300	20	1.98	18.3	3.47	1.56	.42	.388	1.75
300	30	1.87	18.2	3.50	1.23	.50	.388	1.87
300	40	2.34	15.8	3.28	1.62	.38	.487	1.41
300	50	2.63	17.8	4.48	1.64	.58	.603	1.72
300	60	2.61	16.7	3.53	1.67	.48	.571	1.35
300	70	1.93	18.4	3.72	1.44	.47	.419	1.96
	$\bar{X}$	2.85	14.56	3.35	2.11	.41	.620	1.59
Treatment effect[3/]								
	N	**	**	**	**	**	**	-
	P	**	**	**	**	**	**	-
	NP	*	**	**	*	ns	**	-

[1/] Each value represents the mean of three replications.

[2/] Weight of immature needles/weight of mature needles. As number increases tissue maturity decreases.

[3/] *; **; ns = significant at the 5-percent level of probability; significant at the 1-percent level of probability; and nonsignificant, respectively.

the author to believe that some interaction exists beyond the minimum applied rates. This interaction effect is very likely due to the variation in the P response with different levels of N. As shown in Table 5 and Figure 5 the maximum P response occurred at 50 ppm at both 100 and 300 ppm N. However, the maximum P response at 200 ppm N was obtained from 20 ppm P with considerable variation between 20 and 70 ppm P.

Needle length appeared to be strongly dependent on nitrogen supply (Table 5). Phosphorus had a highly significant effect on needle length, but 99 percent of the phosphorus response was found to be due to the difference between 0 and 10 ppm P (Appendix B, Table 17). For this variable 10 ppm P was fully as effective as 70 ppm, the highest rate tested. As was true of needle weight, most of the interaction significance resulted from the inclusion of zero levels of N and P. However, orthogonal comparisons indicated significance in the response beyond 10 ppm P. This indicates that the response to phosphorus varied significantly according to the level of nitrogen. A close examination of needle-length data in Table 5 will reveal shorter needles at 40 ppm P when combined with 100 and 300 N than when this level of P is combined with 0 and 200 ppm N. The considerably longer needles at 0 N-50 ppm P relative to needle length at other levels of P and 0 N may also help account for the significant N x P interaction.

The results of this study seem to support the classical concept that plant maturity is a function of nitrogen supply. The ratio of oven-dry mass of immature needle tissue to oven-dry mass of mature needle tissue was designated "maturity index." These data are presented

in Table 5, and as the magnitude of the numbers increases the proportion of immature to mature tissue increases, thus indicating a decrease in the state of maturity. Considerable variation exists with levels of phosphorus within any given level of nitrogen. However, plants receiving no nitrogen were found to have an average maturity index of 0.232. This compares to the following values for the various levels of applied N: 100 ppm, 0.852; 200 ppm, 1.350; 300 ppm, 1.512. These data, although not subjected to statistical tests, indicate that increasing levels of nitrogen tend to produce more succulent tissue and delayed maturity. According to Meyer, Anderson, and Bohning (1960), if the supply of nitrogen is abundant relative to the quantity of carbohydrate foods, a large quantity of protoplasm will be produced relative to the amount of cell-wall tissue synthesized. The resulting cells are thin-walled and contain an abundance of protoplasm. Tissues composed of such cells are usually soft and succulent.

As is evident in Table 6, number of branches were influenced by variations in N and P. Since 100 ppm N produced greatest shoot growth, one would suspect that the maximum number of branches would develop at this level of nitrogen. Orthogonal comparisons (Appendix B, Table 18) verified this supposition. Phosphorus seemed to have little effect on branching at levels of 10 ppm and greater. The treatment yielding maximum shoot development -- 100 ppm N + 10 ppm P -- resulted in the maximum branching at the second and third internodes (Table 6).

Influence of N and P on Root Growth and Morphology

Nitrogen and phosphorus significantly affected most measures of root development. However, relatively few interactions were

Table 6. Average[1/] effect of nitrogen and phosphorus on number of branches

Levels of		Branches/whorl					Total
N	P	1	2	3	4	5	branches
- ppm -		- - - - - - - - - - - - Number - - - - - - - - - - - -					
0	0	0	0	0	0	0	0
0	10	.1	.6	.2	0	0	.9
0	20	.9	1.1	.3	0	0	2.3
0	30	0	.2	0	0	0	.2
0	40	0	0	0	0	0	0
0	50	1.0	1.0	.8	0	0	2.9
0	60	0	0	0	0	0	0
0	70	0	.5	0	0	0	.5
100	0	0	0	0	0	0	0
100	10	2.1	2.5	3.7	1.5	0	9.8
100	20	3.0	2.3	3.5	1.1	.2	10.1
100	30	3.7	2.5	3.9	2.5	0	12.5
100	40	4.0	2.5	3.8	1.6	0	11.9
100	50	3.8	2.6	3.7	1.8	.8	12.7
100	60	3.0	2.7	3.1	1.8	.3	10.9
100	70	3.5	2.7	3.5	1.8	.3	11.8
200	0	0	0	0	0	0	0
200	10	2.7	1.9	2.8	.7	0	8.1
200	20	3.4	2.0	2.5	2.2	.9	11.0
200	30	3.5	2.1	2.9	1.3	0	9.9
200	40	3.0	2.8	3.1	.8	0	9.7
200	50	3.3	2.1	3.8	1.1	0	10.2
200	60	3.9	2.6	2.5	.6	0	9.5
200	70	3.4	1.9	2.3	1.1	0	8.7

Table 6. Continued

Levels of		Branches/whorl					Total
N	P	1	2	3	4	5	branches
- ppm -		- - - - - - - - - - - - Number - - - - - - - - - - - -					
300	0	0	0	0	0	0	0
300	10	3.4	2.6	1.6	0	0	7.6
300	20	3.8	2.4	2.5	.6	0	9.3
300	30	4.0	2.5	2.2	.5	0	9.2
300	40	3.4	1.8	1.5	.2	0	6.9
300	50	4.2	1.9	2.1	.7	0	8.8
300	60	3.3	2.7	2.3	.2	0	8.5
300	70	3.9	2.2	2.5	1.3	0	9.9
	$\bar{X}$	2.33	1.64	1.66	.73	.08	6.69
Treatment effect[2/]							
	N	**	**	**	**	*	**
	P	**	**	**	**	*	**
	NP	*	ns	ns	ns	**	**

1/ Each value represents the mean of three replications.

2/ *; **; ns = significant at the 5-percent level of probability; significant at the 1-percent level of probability; and nonsignificant, respectively.

significant, and in no cases were there significant interactions at the 1 percent level of probability. Perhaps the relatively few significant interactions can be explained in part by pot-size restrictions on the root system. As mentioned in the methods chapter, five plants were allowed to remain in each pot throughout the experiment. The vigorously growing plants very likely became crowded during the final weeks of the study.

Total oven-dry weight of the root systen reached a maximum at 100 ppm N (Figure 6 and Table 7) with additional increments of N significantly reducing the mass of the root system. This finding is in agreement with Fowells and Krauss (1959) who found maximum root weight at 100 ppm N with significant reductions at lower and higher rates of nitrogen. Phosphorus level also had a significant effect on total root weight. However, 90 percent of the variation due to P can be accounted for by the difference between the zero level and the other rates of P (Appendix B, Table 19). No significant difference was found between 10 ppm and 70 ppm P. Weight of the root system was one of the root characteristics for which a significant N x P interaction was demonstrated. However, when tested by orthogonal comparisons all except an insignificant portion of the interaction sums of squares was accounted for by the comparison involving zero levels of the two elements. It seems likely, therefore, that in terms of root weight the slope of the phosphorus curves does not vary significantly with different levels of N between 100 and 300 ppm. Likewise the response to N is probably independent of phosphorus levels within the range of 10 to 70 ppm P. Taproot weight results were very similar to those of

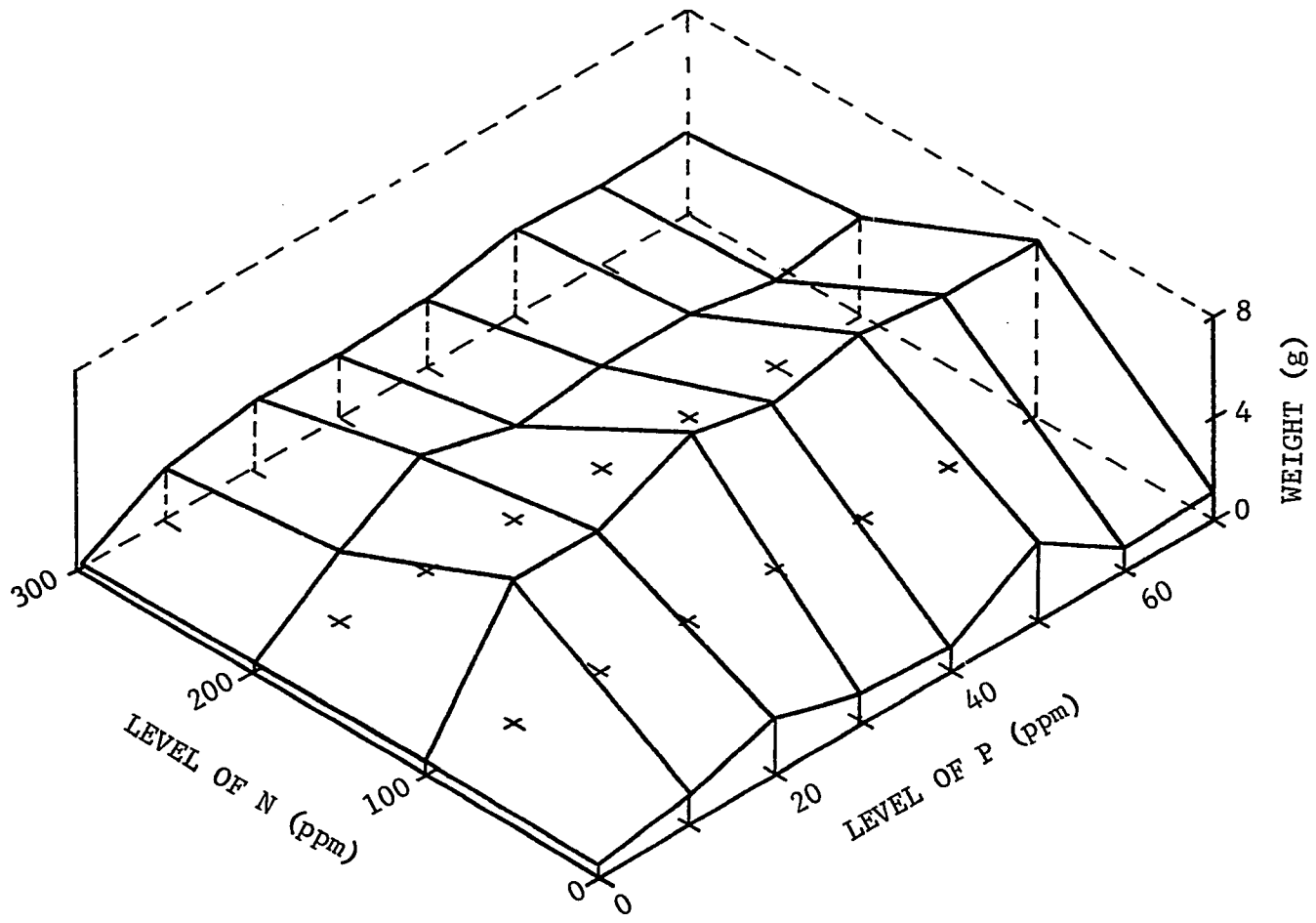


Figure 6. Total weight of root system as affected by nitrogen and phosphorus supply.

Table 7. Average[1/] effect of nitrogen and phosphorus on root weight variables

Levels of N	Levels of P	Weight of taproot	Weight of primary lateral roots per 5-cm segment of taproot[2/]						Total weight of lateral roots	Total weight of root system
			0-5	5-10	10-15	15-20	20-25	25-30		
- ppm -		- - - - - - - - - - - -	- - - - - - - -	- - - - - - - -	- - - - - - - -	- - - - Grams - - - -	- - - - - - - -	- - - - - - - -	- - - - - - - -	- - - - - - - -
0	0	0.07	0.08	0.01	0.01	0.01	0.01	0.01	0.14	0.21
0	10	.29	.43	.14	.09	.17	.09	.01	.94	1.23
0	20	.62	.73	.36	.25	.26	.17	.01	1.79	2.41
0	30	.38	.14	.18	.10	.16	.12	.03	.72	1.11
0	40	.34	.21	.11	.08	.18	.12	.01	.72	1.06
0	50	.91	1.02	.38	.20	.60	.20	.02	2.40	3.32
0	60	.29	.24	.06	.05	.20	.11	.01	.67	.95
0	70	.30	.19	.17	.17	.18	.05	.01	.77	1.08
100	0	.05	.05	0	0	0	0	0	.05	.11
100	10	2.79	1.20	1.05	.44	.29	.12	0	3.10	5.89
100	20	2.30	1.41	1.13	.61	.14	.03	0	3.32	5.62
100	30	3.89	1.37	1.34	.69	.43	.04	0	3.87	7.76
100	40	2.91	1.26	1.48	.74	.18	.01	0	3.67	6.58
100	50	3.49	1.24	1.31	.94	.44	.13	0	4.07	7.56
100	60	2.68	1.82	1.26	.71	.32	.04	0	4.16	6.84
100	70	3.17	1.20	1.51	.62	.23	.06	0	3.62	6.79

Table 7. Continued

Levels of N	Levels of P	Weight of taproot	Weight of primary lateral roots per 5-cm segment of taproot[2/]						Total weight of lateral roots	Total weight of root system
			0-5	5-10	10-15	15-20	20-25	25-30		
- ppm -		- Grams -								
200	0	.08	.07	.02	0	0	0	0	.09	.17
200	10	1.13	.89	.58	.19	.04	0	0	1.70	2.83
200	20	2.03	.15	.77	.28	.14	.03	0	2.72	4.75
200	30	1.93	.77	.67	.22	.31	.05	.01	2.02	3.95
200	40	1.73	1.02	.72	.36	.28	.02	0	2.40	4.14
200	50	1.83	1.15	.73	.34	.15	.05	0	2.42	4.25
200	60	1.54	.89	.57	.15	.17	.02	0	1.80	3.34
200	70	1.70	1.08	.73	.30	.14	.02	0	2.28	3.98
300	0	.05	.03	0	0	0	0	0	.03	.08
300	10	1.00	.85	.21	.17	.08	0	0	1.31	2.31
300	20	1.20	.57	.29	.21	.10	.04	0	1.22	2.42
300	30	1.13	.83	.26	.34	.11	.01	0	1.57	2.71
300	40	1.19	.73	.39	.20	.09	.01	.02	1.44	2.63
300	50	1.42	1.05	.39	.35	.13	.03	0	1.95	3.38
300	60	1.29	.88	.58	.27	.07	0	0	1.81	3.10
300	70	1.23	.79	.77	.27	.13	.02	0	2.00	3.22
	$\bar{X}$	1.41	.760	.568	.292	.179	.050	.004	1.89	3.31

Table 7. Continued

Levels of N	Levels of P	Weight of taproot	Weight of primary lateral roots per 5-cm segment of taproot[2/] 0-5	5-10	10-15	15-20	20-25	25-30	Total weight of lateral roots	Total weight of root system
- ppm -		- - - - - - - - - -	- - - - - - - - - -	- - - - - -	- - - - - -	Grams	- - - - - -	- - - - - -	- - - - - -	- - - - - -
Treatment effect[3/]										
	N	**	**	**	**	**	**	*	**	**
	P	**	**	**	**	**	**	ns	ns	**
	NP	*	*	ns	ns	ns	ns	ns	ns	*

1/ Each value represents the mean of three replications.

2/ Segments begin at root collar and progress toward taproot tip.

3/ *; **; ns = significant at the 5-percent level of probability; significant at the 1-percent level of probability; and nonsignificant, respectively.

total weight of the root system, and weight of lateral roots was found to be a function of nitrogen supply, reaching a maximum at 100 ppm N (Table 7).

Illustrated in Figure 7 is the effect of N and P on volume of the root system. Although the interaction was nonsignificant, the response to the main factors was similar to that of root weight. Orthogonal comparisons indicated that all levels of N produced significantly greater root volume than treatments without N, and that the two higher levels yielded significantly less root volume than the 100 ppm N treatment. According to the statistical tests (Appendix B, Table 20), the variation in the response curve between 10 ppm and 70 ppm P was nonsignificant. The slight increase at 50 ppm P has also been observed for some other variables and could be due to a slight phosphorus comtamination in this treatment at some point in the experiment.

Response curves for total number of primary lateral roots are presented in Figure 8, and data for numbers of lateral roots on individual segments of the taproot are given in Table 8. All three levels of applied N significantly decreased the number of lateral roots below that of plants receiving no nitrogen (Appendix B, Table 21). Nitrogen had a similar depressing effect on taproot length (Table 8). One must bear in mind, however, that the limitations of pot size as previously discussed very likely had an effect on taproot length. Nevertheless, these findings tend to agree with the well-known concept that the relationship between nitrogen supply and root development as mentioned by Bosemark (1954) is an inverse one. He stated that a deficiency of N results in long and slender roots, but as the supply of

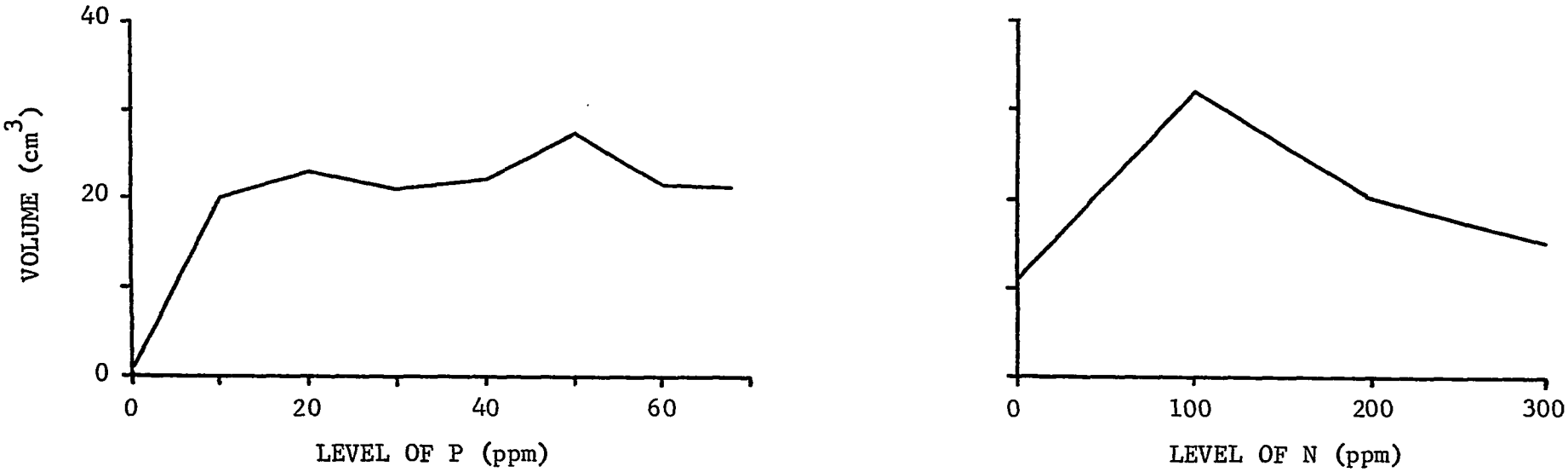


Figure 7. Root volume as affected by nitrogen and phosphorus supply. (Effect of P averaged over all levels of N and effect of N averaged over all levels of P.)

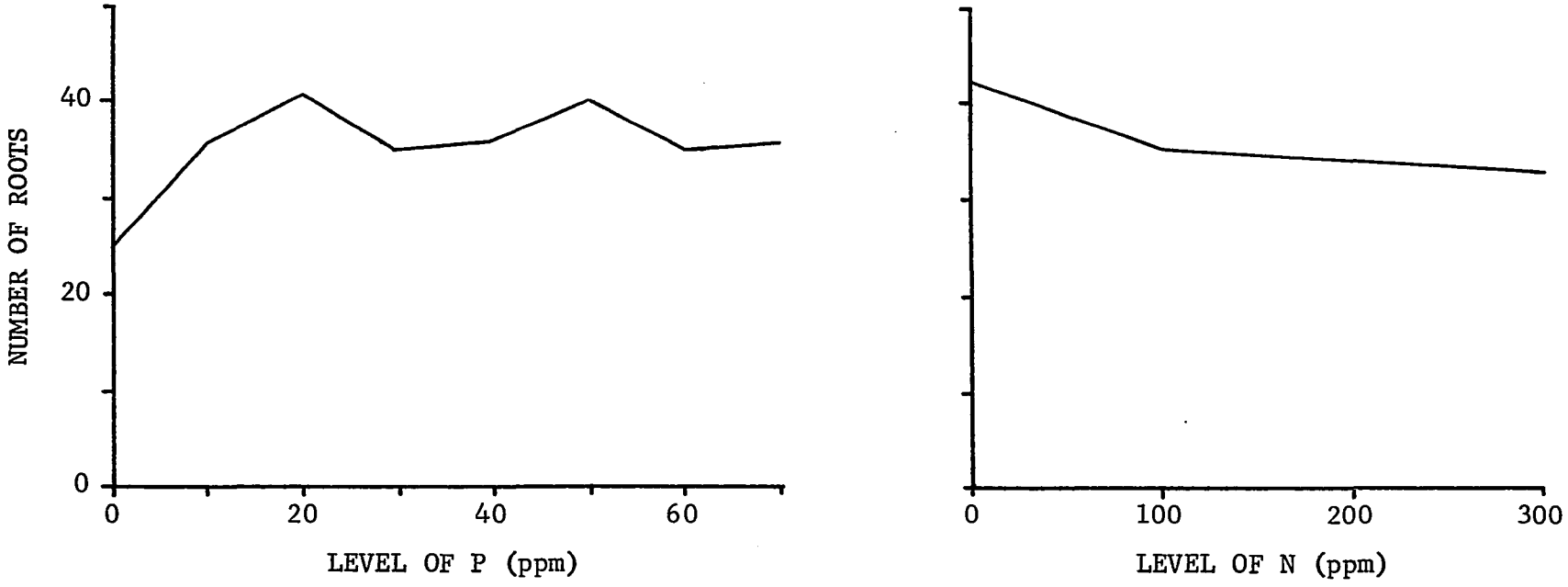


Figure 8. Total number of primary lateral roots as affected by nitrogen and phosphorus supply. (Effect of P averaged over all levels of N and effect of N averaged over all levels of P.)

Table 8. Average[1/] effect of nitrogen and phosphorus on root volume, number of primary lateral roots, and taproot length

Levels of		Root	No. of primary lateral roots per 5-cm segment of taproot[2/]									Total lateral	Taproot
N	P	volume	0-5	5-10	10-15	15-20	20-25	25-30	30-35	35-40	40-45	roots	length
- ppm -		- cm^3 -	- Number -										- cm -
0	0	1.2	11.9	6.5	5.3	4.1	5.3	2.3	1.6	1.2	1.2	39.7	39.0
0	10	12.2	11.4	6.9	5.9	6.4	7.5	1.3	.4	.5	.3	40.9	38.7
0	20	17.5	10.4	8.5	7.2	9.1	9.9	2.7	1.1	.4	.1	49.5	39.8
0	30	7.6	6.5	8.3	6.6	5.7	7.5	3.6	1.1	.1	.3	39.7	41.7
0	40	7.8	9.3	6.9	4.3	6.3	6.3	2.3	1.0	.5	.3	37.1	38.5
0	50	21.4	11.1	7.4	7.2	7.8	12.3	2.9	1.5	.7	.2	51.4	41.4
0	60	9.6	9.5	5.6	4.1	6.7	6.1	1.9	.9	.7	.2	35.8	44.9
0	70	8.1	9.8	7.7	5.8	7.7	7.3	1.5	.4	.2	.1	40.4	37.1
100	0	.6	12.1	5.3	2.9	1.8	2.1	.9	.3	.4	.1	26.0	40.0
100	10	32.4	10.8	7.6	5.5	6.7	5.5	1.3	.4	.1	0	37.8	33.1
100	20	34.1	11.5	6.9	4.3	4.2	4.3	1.3	.4	.2	.1	33.2	31.8
100	30	40.1	10.4	7.5	5.0	6.9	4.9	0	0	0	0	34.8	30.5
100	40	37.6	11.1	6.9	5.6	6.9	3.5	.6	.7	.3	.1	35.7	29.5
100	50	42.5	11.2	8.1	5.9	6.9	6.3	.6	.1	0	0	39.2	33.1
100	60	35.2	10.9	5.9	4.5	5.3	4.8	1.4	.7	.1	0	33.5	33.4
100	70	35.1	9.3	7.4	5.6	5.7	6.2	1.7	.2	.3	0	36.5	33.1

Table 8. Continued

Levels of N	Levels of P	Root volume	No. of primary lateral roots per 5-cm segment of taproot[2/] 0-5	5-10	10-15	15-20	20-25	25-30	30-35	35-40	40-45	Total lateral roots	Taproot length
- ppm -		- cm^3 -	- - - - -	- - - -	- - - -	- - - -	- - - - Number	- - - -	- - - -	- - - -	- - - -	- - - -	- cm -
200	0	.4	9.9	5.1	1.9	1.7	1.3	.4	.1	0	0	20.4	36.2
200	10	19.6	11.7	5.7	4.4	4.8	2.6	.2	0	0	0	29.5	27.5
200	20	26.4	12.6	7.3	5.7	8.8	8.5	1.2	.3	0	0	44.4	31.7
200	30	21.1	8.7	5.8	3.7	7.1	7.1	1.0	1.2	.3	0	34.9	36.3
200	40	24.5	10.6	6.2	4.7	7.7	6.5	1.2	0	0	0	36.9	31.6
200	50	27.3	12.3	6.2	3.3	4.7	6.5	1.1	0	0	0	34.1	32.3
200	60	21.7	10.2	8.0	4.5	7.0	5.5	1.6	.5	.1	0	37.5	32.8
200	70	20.9	10.6	6.1	4.0	4.8	3.2	.7	1.0	.1	0	30.5	30.8
300	0	.4	9.3	3.5	1.1	1.3	3.3	.2	0	0	0	15.7	27.0
300	10	14.1	12.2	5.4	6.6	7.9	4.7	.5	0	0	0	37.2	29.5
300	20	13.5	10.3	5.1	4.6	6.9	8.8	.9	.7	0	0	37.2	31.0
300	30	16.2	10.1	5.2	3.8	5.2	5.0	1.4	.1	0	.5	31.5	31.2
300	40	16.8	10.4	7.5	4.9	6.2	3.0	.5	.3	.1	.1	33.0	28.8
300	50	19.7	11.3	6.8	4.5	6.1	5.7	1.4	0	0	0	35.7	31.4
300	60	19.2	11.1	6.5	5.5	7.0	3.0	0	.1	.2	0	33.4	28.2
300	70	17.9	10.7	6.2	5.3	6.4	4.4	2.7	1.3	.4	.1	37.5	32.3
	$\bar{X}$	19.46	10.60	6.56	4.82	5.99	5.59	1.29	.51	.22	.12	35.64	33.9

Table 8. Continued

Levels of N	Levels of P	Root volume	No. of primary lateral roots per 5-cm segment of taproot[2/]									Total lateral roots	Taproot length
			0-5	5-10	10-15	15-20	20-25	25-30	30-35	35-40	40-45		
- ppm -		- cm^3 -	- Number -										- cm -
Treatment effect[3/]													
N		**	ns	*	**	ns	**	*	*	*	*	**	*
P		**	*	ns	**	**	**	ns	ns	ns	ns	**	ns
NP		ns	ns	ns	*	*	ns	ns	ns	ns	ns	ns	ns

1/ Each value represents the mean of three replications.

2/ Segments begin at root collar and progress toward taproot tip.

3/ *; **; ns = significant at the 1-percent level of probability; significant at the 5-percent level of probability; and nonsignificant, respectively.

nitrogen increases, the roots grow shorter and sturdier. Bosemark also demonstrated, as did the results of the present study, root growth inhibition at high rates of nitrogen. Examination of Figure 8 reveals that the number of roots decreases, as discussed above, with increases in N supply. At the same time the weight of lateral roots (Table 8) and of the entire root system increases as the supply of N increases from 0 to 100 ppm. This relationship seems to indicate larger size per root, which agrees with Bosemark's concept of sturdier roots at higher levels of nitrogen. Plate 9 illustrates the long, slender, and profuse root system of the plants grown without N compared to the shorter, more fleshy root systems of those plants receiving nitrogen. Lyr and Hoffman (1967) also stated that root development is "stronger" in poor soils than in rich ones.

Thompson (1965) also found a significant relationship between nitrogen supply and number of lateral roots. However, he measured a progressive increase in root number up to 220 ppm N and a sharp decrease thereafter. Mitchell (1939) also measured an increase in number of lateral roots with increases in nitrogen supply followed by a decreasing trend as the concentration of nitrogen was further increased. However, the peak observed by Mitchell occurred at 88 ppm N. Perhaps the fewer number of lateral roots at higher N levels can be accounted for if at these rates nitrogen can be absorbed in sufficient quantity without the aid of an extensive root system.

Unlike the results of Thompson (1965) a significant relationship was found between total number of primary lateral roots and phosphorus supply (Figure 8). The response curve reached a maximum at 20 ppm P,

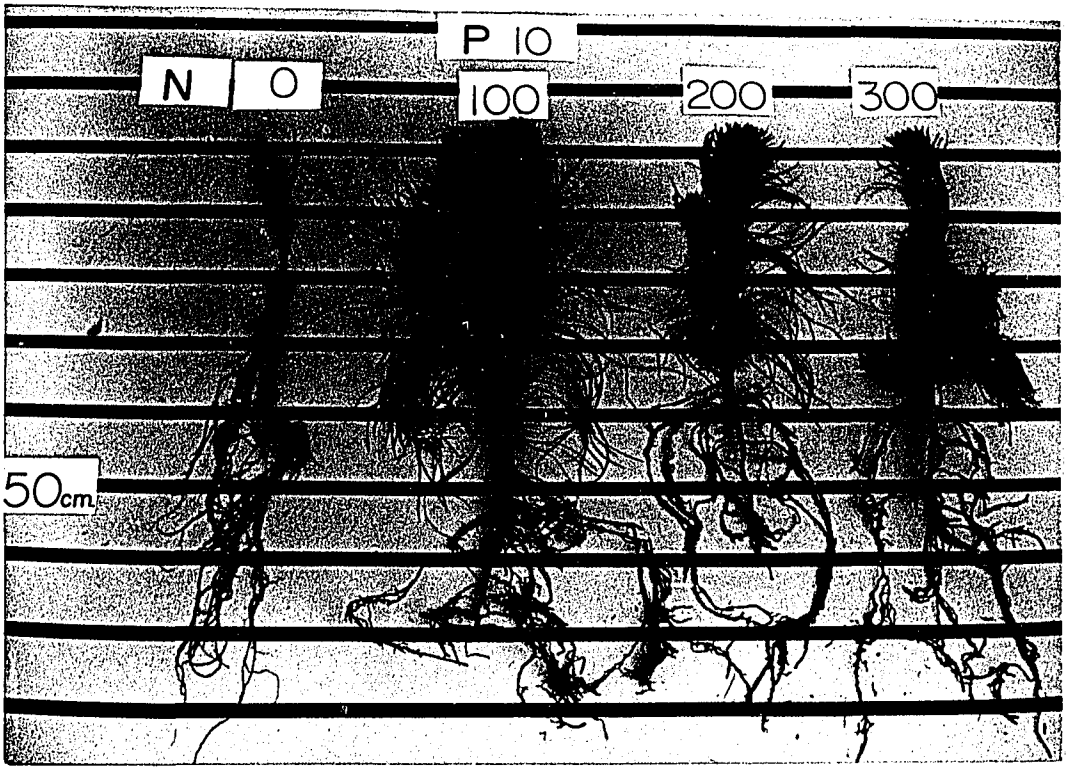


Plate 9. Representative plants treated with 10 ppm P and 0, 100, 200, and 300 ppm N. Note difference in root system development of the plant on the left. Lines on background are spaced at 10-cm intervals.

however, this peak was not significantly different from the 10 ppm rate. The effect of phosphorus on root development is said by Russell (1961) to be an indirect one. Adding phosphorus causes a considerable increase in leaf area resulting in the production of more carbohydrates. This, in turn, allows much greater development in the root system.

Thompson (1965) found, in addition to total number of primary lateral roots, the number of lateral roots on the first 5-centimeter segment of the taproot to be related to nitrogen supply. In the present study the greatest number of lateral roots was found on the uppermost segment of the taproot, but this variable was not related to nitrogen supply. As can be seen in Table 8, only phosphorus had a significant influence on the number of lateral roots on the first segment. The greatest treatment effect appeared at the third segment (Table 8). In terms of weight of the primary lateral roots from individual segments of the taproot, both N and P had a significant influence. Very little interaction was noted, however. Only plants grown without nitrogen developed a measurable mass of lateral roots on the terminal segment of the taproot (Table 7), again supporting the concept of profuse root development in a nitrogen-deficient growth medium.

The disparities between the results of the present study and those of Thompson (1965) could have been caused by differences in methodology. For example, Thompson's cultures were irrigated only on alternate days by manually pouring 2 liters of nutrient on the surface of the culture medium. In contrast, cultures in the present study were irrigated daily with a semi-automatic system as described in the methodology section. Cultures were completely saturated at each irrigation. Also,

Thompson's levels of N and P were applied at a constant level of the other, which may also help account for differences in results of the two studies.

Although no intensive effort was made to identify and characterize mycorrhizae, general observations indicated the presence of very few, if any mycorrhizal roots. Some plants had swollen white root tips characteristic of endotrophic mycorrhizae. However, this condition was found less frequently on nutrient-deficient plants, which seems to indicate that mycorrhizae were not responsible. No evidence of ectotrophic mycorrhizae was found on any plants.

Root/Shoot Ratio

Root/shoot ratios were influenced by both nitrogen and phosphorus but appeared to be largely a function of nitrogen supply. Average root/shoot ratios were as follows:

Level of N	Level of P	Root/shoot ratio
(ppm)		
0	0	1.16
0	10	1.30
0	20	1.49
0	30	1.45
0	40	1.52
0	50	1.30
0	60	1.41
0	70	1.57
100	0	.76
100	10	.30
100	20	.31
100	30	.38

Level of N	Level of P	Root/shoot ratio
(ppm)		
100	40	.32
100	50	.31
100	60	.29
100	70	.30
200	0	.92
200	10	.35
200	20	.33
200	30	.32
200	40	.36
200	50	.34
200	60	.30
200	70	.31
300	0	.69
300	10	.41
300	20	.32
300	30	.38
300	40	.38
300	50	.34
300	60	.36
300	70	.41

Treatment effect	
N	**
P	**
NP	*

Increasing the nitrogen level from 0 to 100 ppm reduced the ratio from 1.40 to 0.37 averaged over all rates of P applied. This indicates an almost fourfold reduction in the proportion of root mass to shoot mass. Likewise, supplying phosphorus at the rate of 10 ppm caused significant,

though lesser, reduction in root/shoot ratio (Figure 9). Orthogonal comparisons (Appendix B, Table 22) for both N and P indicated no significant effect beyond the minimum applied rates -- 100 ppm N and 10 ppm P. Fowells and Krauss (1959) and McGee (1963) obtained similar results.

The effect of interaction for this variable was significant at the 5 percent level of probability, but orthogonal comparisons revealed all the significant variation to be due to differences between zero and all other rates of N and P. Nevertheless, it is interesting to note that, in the absence of nitrogen, additions of phosphorus tended to increase the root/shoot ratio. Increasing increments of nitrogen in the absence of phosphorus, on the other hand, resulted in a decreasing trend in the proportion of root to shoot material.

Meyer, Anderson, and Bohning (1960) attributed root/shoot ratio development to C:N relations within the plant. They explained that a low nitrate level in the growth medium results in most of the absorbed nitrates being utilized in the synthesis of amino acids in the roots. The carbohydrates necessary for this process are transported downward from the leaves. Most of these amino acids are used in protein synthesis during root growth. The result is that only a small quantity of nitrogenous material escapes utilization in the roots and is translocated to the shoot. Therefore, the growth rate of the shoot is relatively low resulting in a high root/shoot ratio. Conversely, when the supply of nitrates is high, only a relatively small proportion of the total uptake is used by the roots. A relatively large quantity of nitrogenous compounds is translocated to the leaves where it is

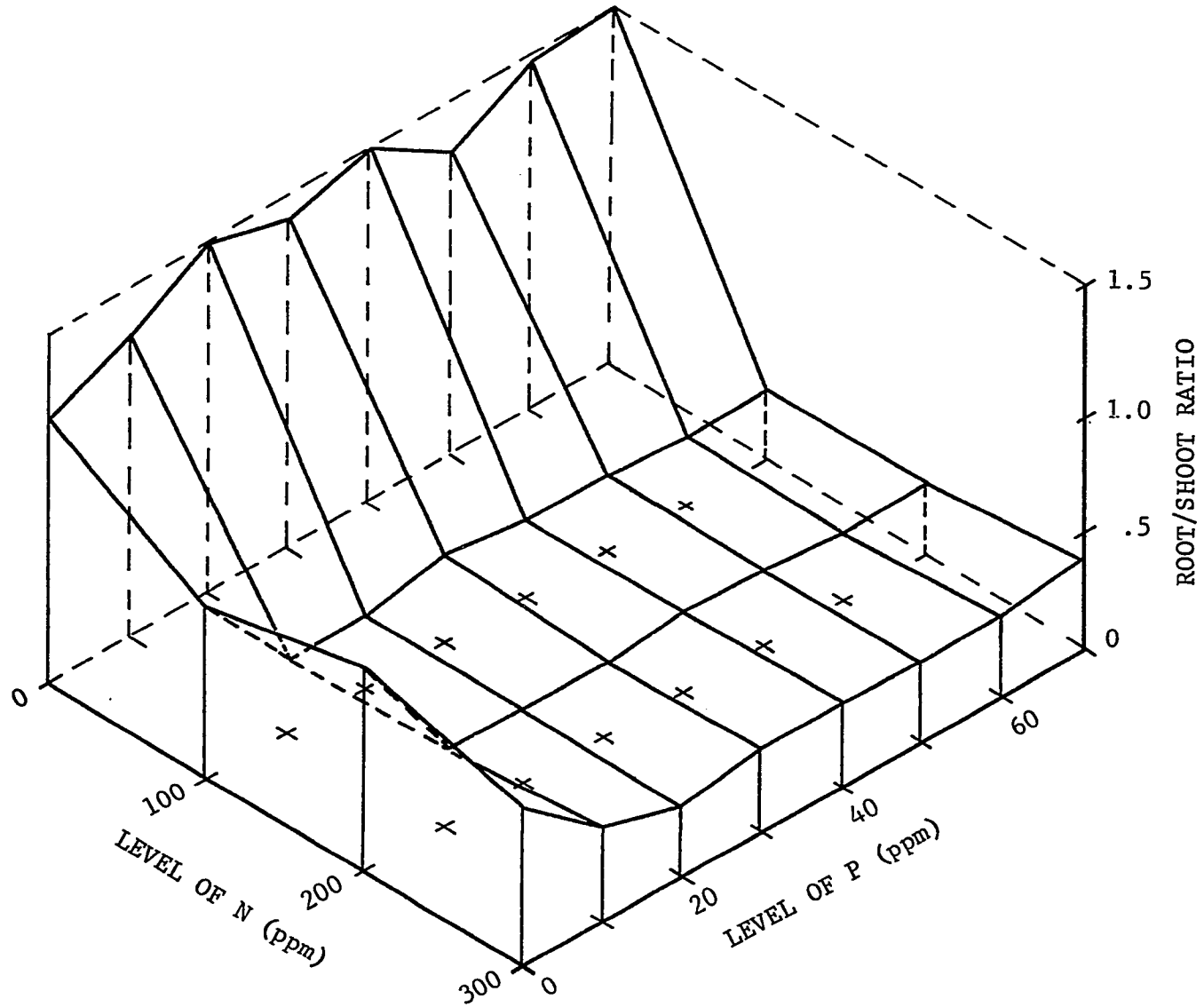


Figure 9. Root/shoot ratio as affected by nitrogen and phosphorus supply.

utilized in the synthesis of proteins. The increased vegetative growth of the shoot portion results in the utilization of more carbohydrates as well as proteinaceous materials. Because of the increased metabolism in the aerial portion of the plant, a relatively small quantity of carbohydrates is translocated into the root system. The roots, according to these authors, are likely to be deficient in carbohydrates and proteins resulting in less root development relative to shoot growth. This situation, of course, yields a smaller root/shoot ratio.

Uptake of Nutrients

The concentrations of nitrogen and phosphorus in all parts of the seedling were directly related to the supply of the respective element. Levels of potassium, calcium, and magnesium, which were supplied at constant rates, were affected to varying degrees by treatments of nitrogen and phosphorus.

Nitrogen uptake.--Increasing the supply of nitrogen resulted in progressive increases in nitrogen concentration of all tissues studied (Table 9 and Figures 10-15). (In Figures 10-15 only elements significantly affected by N and P are shown.) In most cases, however, the concentrations produced by the two highest rates of N were not significantly different. The only real variation among the plant parts was in the magnitude of the concentrations.

Table 9. Nitrogen and phosphorus concentration[1/] in tissues as affected by nitrogen and phosphorus supply

Levels of		Mature needles		Immature needles		Mature stem		Immature stem and branches		Taproot		Lateral roots	
N	P	N	P	N	P	N	P	N	P	N	P	N	P
- ppm -		- Percent -											
0	0	1.23	0.110	1.23	0.110	1.23	0.110	1.23	0.110	1.23	0.110	1.23	0.110
0	10	1.24	.550	1.24	.550	.67	.373	.67	.373	.56	.466	.56	.466
0	20	1.35	.619	1.28	.523	.48	.320	.77	.381	.39	.389	.60	.583
0	30	1.34	.700	1.34	.700	.61	.433	.61	.433	.58	.546	.58	.546
0	40	1.07	.704	1.07	.704	.53	.427	.53	.427	.49	.512	.49	.512
0	50	1.27	.709	.93	.494	.41	.366	.62	.434	.33	.387	.54	.627
0	60	1.26	.733	1.26	.733	.61	.487	.61	.487	.57	.563	.57	.562
0	70	1.25	.860	1.25	.860	.61	.494	.61	.494	.54	.514	.54	.514
100	0	2.88	.107	2.88	.107	2.88	.107	2.88	.107	2.88	.107	2.88	.107
100	10	2.68	.246	2.26	.322	1.06	.184	1.24	.258	1.13	.144	2.28	.311
100	20	3.00	.240	2.60	.323	1.28	.179	1.52	.298	1.37	.164	2.41	.362
100	30	2.67	.249	2.27	.340	1.17	.183	1.37	.316	1.07	.167	2.09	.312
100	40	2.71	.246	2.31	.323	1.08	.184	1.34	.290	1.10	.174	2.14	.397
100	50	2.66	.251	2.33	.332	.98	.182	1.34	.300	1.04	.171	2.18	.385
100	60	2.66	.264	2.27	.329	1.09	.216	1.36	.301	1.25	.209	2.22	.407
100	70	2.57	.276	2.24	.337	.99	.193	1.67	.309	1.06	.225	2.01	.395

Table 9. Continued

Levels of		Mature needles		Immature needles		Mature stem		Immature stem and branches		Taproot		Lateral roots	
N	P	N	P	N	P	N	P	N	P	N	P	N	P
- ppm -		- Percent -											
200	0	2.96	.133	2.96	.133	2.96	.133	2.96	.133	2.96	.133	2.96	.133
200	10	2.96	.258	2.50	.328	1.17	.186	1.38	.310	1.24	.179	2.08	.272
200	20	3.09	.245	2.78	.318	1.33	.203	1.61	.300	1.38	.195	2.55	.364
200	30	3.19	.257	2.78	.314	1.27	.206	1.56	.321	1.30	.194	2.32	.349
200	40	3.03	.259	2.67	.321	1.25	.210	1.55	.328	1.30	.175	2.16	.382
200	50	2.72	.234	2.39	.317	1.17	.184	1.48	.312	1.23	.184	2.35	.382
200	60	2.85	.266	2.43	.320	1.13	.209	1.35	.293	1.10	.189	2.53	.425
200	70	2.80	.292	2.45	.415	1.36	.190	1.45	.250	1.27	.208	2.25	.294
300	0	3.10	.104	3.10	.104	3.10	.104	3.10	.104	3.10	.104	3.10	.104
300	10	3.11	.309	2.84	.303	1.24	.219	1.73	.323	1.44	.217	2.58	.340
300	20	3.06	.276	2.63	.336	1.26	.203	1.70	.352	1.40	.188	2.74	.346
300	30	3.03	.264	2.60	.337	1.45	.210	1.58	.331	1.45	.188	2.20	.361
300	40	3.02	.290	2.72	.354	1.46	.221	1.66	.333	1.41	.230	2.94	.373
300	50	2.87	.261	2.61	.316	1.35	.187	1.57	.301	1.42	.188	2.51	.390
300	60	2.87	.272	2.53	.330	1.30	.217	1.55	.332	1.31	.216	2.47	.392
300	70	3.17	.303	2.57	.313	1.37	.227	1.58	.339	1.45	.217	2.35	.352
	$\bar{x}$	2.49	.340	2.23	.373	1.25	.234	1.44	.312	1.26	.245	1.98	.370

Table 9. Continued

Levels of		Mature needles		Immature needles		Mature stem		Immature stem and branches		Taproot		Lateral roots	
N	P	N	P	N	P	N	P	N	P	N	P	N	P
- ppm -		- - - - - - - - - - - - - - - - - - - -						Percent - - - - - - - - - - - - - - - - - -					
Treatment effect[2/]													
N		**	**	**	**	**	**	**	**	*	**	**	**
P		ns	**	**	**	**	**	**	**	**	**	**	**
NP		ns	**	ns	*	**	ns	ns	ns	**	**	ns	*

1/ Each value represents the mean of three replications.

2/ *; **; ns = significant at the 5-percent level of probability; significant at the 1-percent level of probability; and nonsignificant, respectively.

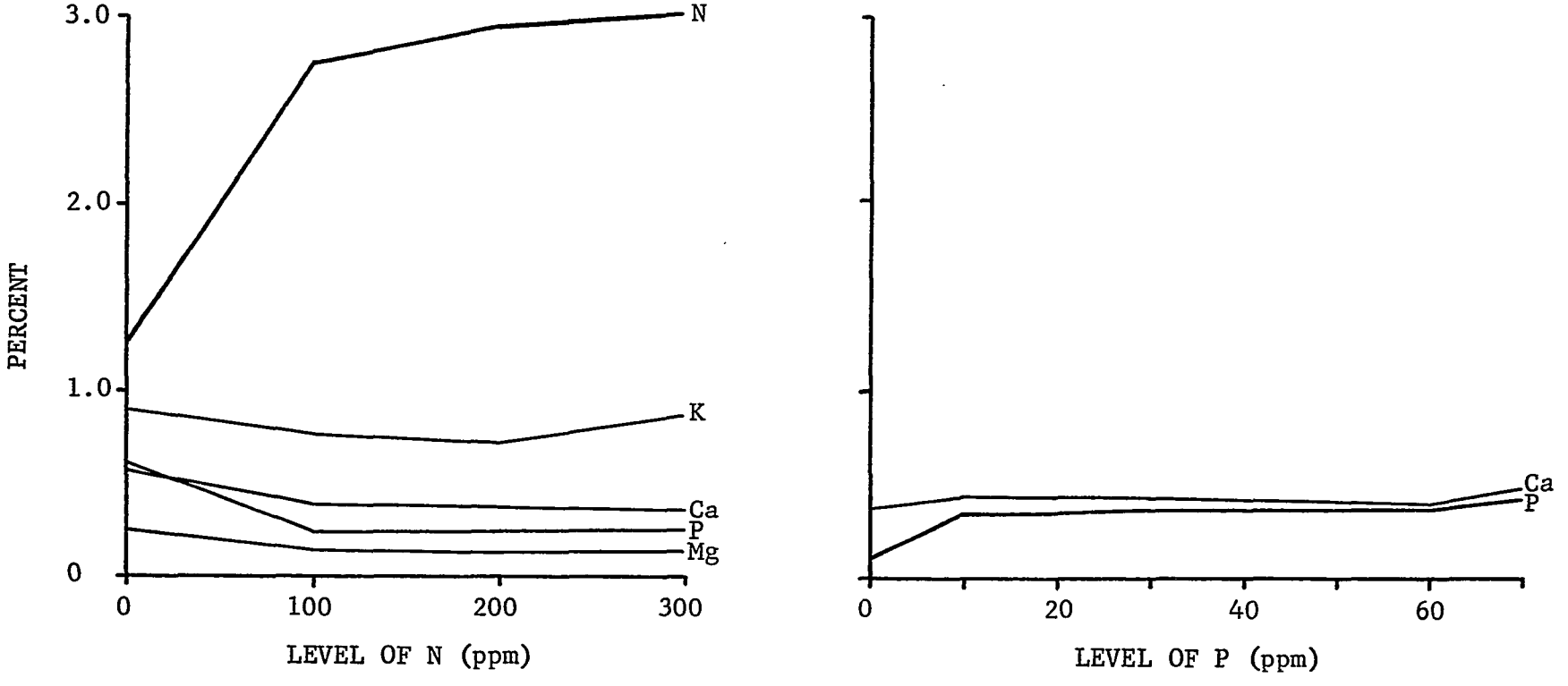


Figure 10. Effect of nitrogen and phosphorus on nutrient concentration of mature needles.

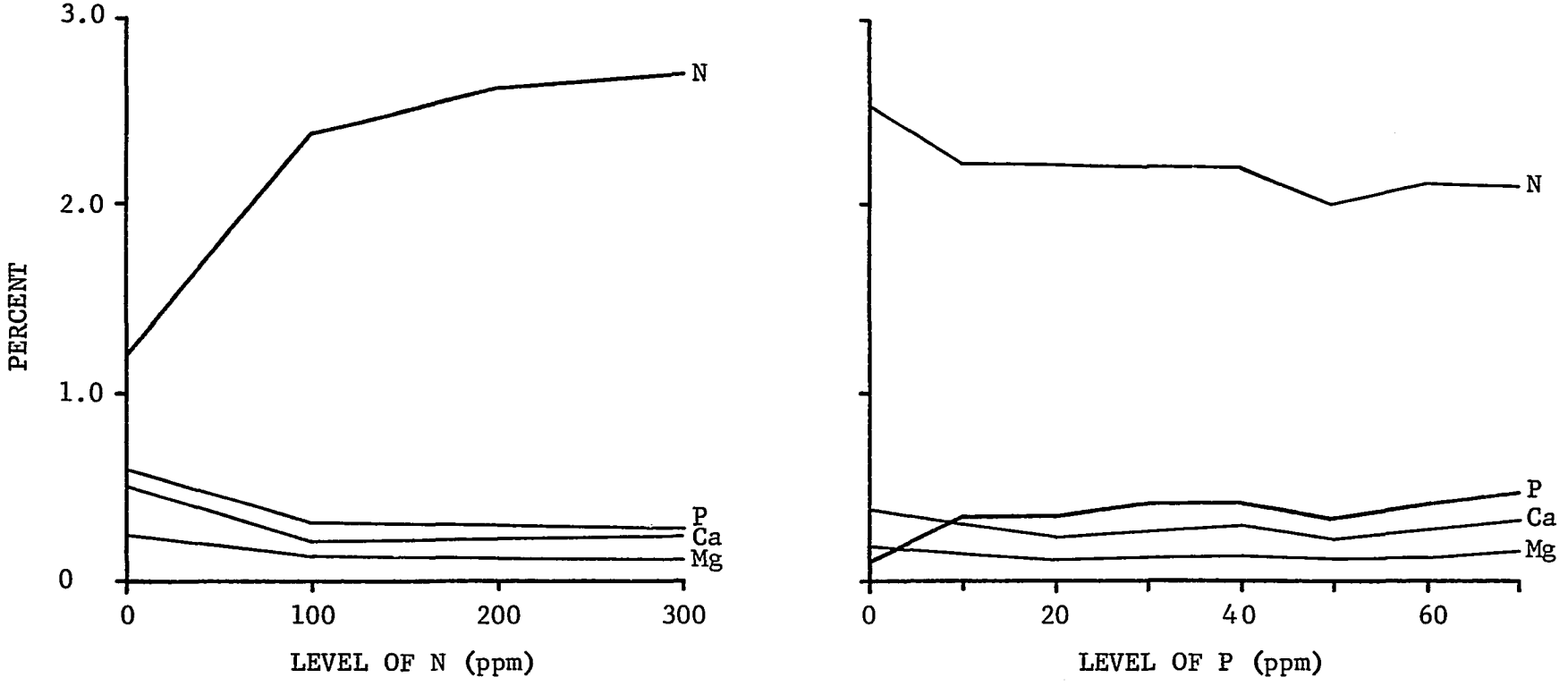


Figure 11. Effect of nitrogen and phosphorus on nutrient concentration of immature needles.

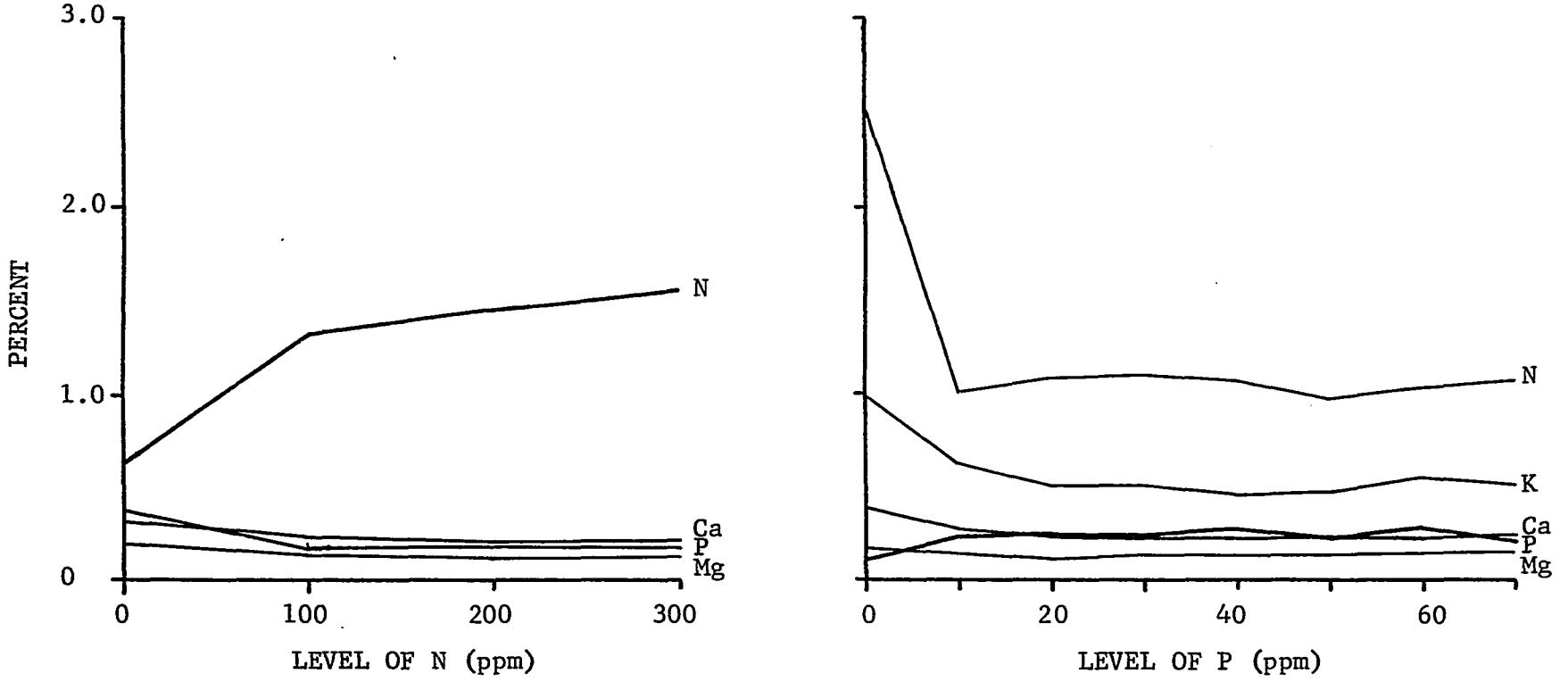


Figure 12. Effect of nitrogen and phosphorus on nutrient concentration of mature stem.

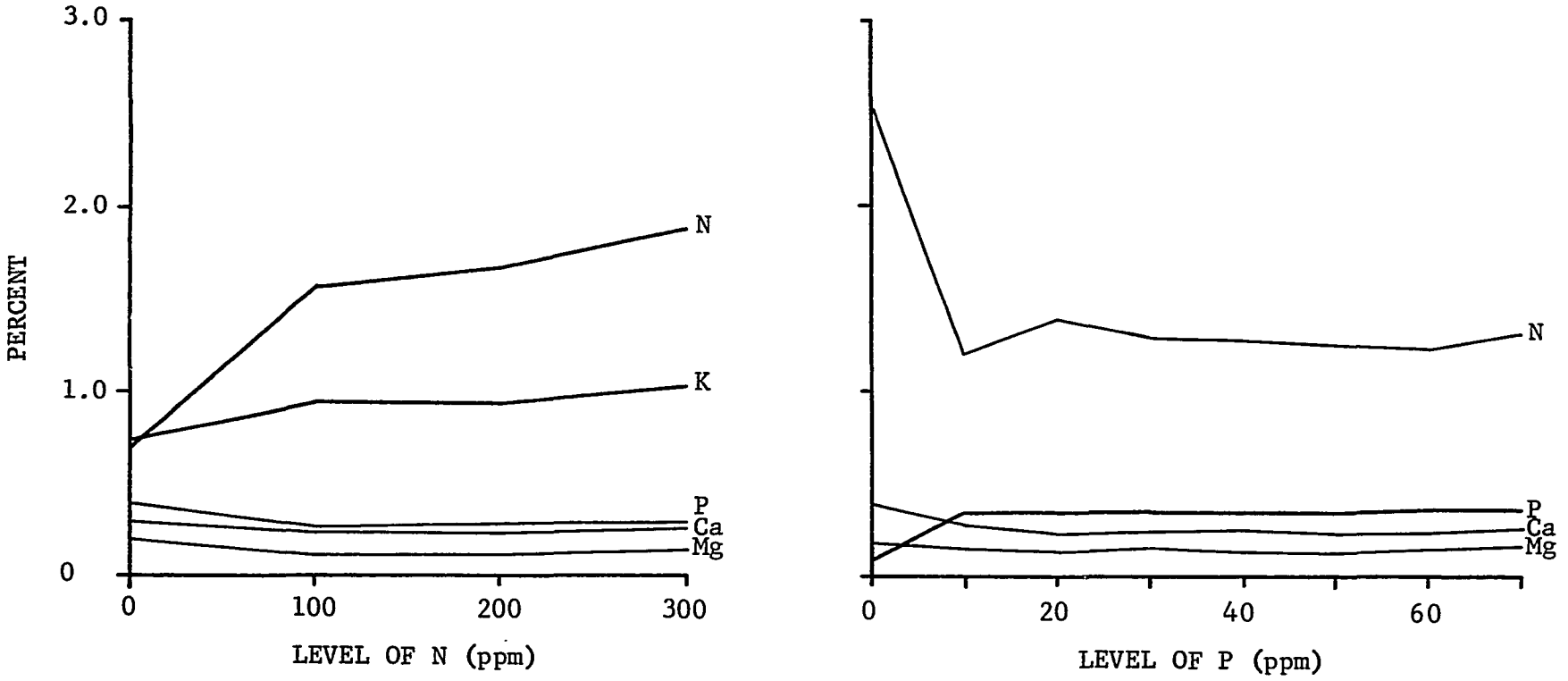


Figure 13. Effect of nitrogen and phosphorus on nutrient concentration of immature stem.

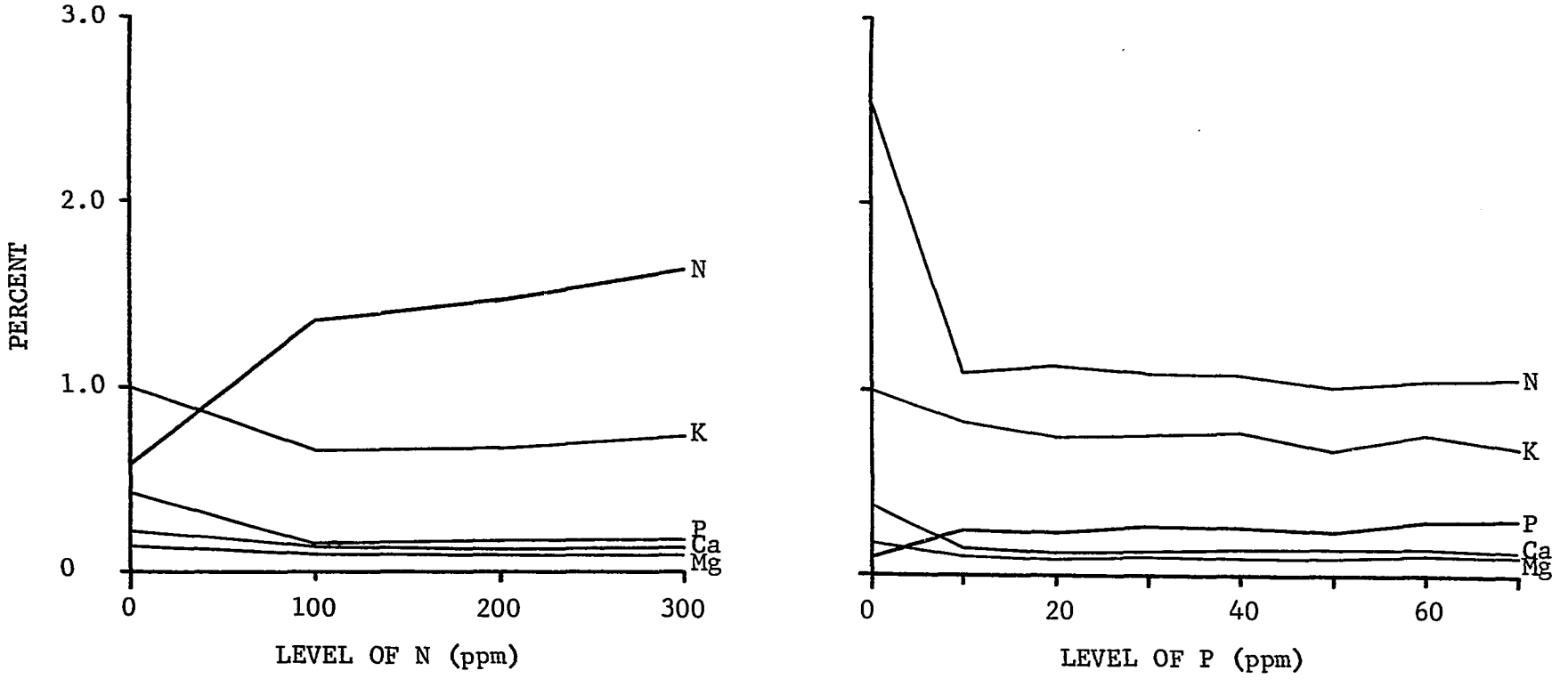


Figure 14. Effect of nitrogen and phosphorus on nutrient concentration of taproot.

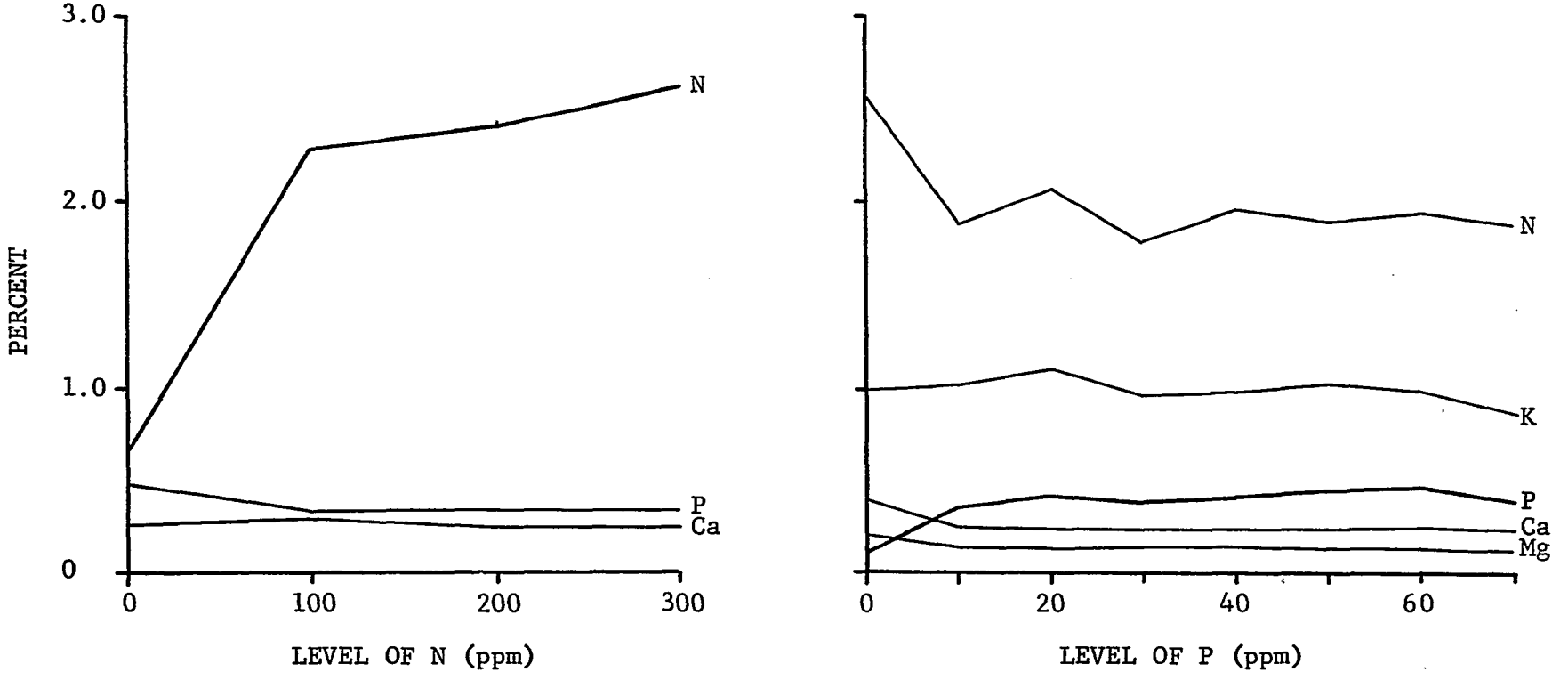


Figure 15. Effect of nitrogen and phosphorus on nutrient concentration of lateral roots.

Ranges in nitrogen concentration in tissues with increasing rates of application of this element, averaged over all levels of applied phosphorus, are given below.

Component	Percent nitrogen at	
	0 N	300 N
Mature needles	1.25	3.03
Immature needles	1.20	2.70
Lateral roots	0.65	2.60
Immature stem	0.71	1.89
Taproot	0.58	1.61
Mature stem	0.64	1.55

Few other studies have made separate analyses on so many plant parts; however, Thompson (1965) did observe greatest N concentration in the mature needles. Fowells and Krauss (1959) also found lower nitrogen levels in stems and roots than in needles.

Increases in phosphorus supply significantly reduced nitrogen concentrations in all tissues except mature needles. The response curves were almost an inverse of those produced by nitrogen supply (Figures 10-15). Levels of phosphorus between 10 and 70 ppm resulted in no significant change in percent N. These results are somewhat different to those of Fowells and Krauss (1959) who found the foliar N concentration in a medium containing 1 ppm P to be lower than the other treatments. Meyer, Anderson, and Bohning (1960), however, reported that inorganic nitrogen accumulates in tissues when available phosphates are low. In the present study the percentage of N in the various plant parts with increasing levels of applied phosphorus is shown in the following tabulation.

Component	Percent nitrogen at	
	0 P	70 P
Mature needles	2.54	2.42
Immature needles	2.54	2.10
Lateral roots	2.54	1.89
Immature stem	2.54	1.30
Taproot	2.54	1.05
Mature stem	2.54	1.07

The sharp decreases in percent nitrogen with 10 ppm or more of phosphorus has two possible explanations. First, the increased growth from addition of P resulted in dilution of nitrogen in the plant tissue. This will be discussed more fully in the next section. Secondly, as was pointed out in the previous chapter, plants receiving no phosphorus were very small. Enough material could be obtained for chemical analysis only by combining all components into one sample. The result, of course, was a single value for each element, which represented the nutrient content of the entire plant rather than any individual component. The author was advised[6/] that, in order to avoid missing values in the analysis of variance, the single values for the whole plant should be used as the nutrient content of each of the six plant components. From a biometrical standpoint this was the simplest solution. However, the nitrogen content, as were the concentrations of the other nutrients, was rather high in these small plants. Therefore, the data for each variable, except mature needles, revealed marked decreases in nitrogen concentration with addition of 10 ppm P. The problem created by substituting entire plant analyses for individual component values apparently did not affect mature needle data as much as data of the other components.

6/ Personal communication, Dr. Barton R. Farthing, Department of Experimental Statistics, Louisiana State University, Baton Rouge.

Analyses of variance (Appendix B, Table 23) indicated only nitrogen accumulation in the mature stem and taproot to be influenced by N x P interaction. This relationship for mature stems is depicted in Figure 16. The significant interaction is very likely due to the curve representing the zero level of phosphorus over various levels of nitrogen. This curve probably represents abnormally high nitrogen contents for woody tissues of loblolly pine seedlings. The response surface for percent nitrogen in the taproot was similar in trend.

Phosphorus uptake.--As shown in Figures 10-15 and Table 9, nitrogen supply significantly decreased the concentration in phosphorus in all components studied. Ranges for tissue concentrations of phosphorus as affected by increasing nitrogen supply are shown below.

Component	Percent phosphorus at	
	0 N	300 N
Immature needles	0.584	0.299
Lateral roots	.489	.325
Mature needles	.623	.235
Immature stem	.392	.272
Taproot	.436	.170
Mature stem	.376	.190

The accumulation of the highest concentration of phosphorus in immature needles and lateral roots is in agreement with Meyer, Anderson, and Bohning (1960), who observed that in growing plants phosphorus is most abundant in meristematic tissue. In these tissues this element is used in the synthesis of nucleoproteins and other phosphorus-containing compounds.

Fowells and Krauss (1959) also found the greatest concentration of phosphorus in plants treated with very low levels of nitrogen. These

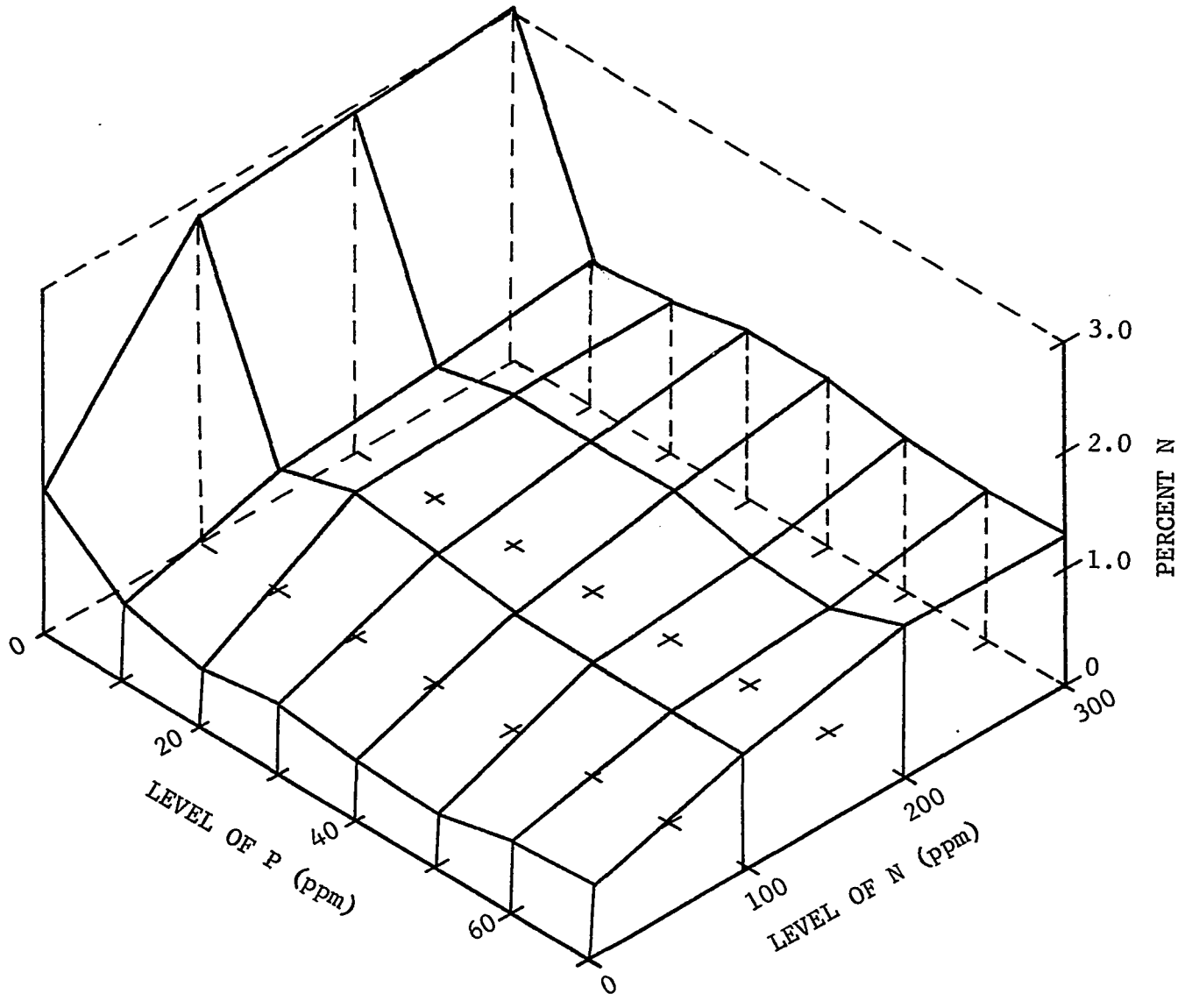


Figure 16. Effect of nitrogen and phosphorus on nitrogen concentration of mature stem tissue.

authors, as did Van Goor (1953), suggested an antagonism between nitrate and phosphate ions. However, virtually all the decrease in phosphorus concentration in the present study resulted from the addition of the first increment (100 ppm) of nitrogen. The fact that 100 ppm N produced a many-fold increase in growth was well established in a previous section. This strongly suggests, therefore, that the reduction in percent P caused by adding 100 ppm N is the result of the element being diluted in a greater volume of plant tissue. One must not discount the possibility of N-P antagonism; however, using percentages to express nutrient uptake does not permit differentiation between antagonistic and dilution effects.

Probably a better reference basis for the analytical data would have been amount of nutrients per 100 needles (Tamm 1964) rather than percentages. Absolute quantity of nutrients per plant is often used; however, this expression is almost as much a function of plant size as is percentage. Therefore, little is gained by this method of expression.

Increasing the level of phosphorus in the nutrient solution from 0 to 10 ppm resulted in increases in concentration of this element in all tissues. However, there was apparently no difference between the 10 ppm P and the 70 ppm P treatment. Ranges in tissue P resulting from increasing levels of phosphorus in the growth medium were as follows:

Component	Percent phosphorus at	
	0 P	70 P
Immature needles	0.114	0.481
Lateral roots	.114	.398
Mature needles	.114	.433
Immature stem	.114	.353
Taproot	.114	.293
Mature stem	.114	.215

The substitution of whole plant analyses for individual component values accounts for the uniformity of the lower values in the above ranges.

The significant effect of the N x P interaction on percent P in mature needles (Figure 17 and Appendix B, Table 24) is thought to be due to (1) the increases in concentration of P when P increments were added without N, and/or (2) the effect of 10 ppm P in increasing P concentration over all levels of N applied. Very little, if any, significant interaction exists in the portion of the response surface representing combinations of applied nitrogen and phosphorus.

K, Ca, and Mg uptake.--Figures 10-15 and Tables 10-11 reveal that in most cases increasing the supply of nitrogen and phosphorus significantly reduced the concentration of potassium, calcium, and magnesium in all six plant components. Again practically all the reduction in nutrient percentages resulted from supplying N and P at the lowest rates of application. Further increases in nutrient supply beyond 10 ppm P and 100 ppm N had no effect on concentrations of K, Ca, and Mg. There could be an antagonistic effect between nitrogen and phosphorus and K, Ca, and Mg. In fact, Thompson (1965) suggested such an effect between N and K. However, Thompson was not, nor am I from the present study, able to separate the effects of plant size at higher rates of nitrogen. Increased growth resulting in dilution of K, Ca, and Mg is thought to be the major factor producing the trends in the present study.

Shown in Table 12 are average K, Ca, and Mg percentages found in the various plant components. The greatest concentration of potassium occurred in the meristematic tissue, being highest in immature needles and lateral roots. Lowest concentration of this element was in woody

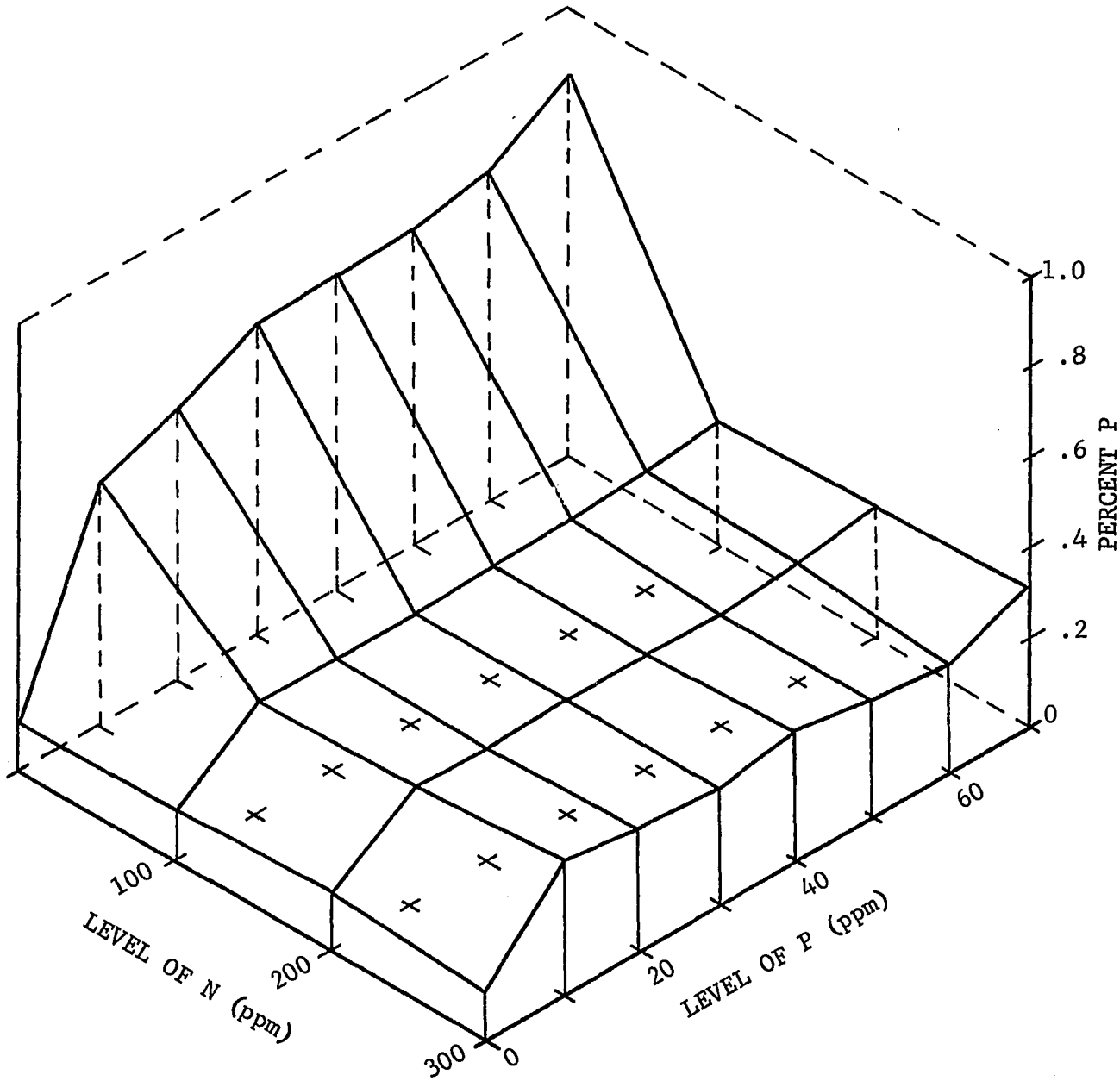


Figure 17. Effect of nitrogen and phosphorus on phosphorus concentration of mature needles.

Table 10. Potassium, calcium, and magnesium concentrations[1/] in shoot tissue as affected by nitrogen and phosphorus supply

Levels of		Mature needles			Immature needles			Mature stem			Immature stem and branches		
N	P	K	Ca	Mg	K	Ca	Mg	K	Ca	Mg	K	Ca	Mg
- ppm -		- Percent -											
0	0	1.16	.403	.201	1.16	.403	.201	1.16	.403	.201	1.16	.403	.201
0	10	.98	.583	.250	.98	.580	.250	.53	.325	.202	.53	.325	.202
0	20	.64	.572	.226	.94	.401	.196	.41	.281	.178	.82	.234	.160
0	30	.83	.599	.264	.83	.599	.264	.58	.322	.203	.58	.322	.203
0	40	.76	.595	.258	.76	.595	.258	.37	.323	.191	.37	.323	.191
0	50	.86	.639	.261	1.35	.366	.198	.48	.301	.162	1.06	.219	.145
0	60	.93	.550	.268	.93	.550	.268	.68	.293	.210	.68	.293	.210
0	70	.99	.598	.290	.99	.598	.290	.63	.304	.286	.63	.304	.286
100	0	.78	.289	.143	.78	.289	.143	.78	.289	.143	.78	.289	.143
100	10	.75	.483	.188	1.15	.232	.127	.74	.247	.152	.92	.300	.141
100	20	.73	.435	.159	1.05	.206	.108	.50	.254	.142	1.04	.261	.132
100	30	.68	.394	.135	1.06	.192	.112	.52	.249	.147	1.05	.236	.128
100	40	.77	.406	.144	1.03	.188	.126	.48	.234	.153	.93	.225	.126
100	50	.81	.380	.143	1.32	.173	.115	.51	.216	.136	.99	.226	.134
100	60	.95	.369	.138	1.12	.204	.105	.52	.234	.146	.93	.263	.134
100	70	.67	.394	.122	1.07	.200	.108	.47	.225	.115	.92	.246	.126

Table 10. Continued

Levels of		Mature needles			Immature needles			Mature stem			Immature stem and branches		
N	P	K	Ca	Mg	K	Ca	Mg	K	Ca	Mg	K	Ca	Mg
- ppm -		- Percent -											
200	0	.69	.335	.170	.69	.335	.170	.69	.335	.170	.69	.335	.170
200	10	.80	.377	.119	1.10	.228	.116	.56	.188	.127	1.10	.263	.148
200	20	.65	.388	.130	1.09	.200	.104	.48	.220	.127	.93	.238	.127
200	30	.72	.367	.120	1.01	.199	.101	.44	.197	.128	.81	.228	.127
200	40	.66	.386	.121	1.01	.203	.105	.51	.197	.115	.88	.254	.128
200	50	.76	.328	.118	.99	.165	.101	.46	.199	.120	.99	.243	.120
200	60	.78	.353	.121	1.06	.195	.103	.56	.209	.137	1.05	.245	.128
200	70	.71	.480	.183	1.21	.392	.198	.43	.199	.135	.95	.230	.145
300	0	1.35	.503	.250	1.35	.503	.250	1.35	.503	.250	1.35	.503	.250
300	10	.90	.345	.121	.89	.213	.107	.59	.150	.134	.95	.279	.157
300	20	.85	.365	.132	1.10	.229	.115	.64	.158	.131	1.11	.239	.144
300	30	.76	.325	.118	1.07	.201	.118	.50	.168	.138	1.04	.236	.145
300	40	.86	.334	.128	1.01	.220	.119	.51	.182	.124	.90	.259	.145
300	50	.76	.357	.108	.96	.224	.109	.47	.181	.113	.85	.260	.133
300	60	.86	.305	.117	1.06	.196	.114	.50	.160	.118	.99	.224	.133
300	70	.75	.384	.129	.93	.227	.113	.59	.165	.112	1.07	.253	.129
	$\bar{X}$	.82	.426	.168	1.03	.303	.153	.58	.247	.155	.91	.274	.156

Table 10. Continued

Levels of		Mature needles			Immature needles			Mature stem			Immature stem and branches		
N	P	K	Ca	Mg	K	Ca	Mg	K	Ca	Mg	K	Ca	Mg
- ppm -		- Percent -											
Treatment effect[2/]													
N		*	**	**	ns	**	**	ns	**	**	**	**	**
P		ns	ns	ns	ns	*	*	**	**	ns	ns	**	*
NP		ns	*	*	ns	*	ns	ns	**	ns	ns	ns	ns

1/ Each value represents the mean of three replications.

2/ *; **; ns = significant at the 5-percent level of probability; significant at the 1-percent level of probability; and nonsignificant, respectively.

Table 11. Potassium, calcium, and magnesium concentrations[1/] in root tissue as affected by nitrogen and phosphorus supply

Levels of		Taproot			Lateral roots		
N	P	K	Ca	Mg	K	Ca	Mg
- ppm -		- - - - - - - - - - Percent - - - - - - - - - -					
0	0	1.16	.403	.201	1.16	.403	.201
0	10	1.03	.230	.130	1.03	.230	.130
0	20	.95	.153	.116	1.30	.232	.117
0	30	1.17	.239	.140	1.17	.239	.140
0	40	1.06	.233	.131	1.06	.233	.131
0	50	.72	.158	.093	1.19	.262	.128
0	60	1.03	.236	.132	1.03	.236	.132
0	70	.97	.215	.130	.97	.215	.130
100	0	.78	.289	.143	.78	.289	.143
100	10	.67	.156	.129	1.04	.388	.168
100	20	.72	.137	.121	1.03	.338	.142
100	30	.50	.146	.115	.79	.301	.145
100	40	.71	.140	.126	.98	.266	.149
100	50	.64	.128	.114	.98	.272	.138
100	60	.71	.152	.117	.80	.314	.132
100	70	.55	.111	.096	.89	.223	.138
200	0	.69	.335	.170	.69	.335	.170
200	10	.89	.103	.099	.94	.177	.107
200	20	.63	.117	.104	1.06	.208	.130
200	30	.71	.105	.098	.95	.211	.122
200	40	.70	.103	.085	1.12	.206	.127
200	50	.71	.114	.095	.92	.226	.124
200	60	.62	.095	.094	1.20	.208	.128
200	70	.58	.115	.115	.81	.250	.143

Table 11. Continued

Levels of		Taproot			Lateral roots		
N	P	K	Ca	Mg	K	Ca	Mg
- ppm -		- - - - - - - - - - Percent - - - - - - - - - -					
300	0	1.35	.503	.250	1.35	.503	.250
300	10	.65	.099	.092	1.04	.191	.121
300	20	.71	.103	.099	1.02	.223	.126
300	30	.71	.092	.090	.92	.213	.121
300	40	.64	.118	.093	.79	.236	.125
300	50	.64	.109	.086	1.01	.217	.119
300	60	.70	.099	.107	.95	.188	.114
300	70	.65	.101	.077	.78	.172	.097
	$\bar{X}$	.78	.170	.119	.99	.256	.137
Treatment effect[2/]							
	N	**	**	**	ns	*	ns
	P	*	**	**	ns	**	**
	NP	ns	**	*	ns	ns	ns

[1/] Each value represents the mean of three replications.

[2/] *; **; ns = significant at the 5-percent level of probability; significant at the 1-percent level of probability; and nonsignificant, respectively.

Table 12. Concentrations of K, Ca, and Mg in various plant tissues averaged over all levels of nitrogen and phosphorus

Component	Nutrient		
	K	Ca	Mg
	- - - - - Percent - - - - -		
Mature needles	0.82	0.426	0.168
Immature needles	1.03	.303	.153
Immature stem	.91	.274	.156
Mature stem	.58	.247	.155
Taproot	.78	.170	.119
Lateral roots	.99	.256	.137

tissue (mature stem and taproot). Calcium accumulated to a greater degree in the mature needles, followed by immature needles. Lowest levels again were found in the mature stem and taproot. Since the mature needles no doubt contain the greatest concentration of chlorophyll, one would suspect magnesium to accumulate in this component. This was found to be true in the present study (Table 12).

These findings agree with observations of Meyer, Anderson, and Bohning (1960). They stated that potassium is found to be highest in actively growing tissues such as young leaves and root tips. The proportion of potassium is usually lower in seeds and mature tissues. They also indicated that a large part of plant calcium is found in the leaves, with more accumulating in mature than immature leaves. In the present study this was found to be true of loblolly pine seedlings.

Nutrient uptake in relation to maximum growth.--In terms of net biomass production of shoot and root systems (Table 4, 5, and 7) the treatment containing 100 ppm N and 10 ppm P was superior to the other combinations of nitrogen and phosphorus. Table 13 illustrates nutrient content of the various tissues of plants receiving the "optimum" treatment. Even though a direct comparison with the results of Thompson (1965) cannot be made, he found at 95 ppm N the following nitrogen concentrations: mature needles, 2.15 percent; immature stems and needles, 1.97 percent; woody stems and branches, 0.81 percent; and roots, 1.43 percent. The concentrations shown in Table 13 are in fair agreement with Thompson's except in roots. The difference, no doubt, is due to the fact that Thompson's value represents the nitrogen

Table 13. Nutrient concentrations of various tissues of plants treated with 100 ppm N and 10 ppm P and displaying maximum growth

Component	Nutrient				
	N	P	K	Ca	Mg
	- - - - - - - Percent - - - - - - -				
Mature needles	2.68	0.246	0.75	0.483	0.188
Immature needles	2.26	.322	1.15	.232	.127
Immature stem	1.24	.258	.92	.300	.141
Mature stem	1.06	.184	.74	.247	.152
Taproot	1.13	.144	.67	.156	.129
Lateral roots	2.28	.311	1.04	.388	.168

percentage of the entire root system. The presence of taproot tissue, which is relatively low in nitrogen, reduced his value for roots.

Thompson (1965) found phosphorus percentages of 0.323, 0.163, and 0.297 in immature stems and needles, woody stem, and roots, respectively, of plants displaying maximum growth. These values compare favorably with those found in the present study.

In the present study N and P concentrations coincident with maximum growth were somewhat higher than those of Fowells and Krauss (1959). They found growth of loblolly pine to be maximum at needle concentrations ranging from 1.7 to 2.3 percent N and 0.14 to 0.18 percent P. Differences in techniques, i.e., irrigation interval, length of growth period, etc., likely account for the difference.

Luxury consumption of nitrogen and phosphorus was apparent in this study. Maximum growth as previously mentioned was associated with the treatment containing 100 ppm N and 10 ppm P. As shown in Table 9 mature needles contained 2.68 percent N and 0.246 percent P. Increasing the supply of nitrogen to 200 ppm and 300 ppm reduced growth significantly, while increasing the nitrogen concentration of mature needles to 2.96 percent and 3.10 percent, respectively. Trends for the other components were similar. This observation tends to indicate luxury consumption of nitrogen at the higher rates of N supply.

Increasing the levels of phosphorus supply beyond 10 ppm P did not result in significant increases in phosphorus concentration of tissue. Rates of P greater than 10 ppm also had little effect on growth regardless of the N level. These observations tend to indicate that,

if luxury consumption of phosphorus occurred, it did so to a lesser degree than luxury consumption of nitrogen.

Nutrient Deficiency Symptoms

Deficiencies of both nitrogen and phosphorus resulted in reduced growth and development as well as conspicuous color abnormalities.

Nitrogen deficiency.--Plants grown in the absence of nitrogen (Plate 10) were stunted, developed few secondary needles, and were characterized by a pale green color. Abnormal coloration was not limited to any specific region but was more obvious on the secondary needles. Tips of the lower needles of a few plants developed necrosis late in the study. Needle length averaged only 10 cm as compared to approximately 20 cm for plants receiving 100 ppm N. Nitrogen-deficient plants produced long slender roots (Plate 9).

Nitrogen deficiency symptoms observed in this study were generally the same as has been observed for plants in general (Kramer and Kozlowski 1960); shortleaf pine, white pine, pitch pine, and red pine (Hobbs 1944); longleaf pine (Pessin 1937); loblolly pine (Fowells and Krauss 1959); jack pine (Swan 1960); and Scots pine (Hacskaylo, Finn, and Vimmerstedt 1969).

Although not measured, the angle formed between the secondary needles and stem was noted to be much more acute on plants receiving no nitrogen than those grown in complete solutions. The author was able to find no report of this characteristic in literature concerning conifers; however, Davidson and Judkins (1949) report that leaf petioles of nitrogen-deficient apple trees tend to form narrow angles with the stems.

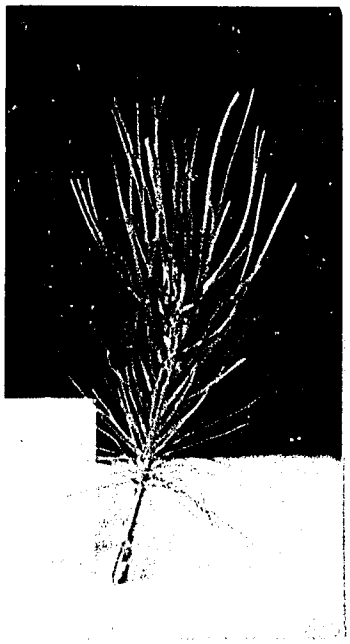


Plate 10. A typical nitrogen-deficient plant.

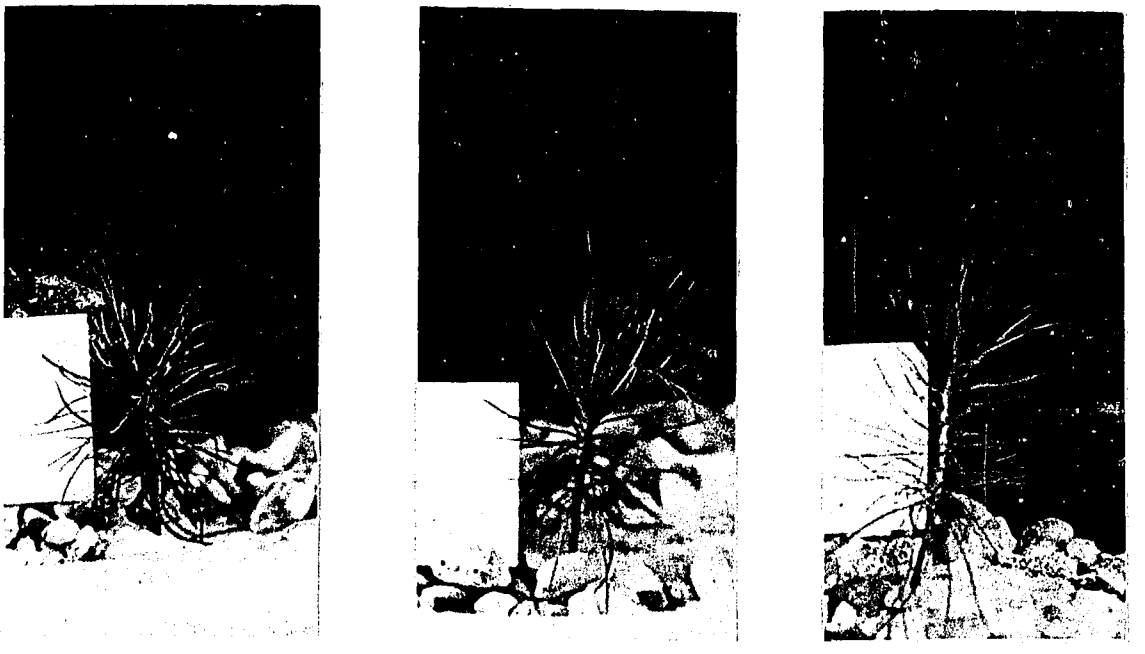
Levels of phosphorus apparently had little effect on the appearance of nitrogen-deficient plants.

Phosphorus deficiency.--Omission of phosphorus resulted in greatly stunted seedlings (Plate 11). With few exceptions, these plants produced only primary needles, which were very short and stiff. Needles turned bluish-green, then developed brown tips, and the necrotic condition finally extended to the base of the needles. Phosphorus-deficient plants, therefore, were characterized by brown needles on the lower part of the seedling and bluish-green needles concentrated in the terminal region. Although very little shoot elongation occurred, most plants grown in the absence of phosphorus survived throughout the study.

Roots of these plants were long, dark brown (almost black), with very little branching.

Phosphorus deficiency symptoms observed in this study were very similar to those described by Hobbs (1944), Swan (1960), and Hacskaylo, Finn, and Vimmerstedt (1969). However, with longleaf pine, Pessin (1937) found very little adverse effect of phosphorus deficiency. Plants grown without this element possessed normal green color, characteristic of plants grown in the complete nutrient solution. Fowells and Krauss (1959) also failed to observe any abnormal needle coloration but observed early needle abscision as the only phosphorus deficiency symptoms. Likewise, the work of Thompson (1965) produced no phosphorus deficiency symptoms; however, Thompson did not include zero levels in his experiment.

Increases in the level of nitrogen supplied to phosphorus-deficient plants in the present study seemed to accentuate phosphorus deficiency



a b c

Plate 11. Phosphorus-deficient plants, having been supplied with 100 ppm N (a), 200 ppm N (b), and 300 ppm N (c).

symptoms. As can be seen in Plate 11c, plants receiving 300 ppm N but no P displayed the bluish-green needle cast to a greater extent than did plants receiving lower rates of nitrogen.

Withholding both nitrogen and phosphorus resulted in plants similar to the one shown in Plate 12. These plants were similar to those deficient only in phosphorus. Plants deficient in both elements produced slightly more shoot elongation than the phosphorus-deficient plants, but less shoot growth than plants deficient only in nitrogen.

Results of Supplementary Test

As was mentioned in the methods chapter, a supplementary test with only one replication was established in an effort to obtain information relative to plant response to nitrogen and phosphorus levels not included in the main study. Figures 18 and 19 illustrate the shoot growth response to these treatments. The dashed line represents response to the supplementary treatments while the solid line depicts response to the main study treatments.

In the case of nitrogen, the two rates -- 25 and 75 ppm -- produced greater shoot elongation than did 100 ppm N (Plate 13). Although these data cannot be analyzed statistically, indications are that the lowest level of applied N (100 ppm) used in the main study may have been in the super-optimum range of nitrogen concentrations. One must bear in mind that the supplementary nitrogen treatments contained only one rate of P -- 30 ppm. However, results reported earlier in this paper have clearly indicated that 30 ppm is within the optimum range of phosphorus levels.

Plate 12. Seedling deficient in both nitrogen and phosphorus.

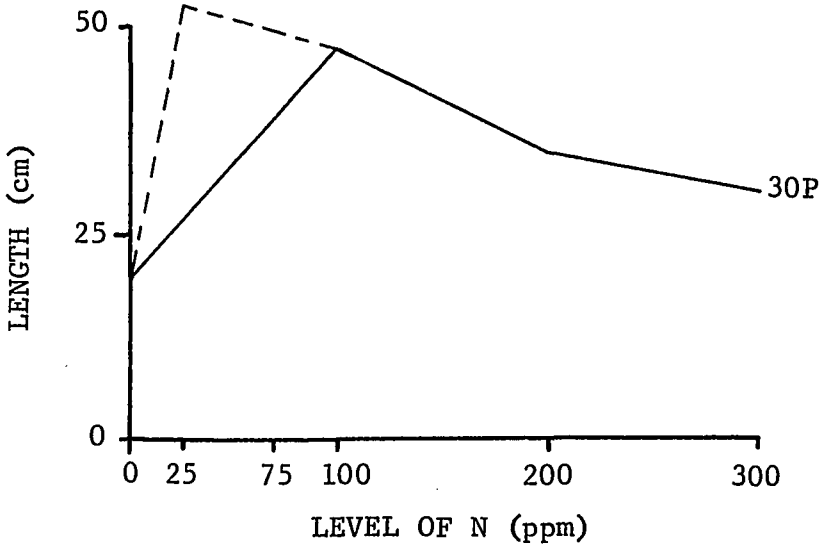


Figure 18. Shoot length response to nitrogen. Dashed line represents response to supplementary treatments.

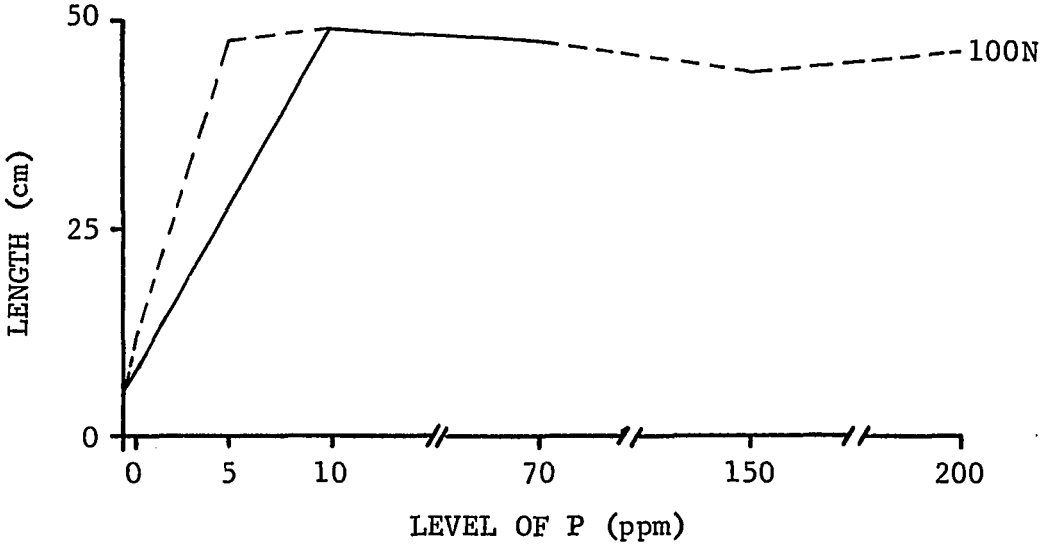


Figure 19. Shoot length response to phosphorus. Dashed line represents response to supplementary treatments.

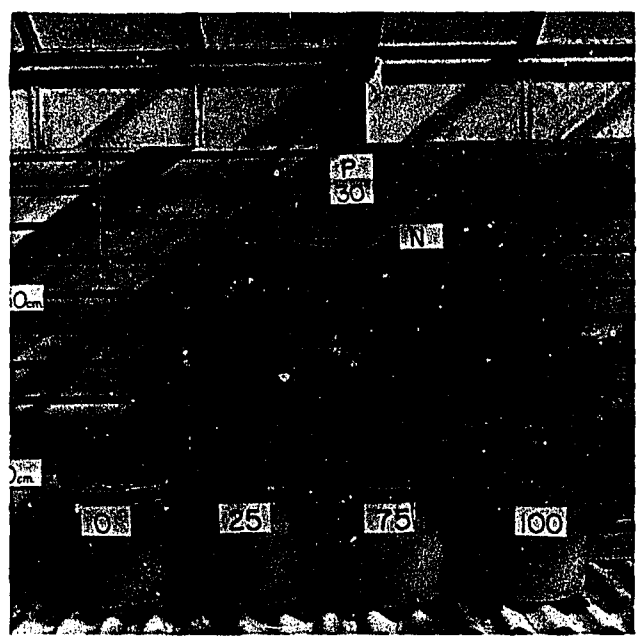


Plate 13. Seedlings supplied with 25 and 75 ppm N from the supplementary test compared to plants grown with 0 and 100 ppm N in the main experiment.

In the supplementary phosphorus series, two P levels (0.5 and 5 ppm) below those used in the main experiment and two higher levels (150 and 200 ppm) were tested (Figure 19). Shoot elongation of plants supplied with 0.5 ppm P was slightly greater than growth of plants receiving no phosphorus. The difference, however, is probably not significant. The supplementary treatment supplying 5 ppm P, on the other hand, yielded shoot length almost as great as those of plants receiving 10 ppm P. Although these values cannot be compared statistically, the differences between shoot length for 0.5 ppm P and 5 ppm P are thought to be real. In terms of plant height, the effects of 5 and 10 ppm P are not likely to be significantly different; however, seedlings treated with 5 ppm P were otherwise less vigorous than plants which received 10 ppm P (Plate 14). Fowells and Krauss (1959) found 1 ppm to be an adequate rate of phosphorus. The two higher phosphorus rates (150 and 200 ppm) used in the supplementary test produced shoot lengths which did not appear to differ significantly from 70 ppm P used in the main study. Other workers (Fowells and Krauss 1959 and McGee 1963) have also found that pines grow well over a wide range of phosphorus concentrations.

Results of the supplementary test, therefore, indicate that the optimum levels of N and P are somewhat lower than the 100 ppm N and 10 ppm P rates observed in the main experiment. Values of 25 to 75 ppm N and 6 to 8 ppm P may be nearer the true optimum levels of these elements.

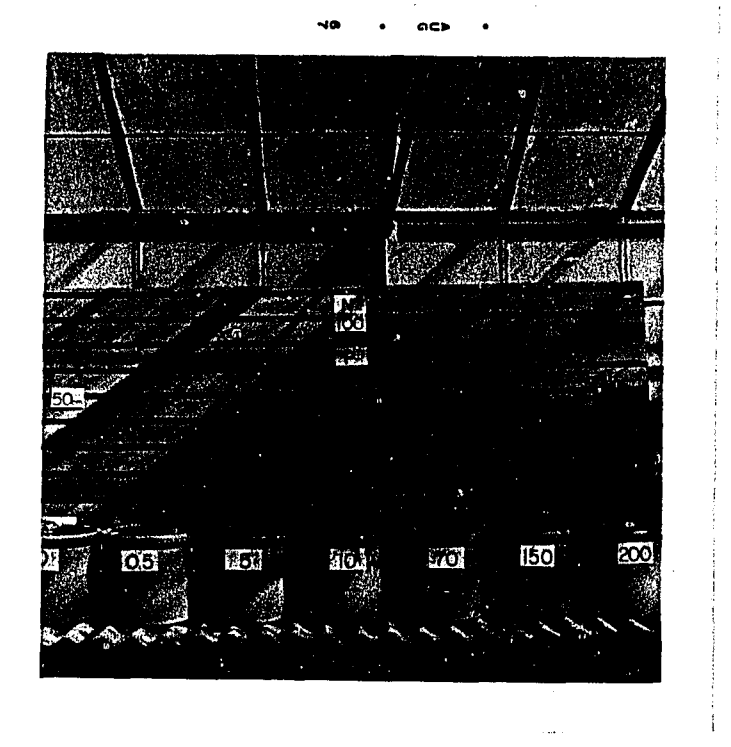


Plate 14. Seedlings supplied with 0.5, 5, 150, and 200 ppm P from the supplementary test compared to plants grown with 0, 10, and 70 ppm P in the main experiment.

SUMMARY AND CONCLUSIONS

This experiment was designed and conducted to investigate the effects of various levels and combinations of levels of nitrogen and phosphorus on the growth and development of loblolly pine seedlings. The study was conducted during the summer and fall of 1966 with a sand-culture technique in the School of Forestry and Wildlife Management greenhouse located on the Baton Rouge campus of Louisiana State University.

Four levels of nitrogen -- 0, 100, 200, and 300 ppm -- and eight levels of phosphorus -- 0, 10, 20, 30, 40, 50, 60, and 70 ppm -- were supplied singly and in all combinations. Other macro- and micronutrient elements were supplied at constant rates considered adequate for loblolly pine. A randomized block design with three replications was used, and within each block treatments were randomly assigned in a complete factorial. Once each day the cultures were irrigated with a semi-automatic device, each culture being completely saturated with nutrient solution. Solutions were recycled through the cultures for three weeks and then discarded and replaced with new solutions. Five seedlings per pot were grown for a period of nine months after initiation of treatments.

A supplementary test with only one replication was conducted simultaneously with the main study to test additional levels of nitrogen

and phosphorus. In this test phosphorus was supplied at 0.5, 5, 150, and 200 ppm, and nitrogen was supplied at 25 and 75 ppm. In the nitrogen series phosphorus was held constant at 30 ppm, and in the phosphorus series nitrogen was supplied at a constant rate of 100 ppm. These supplementary cultures were otherwise treated in the same manner as those in the main experiment.

After harvesting, the plants were stored in tightly sealed polyethylene bags at 2°C until they could be measured, dissected, and prepared for chemical analyses. The following measurements were made on each green plant: root volume, taproot length, number of primary lateral roots per 5-cm segment of the taproot, total length, length of each internode, shoot length, number of branches per whorl, and needle length. After dissecting and drying the plant parts at 70°C, weights of the following components were obtained: mature needles, immature needles, mature stem, immature stem, branches, entire shoot, taproot, lateral roots from each 5-cm segment of the taproot, and entire root system. Root/shoot ratios were calculated by dividing root weight by shoot weight. The ratio of immature needle mass to mature needle mass was designated "maturity index." The various plant components were then ground in a Wiley mill to pass through a 40-mesh screen for chemical analyses.

Nitrogen, phosphorus, potassium, calcium, and magnesium concentrations were determined for mature needles, immature needles, mature stem, immature stem, taproot, and lateral roots. Total nitrogen was determined by the improved boric acid Kjeldahl method, phosphorus by absorption spectrophotometry, potassium by flame emission

spectrophotometry, and calcium and magnesium by atomic absorption spectrophotometry.

The overall effects of nitrogen and phosphorus were tested by analysis of variance. Individual means were compared using orthogonal comparisons. Including growth variables and chemical concentration data, a total of 78 variables were examined.

Results of this study lead to the following conclusions:

1. Combinations of nitrogen and phosphorus had a significant effect on almost every variable measured.

2. Orthogonal comparisons conducted on shoot variables indicated 100 ppm to be the optimum level of nitrogen for maximum shoot growth and development. The two highest levels of nitrogen depressed growth and are therefore considered to be in excess of the optimum level of nitrogen.

3. Increasing the level of applied nitrogen delayed shoot-tissue maturity.

4. The greatest mass of roots was produced at 100 ppm N; however all levels of applied nitrogen reduced root length and numbers of primary lateral roots.

5. Root/shoot ratio was found to be a function of nitrogen supply, being reduced to approximately the same ratio by all three rates of applied nitrogen.

6. Phosphorus significantly increased both shoot and root growth; however, 10 ppm P appeared to be as effective as the other rates of this element.

7. Percent nitrogen and phosphorus increased in all tissues as the level of the respective element in the growth medium was increased.

8. The concentrations of K, Ca, and Mg were, in most cases, decreased with increases in nitrogen and phosphorus supply.

9. The nitrogen-phosphorus interaction was significant for many shoot and for some root variables. Orthogonal comparisons, however, revealed virtually all of the interaction effect to be due to the inclusion of zero levels of nitrogen and phosphorus. The author concludes, therefore, that for rates in excess of 100 ppm N and 10 ppm P the response to nitrogen occurred independently of the rate of applied phosphorus and vice versa, thus indicating the absence of interaction beyond these levels. Since the phosphorus response curves were found to be virtually flat between 10 and 70 ppm P, one may further conclude that the plant reacted to these rates of P as though only one level of this element was being supplied. All non-zero rates apparently were within the optimum range of P concentrations. A meaningful interaction between N and P would likely have been observed had rates of applied phosphorus above and below the optimum range been included in the study.

10. Nitrogen and phosphorus deficiency symptoms of loblolly pine are very similar to those of other pines. Nitrogen deficiency was characterized by poor shoot growth and pale green foliage. Phosphorus-deficient plants were severly stunted, and needles were bluish-green in the terminal region and brown on the lower part of the seedling.

The above statements are, of necessity, based on results of the main experiment. However, the trends noted from the supplementary test should not be disregarded. Indications are that nitrogen rates of 25

and 75 ppm were as effective as 100 ppm N. The optimum level of nitrogen for loblolly pine very likely is somewhat less than 100 ppm. Similarly, 5 ppm of phosphorus was almost as effective as 10 ppm; however 0.5 was no more effective than the zero level. The lower limit of the optimum range for phosphorus is probably near 6 to 8 ppm. No real decrease in growth was observed at 200 ppm P. This paper then supports the thesis that the phosphorus requirement of loblolly pine is relatively low, but the species grows vigorously over a wide range of phosphorus concentrations.

The ultimate practical aim of loblolly pine nutrition research is the collection of enough sound data to enable the formulation of fertilizer recommendations for this species. There are, no doubt, many fundamental physiological questions remaining to be answered through sand or solution culture methods; however, before fertilizer recommendations can be made, responses to added nutrients must be measured on numerous soil types on which loblolly pine occurs. The author feels that there are three basic needs in loblolly pine fertilization research: (1) the continuance of factorially arranged experiments, designed to detect interactions among nutrient elements, (2) investigations of genetic x nutritional interactions, and (3) coordination of research techniques.

To fulfill the first need, future investigators should begin with short term soil-pot studies in the greenhouse, using selected soils as the growth medium. In the greenhouse one may test all combinations of a wide range of rates in a study that would be prohibitively large using field-plot techniques. A logical follow-up to this type of study

would be the field testing of certain combinations of nutrient rates which appear most promising in the greenhouse. Eventually researchers must, of course, consider a wide spectrum of factors such as age, stand density, competing vegetation, site variation, and many others. Beginning in the greenhouse one could perhaps identify certain soils which are likely to respond to fertilizers in the field environment.

The second need involves consideration of the possibility that fertilizer response is partially a function of genetic composition of individual trees. Again, this research can begin with soil-pot studies in the greenhouse. This work should be closely coordinated with geneticists in an effort to identify genetic stock with the capacity to efficiently utilize added nutrients.

Thirdly, an effort should be made to better coordinate research in this area. Obviously one researcher cannot study the fertilizer requirements of loblolly pine on all soils within the natural range of this species. Those concerned with this problem should attempt to employ similar technique, but under different environments. Lack of coordination in methodology is a major cause for disparity in published results today.

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APPENDIX A

ANALYTICAL PROCEDURES FOR CHEMICAL ANALYSES

ANALYTICAL PROCEDURES FOR CHEMICAL ANALYSES

Nitrogen (Horwitz et al. 1960)

Reagents.--

H_2SO_4, concentrated.

Kel-Pac Powders (15 g K_2SO_4 + 0.7 g HgO).

NaOH solution, 50% and containing 7 to 8 g of $Na_2S_2O_3 \cdot 5H_2O$ per liter.

H_3BO_3 solution, 4%.

Methyl-red indicator, 0.1%.

HCl, 0.1 N.

Sample preparation.--Ground plant material weighing 1.4 g was placed in a 500-ml Kjeldahl flask with one Kel-Pak. Twenty-five ml of concentrated sulfuric acid was then added to each flask.

Procedure.--The flask was then placed on a digestion rack and allowed to digest at approximately 350°C for 2 hours. Every 30 minutes the flask was rotated 180° to insure complete oxidation of carbonaceous material. The sample was allowed to cool for 30 minutes, then diluted with 150 ml of distilled water, mixed, and allowed to cool for an additional 30 minutes. Twenty-five ml of 4 percent boric acid containing methyl-red indicator along with 50 ml of distilled water was added to a 500-ml Erlenmeyer flask. The flask was then placed on the distillation unit with the glass delivery tube just under the surface

of the boric acid. After adding three or four pieces of mossy zinc to the Kjeldahl flask, 125 ml of 50 percent sodium hydroxide-sodium thiosulfate solution was carefully added to each Kjeldahl flask. The sample solution was gently mixed and placed on the distillation unit. After approximately 30 minutes of distillation and only 25 to 30 ml of the sample solution remaining in the Kjeldahl flask, the Erlenmeyer flask containing the distillate was removed from the distillation unit, and the solution was titrated with 0.1 N HCl to an end point indicated by a color change from yellow to red. Two blank determinations were made with each set of unknowns. Blank samples were processed by the above procedure but contained no plant material.

Percent nitrogen was calculated by the following equation:

$$\%N = (T - B) \times N \times \frac{1.4}{s}$$

in which,

T = sample titration, ml standard acid.

B = blank titration, ml standard acid.

N = normality of standard acid.

s - sample weight, g.

Phosphorus, potassium, calcium, and magnesium (Jackson 1958)

Reagents.--

HCl, 3 M.

$LaCl_3$, 10%.

Vanadomolybdate reagent, prepared by dissolving 40 g of ammonium tetrahydrate in 400 ml of hot distilled H_2O and cooled. Two grams of ammonium metavanadate were then dissolved in 250 ml of hot distilled H_2O, cooled, and mixed with 250 ml of 70% perchloric acid. The

molybdate solution was then slowly added to the vanadate solution and diluted to 2 liters.

Phosphorus stock solution (1000 ppm P), prepared by dissolving 4.394 g of KH_2PO_4 in distilled water. Ten ml of vanadomolybdate reagent was added and the solution diluted to 1 liter with distilled water.

Potassium stock solution (1000 ppm K), prepared by dissolving 1.907 g of KCl in 1 liter of distilled water.

Calcium stock solution (1000 ppm Ca), prepared by dissolving 2.500 g of clear calcite ($CaCO_3$) in 10 ml of N HCl. The solution was then boiled to expel CO_2, then diluted to 1 liter with distilled water.

Magnesium stock solution (1000 ppm Mg), prepared by dissolving 1.000 g of metallic Mg foil in 10 ml of N HCl, then diluted with distilled water to 1 liter.

Sample preparation.--A 2-gram sample of plant material was placed in a porcelain crucible and dry-ashed in a muffle furnace at 500°C for 8 hours. The ash was then taken up in 3 M HCl. The crucible was placed on a hot plate and heated until vapor ascended from the solution but was removed before boiling occurred. This step helped to insure complete dissolution of the elements contained in the ash. This solution was then transferred to a 100-ml volumetric flask and brought to volume with distilled water and mixed thoroughly. Appropriate aliquots of the working solution were then removed for the subsequent determination of P, K, Ca, and Mg.

Procedure for phosphorus determination.--A 5-ml aliquot of the working solution was transferred to a 50-ml volumetric flask. Ten ml

of vanadomolybdate reagent were then added to the 50-ml flask. The solution was brought to volume with distilled water. Standard solutions of 0, 2, 4, 6, 8, and 10 ppm P were prepared to diluting appropriate aliquots of a 1000 ppm P stock solution as described above. With the wave length set at 400 millimicrons, absorbance (optical density) was measured using the Bausch and Lomb Model 20 colorimeter. Parts per million phosphorus in the sample was read from the standard curve prepared from absorbance values of the standard solutions. Data were later converted to percent.

Procedure for K, Ca, and Mg.--A 5-ml aliquot of the working solution was transferred to a 50-ml volumetric flask. Five ml of 10 percent $LaCl_3$ were then added to reduce interference from phosphate and sulfate ions. The solution was then brought to volume with distilled water and mixed thoroughly. Portions of this solution were used for the determination of potassium with the Beckman DU flame photometer, and calcium and magnesium with the Jerrell-Ash atomic absorption analyzer. Standard solutions of the following concentrations were used in construction of standard curves for each element.

K-- 0, 5, 10, 20, 40, and 60 ppm.

Ca-- 0, 2.5, 5, 10, 15, 20, and 25 ppm.

Mg-- 0, 0.25, 0.5, 1, 1.5, 2, 2.5, 3, and 4 ppm.

Potassium, calcium, and magnesium concentration in the unknown samples were read from the standard curve for the respective element. Data were later converted to percent.

APPENDIX B

STATISTICAL ANALYSES

In all tables in Appendix B the following notations are used:

** = Significant at the 0.01 level of probability

* = Significant at the 0.05 level of probability

ns = Nonsignificant.

Table 14. Analysis of variance of effect of treatments on shoot length

Source of variation	Degrees of freedom	Sums of squares	Mean squares	F
Block	2	222.15		
N	3	8269.67	2756.56	68.9**
ON vs 100-300N	1	5070.25	5070.25	126.7**
100N vs 200&300N	1	2754.15	2754.15	68.8**
200N vs 300N	1	440.68	440.68	11.0**
P	7	7321.73	1045.96	26.1**
OP vs 10-70P	1	7148.79	7148.79	193.0**
Remainder	6	172.94	28.82	<1ns
NP	21	1506.51	71.74	1.8*
(ON vs 100-300N)(OP vs 10-70P)	1	766.38	766.38	18.2**
Remainder	20	740.11	37.00	<1ns
Error	62	2480.51	40.008	
Total	95	19,800.56		

Table 15. Analysis of variance of effect of treatments on shoot weight

Source of variation	Degrees of freedom	Sums of squares	Mean squares	F
Block	2	54.53		
N	3	3837.12	1279.04	103.8**
ON vs 100-300N	1	2176.02	2176.02	176.6**
100N vs 200&300N	1	1511.65	1511.65	122.7**
200 vs 300N	1	148.68	148.68	12.1**
P	7	1241.86	177.41	14.4**
OP vs 10-70P	1	1128.26	1128.26	91.6**
Remainder	6	113.60	18.93	1.5ns
NP	21	660.51	31.45	2.6**
(ON vs 100-300N)(OP vs 10-70P)	1	312.29	312.29	25.4**
Remainder	20	339.22	16.97	1.4ns
Error	62	763.89	12.32	
Total	95	6557.90		

Table 16. Analysis of variance of effect of treatments on mature needle weight

Source of variation	Degrees of freedom	Sums of squares	Mean squares	F
Block	2	6.46		
N	3	405.17	135.06	69.1**
ON vs 100-300N	1	173.72	173.72	88.9**
100N vs 200&300N	1	218.08	218.08	111.6**
200N vs 300N	1	13.28	13.28	6.8**
P	7	116.94	16.71	8.6**
OP vs 10-70P	1	103.09	103.09	52.8**
Remainder	6	13.85	2.31	1.2ns
NP	21	79.52	3.79	1.9*
(ON vs 100-300N)(OP vs 10-70P)	1	9.12	9.12	4.7**
Remainder	20	70.40	3.52	1.8*
Error	62	121.13	1.95	
Total	95	729.22		

Table 17. Analysis of variance of effect of treatments on needle length

Source of variation	Degrees of freedom	Sums of squares	Mean squares	F
Block	2	7.39		
N	3	1084.37	361.46	107.6**
ON vs 100-300N	1	1017.01	1017.01	303.1**
100N vs 200&300N	1	58.37	58.37	17.4**
200N vs 300N	1	9.29	9.29	2.7ns
P	7	2281.95	325.99	97.2**
OP vs 10-70P	1	2259.69	2259.69	673.5**
Remainder	6	22.26	3.71	1.1ns
NP	21	247.26	11.77	3.5**
(ON vs 100-300N)(OP vs 10-70P)	1	26.66	26.66	7.9**
Remainder	20	220.60	11.03	3.3**
Error	62	208.02	3.35	
Total	95	3828.99		

Table 18. Analysis of variance of effect of treatments on number of branches

Source of variation	Degrees of freedom	Sums of squares	Mean squares	F
Block	2	3.82		
N	3	1150.38	383.46	92.7**
ON vs 100-300N	1	1079.34	1079.34	260.9**
100N vs 200&300N	1	66.72	66.72	16.1**
200N vs 300N	1	8.96	8.96	2.2ns
P	7	648.89	92.70	22.4**
OP vs 10-70P	1	614.18	614.18	148.5**
Remainder	6	34.71	5.79	1.4ns
NP	21	212.60	10.12	2.4**
(ON vs 100-300N)(OP vs 10-70P)	1	51.28	51.28	12.4**
Remainder	6	161.28	8.06	1.9*
Error	62	256.48	4.14	
Total	95	2272.14		

Table 19. Analysis of variance of effect of treatments on total weight of root system

Source of variation	Degrees of freedom	Sums of squares	Mean squares	F
Block	2	4.94		
N	3	263.00	87.67	55.5**
ON vs 100-300N	1	113.77	113.77	71.9**
100N vs 200&300N	1	138.43	138.43	87.4**
200N vs 300N	1	10.76	10.76	6.8*
P	7	152.99	21.87	13.8**
OP vs 10-70P	1	137.32	137.32	86.7**
Remainder	6	15.68	2.61	1.7ns
NP	21	59.08	2.81	1.8*
(ON vs 100-300N)(OP vs 10-70P)	1	5.79	5.79	3.6**
Remainder	20	53.29	2.66	1.6ns
Error	62	98.12	1.58	
Total	95	578.13		

Table 20. Analysis of variance of effect of treatments on root volume

Source of variation	Degrees of freedom	Sums of squares	Mean squares	F
Block	2	164.64		
N	3	6318.82	2106.27	36.9**
ON vs 100-300N	1	2483.72	2483.72	43.5**
100N vs 200&300N	1	3473.92	3473.92	60.9**
200N vs 300N	1	366.97	366.97	6.4*
P	7	5365.67	766.52	13.4**
OP vs 10-70P	1	4858.03	4858.03	85.2**
Remainder	6	507.64	84.61	1.5ns
NP	21	1446.87	68.90	1.2ns
Error	62	3536.15	57.03	
Total	95	16,832.15		

Table 21. Analysis of variance of effect of treatments on number of primary lateral roots

Source of variation	Degrees of freedom	Sums of squares	Mean squares	F
Block	2	44.62		
N	3	1261.56	420.52	9.4**
ON vs 100-300N	1	1218.20	1218.20	27.3**
100N vs 200&300N	1	35.76	35.76	<1ns
200N vs 300N	1	9.08	9.08	<1ns
P	7	1857.56	265.37	5.9**
OP vs 10-70P	1	1426.83	1426.83	31.9**
Remainder	6	430.73	71.79	1.6ns
NP	21	1278.07	60.86	1.4ns
Error	62	2769.63	44.67	
Total	95	7211.44		

Table 22. Analysis of variance of effect of treatments on root/shoot ratio

Source of variation	Degrees of freedom	Sums of squares	Mean squares	F
Block	2	0.2050		
N	3	18.0850	6.030	181.1**
ON vs 100-300N	1	18.0710	18.0710	542.7**
100N vs 200&300N	1	.0130	.0130	<1ns
200 vs 300N	1	.0006	.0006	<1ns
P	7	.8139	.1163	2.2**
OP vs 10-70P	1	.7486	.7486	22.7**
Remainder	6	.0653	.0108	<1ns
NP	21	1.3060	.0622	1.8*
(ON vs 100-300N)(OP vs 10-70P)	1	.3405	.3405	10.3**
Remainder	20	.9653	.0483	1.4ns
Error	62	2.0640	.0333	
Total	95	22.4740		

Table 23. Analysis of variance of effect of treatments on percent N in mature stems

Source of variation	Degrees of freedom	Sums of squares	Mean squares	F
Block	2	0.0564		
N	3	12.312	4.104	109.7**
P	7	23.217	3.317	88.7**
NP	21	2.778	.1323	3.5**
Error	62	2.318	.0374	
Total	95	40.682		

Table 24. Analysis of variance of effect of treatments on percent P in mature needles

Source of variation	Degrees of freedom	Sums of squares	Mean squares	F
Block	2	0.0147		
N	3	2.5690	0.8562	93.8**
P	7	.7717	.1102	12.1**
NP	21	.4948	.0236	2.6**
Error	62	.5660	.0091	
Total	95	4.416		

VITA

Bobby G. Blackmon was born on May 17, 1940, in Rodessa, Caddo Parish, Louisiana, to William Joshua and Myrtie Wiggins Blackmon. He attended primary and secondary school in Logansport, Desoto Parish, Louisiana, and was graduated from Logansport High School in 1958.

During the summer of 1958 he attended Stephen F. Austin State College. In September 1958 he transferred to Louisiana Polytechnic Institute from which he was granted the Bachelor of Science degree with a major in forestry in June 1962.

He enrolled as a graduate student at Duke University in June 1962 and was graduated with the Master of Forestry degree with a major in forest soils in June 1963.

In July 1965 Blackmon entered Louisiana State University as a graduate student in forest soils. Until August 1967 he was a graduate research assistant in the School of Forestry and Wildlife Management. He is now a candidate for the Doctor of Philosophy degree.

His professional experience includes two years as a research assistant in soil fertility at the University of Arkansas, Rice Branch Experiment Station, Stuttgart, Arkansas, from 1963 to 1965. Since September 1967 he has been employed as associate silviculturist in forest soil fertility research with the U. S. Forest Service, Southern Forest Experiment Station, at Stoneville, Mississippi.

He is married to the former Sarah Avery and they are the parents of three sons, Glenn, Bryan, and Douglas.

EXAMINATION AND THESIS REPORT

Candidate: Bobby Glenn Blackmon

Major Field: Forestry

Title of Thesis: RESPONSE OF LOBLOLLY PINE (Pinus taeda L.) SEEDLINGS TO VARIOUS LEVELS AND COMBINATIONS OF NITROGEN AND PHOSPHORUS

Approved:

Norwin E. Linnartz
Major Professor and Chairman

Max Goodrich
Dean of the Graduate School

EXAMINING COMMITTEE:

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Date of Examination:

June 30, 1969