MINERAL NUTRITION OF FOREST TREE SEEDLINGS

by

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INTRODUCTION

The application of inorganic fertilizers to correct mineral nutrient deficiencies of planting sites may significantly improve the establishment and growth of hardwood forest plantations. It is well known that some soils do not have a sufficient supply or even an initial supply of these elements for the seedlings' needs. The major problems confronting the use of fertilizers to increase the growth of planted trees, therefore, are proper choice of fertilizer and determination of the amount to be used. The ability of tree seedlings to absorb and utilize mineral nutrients from the soil must be understood more thoroughly, however, before fertilizers can be used efficiently and economically.

Many fertilizer experiments have been conducted with forest tree seedlings, but because they usually were on a trial-and-error basis, little information has been gained as to the mineral nutrient requirements. For various reasons, past experiments have included too few observations on mineral nutrient status of soils and tree seedlings to determine if mineral deficiencies really existed, and if so, to what extent they were corrected by the fertilizer application. It is imperative that the nutrient needs of each forest tree species be known in order to evaluate properly the benefit and future place of fertilization in the establishment of forest plantations.

Three general approaches have been used to evaluate the mineral nutrient requirements of forest tree seedlings: (1) soil analysis, (2) fertilizer trials, and (3) foliar analysis. Each method has proven to have only limited value when used alone in diagnosing nutrient

deficiencies. It is now commonly believed that all three methods must be coordinated to evaluate accurately the soil-plant relationships that affect the nutrition and growth of tree seedlings.

The mineral nutrition of forest tree seedlings is conditioned by a number of factors seldom considered to be very critical with agricultural and horticultural crops. For example, (1) planting often is done on rather adverse sites where mineral nutrients, organic matter, soil moisture, and available light are deficient, and (2) many forest tree species are able to extract and utilize mineral nutrients efficiently from difficultly soluble sources by means of a symbiotic association with mycorhizal fungi. Very few studies have been conducted with tree seedlings where these factors were investigated under controlled conditions, and even fewer studies have been concerned specifically with the hardwood species that are commonly planted.

Investigations were started in 1962 to evaluate the mineral nutrition of hardwood tree seedlings, using the three general approaches previously mentioned, in relation to several soil and site factors associated with some frequently planted forest, prairie, and old field soils in Iowa and Missouri. Northern red oak (Quercus rubra L.) was used as the major test species, but black walnut (Juglans nigra L.), green ash (Fraxinus pennsylvanica Marsh.), and cottonwood (Populus deltoides Bartr.) also were included in the study. Emphasis was placed on use of seedlings because many hardwood plantings have not been successful because of unfavorable conditions during the critical first year or two after establishment. The soil-site factors investigated

are believed to have contributed significantly to these unfavorable conditions.

Specifically, the investigations reported here were designed to: (1) evaluate the nutrient status of the soils and the fertilizer response of red oak seedlings; (2) establish optimum rates of nitrogen fertilization and optimum foliar nitrogen content of red oak seedlings; (3) evaluate the benefit of lime to red oak seedlings; (4) evaluate light intensity-fertilizer interactions in the growth and nutrition of red oak seedlings; (5) explore the mycorhizal relationships of red oak seedlings; and (6) compare the growth and nutrient relationships among the various tree species on the different soils.

The results of these investigations provide an insight into the basic problem in the use of fertilizers in establishing hardwood plantations on the soils tested. Some specific fertilizer recommendations can be made at the present time but the major contribution of these studies is to demonstrate that nutrition and growth of hardwood tree seedlings is affected by a number of factors, and that a more scientific approach must be followed if fertilization is to be taken from the trial-and-error stage and become an integral step in the establishment of hardwood plantations.

REVIEW OF LITERATURE

Interest in forest tree nutrition has increased rapidly in the past decade. A recent symposium published by Duke University (1959) considered a number of topics relating to basic and applied research in the field of inorganic nutrition of forest trees. Excellent reviews of the progress and problems in mineral nutrition of forest trees have been prepared by Gessel (1962) and Leyton (1958).

In general, the research in forest tree nutrition has been conducted to: (1) determine the relative mineral nutrient requirements of various tree species; (2) determine factors affecting the mineral nutrition of forest trees; and (3) develop methods of diagnosing nutrient needs.

Soil Fertility and Forest Fertilization

Soil fertility requirements

Many investigators have been misled by the fact that tree species may grow satisfactory on relatively infertile soils and have concluded that they have low mineral nutrient requirements. This only partly is true because forest trees appear to have a greater ability to extract sufficient nutrients, even from the poorest soils, than many plants.

Rennie (1955) observed for several forest tree species groups that the uptakes of potassium and phosphorus were considerably lower than those for agricultural crops, but hardwood forest took up almost as much calcium, pine one-fifth, and other conifers one-half as much as crops. He believed, however, that a truer picture of nutrient demands

of the two crops may be obtained by comparing uptake relative to the soil nutrient-status of their respective sites. Following this approach, he found that the nutrient demands of forest trees relative to the soil nutrient-status of their sites were all greater than the nutrient demands of agricultural crops upon agricultural soils.

Mayer-Krapoll (1956) has cited some nutrient requirements of plantings of several forest tree species. From the quantities cited, it would appear that supplemental fertilization would be necessary on most sites to obtain maximum yields. For example, oak plantings may require 50 to 60 kg N, 80 kg P_2O_5, 80 to 100 kg K_2O, and 40 to 50 kg CaO per hectare. Only a part of these nutrients could be supplied by the soil on an average site.

Individual forest tree species often show varying degrees of response to differences in soil fertility. Some investigators have taken this as evidence of differences in mineral nutrient requirements.

Wilde and Patzer (1940) and Wilde (1958) have established nursery soil fertility standards for several hardwood species on the basis of soil fertility measurements under stands with good growth rates. In general, the hardwood species appear to require a moderate to high level of nursery soil fertility in comparison with some less-exacting pine species. Hardwood species such as black walnut, white ash, white oak, tulip poplar, and basswood require high fertility, whereas yellow birch, northern red oak, and largetooth aspen do well under moderate but stable soil fertility levels.

Mitchell and Chandler (1939) compared the relative nitrogen requirements of several hardwood species and found rather large differ-

ences with which they were able to categorize the various species. Species such as red, white, and chestnut oak, red maple, and aspen made satisfactory growth on relatively nitrogen deficient soils, beech, sugar maple, pignut hickory, and black gum were intermediate in their nitrogen requirements, and yellow poplar, white ash, and basswood attained maximum growth only on sites with high nitrogen supplying capacity.

Other workers have observed differences in response to the application of fertilizers, which also indicates differences in mineral nutrient requirements. For example, McComb (1949) applied fertilizers to three hardwood species growing on surface soils and found that black locust did not respond to nitrogen, whereas the same soils were nitrogen deficient for ash, elm, and oak. Curlin (1961) observed that nitrogen stimulated the height growth of hazel in the first growing season, phosphorus that of white oak in the second and third, but red oak and sugar maple showed no response on his soils.

Previous fertilizer trials

A rather voluminous literature now exists in the field of forest fertilization. Several hundred abstracts of research results from fertilizer trials made over the world have been compiled by White and Leaf (1956). More general treatments of the practical aspects of this subject have been given by Brüning (1959), Galoux (1954), Mayer-Krapoll (1956), Stoeckeler and Arneman (1960) and Wilde (1958, 1961).

The application of fertilizers to correct mineral nutrient deficiencies on planting sites for forest tree seedlings has been tested by a number of investigators. The results of these experiments, in

general, have been variable. Only a few of the earlier studies which deal specifically with fertilizing newly planted hardwoods will be reviewed.

Cummings (1941) applied 27 mixtures of nitrogen, phosphorus, and potassium fertilizers, peat and limestone to three forest tree species at the time of planting on adverse sites. No marked superiority over untreated trees was noted in height increment during the first two years, although differential effects of the individual nutrients were indicated for the different species.

The application of a complete fertilizer to black locust planted on a compact subsoil deficient in mineral nutrients was found, by Denuyl (1944), to result in a marked increase in height, diameter, and root growth in comparison with untreated controls. The effect of the fertilizer was still evident after four years, when the study was concluded.

Holsoe (1941) studied the effect of a complete fertilizer on tree growth on eroded soils, and showed that, even when the fertilizer was placed six inches below the soil surface, weed growth was increased and only the fast-growing tree species could compete with it. He recommended that slow-growing, intolerant tree species should not be fertilized when planted unless weed competition could be prevented.

McComb (1949) tested the response of planted hardwood seedlings to nitrogen and phosphorus applied in both loose and briquetted form. He concluded that under average conditions in eroded old fields in Iowa, fertilizer response with transplant and seedling stock will be small and of little practical significance for most hardwood species.

His investigations also indicated that as the residual soil nitrogen supply increased, growth response to nitrogen fertilizer decreased. On a soil with residual soil nitrogen at 600 pounds per acre the response of elm to added nitrogen was 600 percent, while on another soil containing 1900 pounds residual nitrogen, responses were small. The evidence suggested that about 2000 pounds total nitrogen per acre is a level above which seedling nitrogen responses would not be expected.

McComb also found that phosphorus was consistently and significantly deficient in the subsoils of the Lindley series. Seedling responses to phosphorus, however, were smaller than to nitrogen. On O'Neill soil, a marked root growth response to phosphorus was obtained with red oak. Potassium was not deficient on O'Neill or Clarion soils.

Better growth of red oak and green ash on Lindley forest soil, as compared to prairie Clarion and Tama, was noted. Differences in soil organic matter and mycorhizal factors were used to explain the superiority of the forest soil.

After reviewing the early work with fertilizers, Wilde (1958) concluded that the conflicting results of these trials could be attributed to several factors, the first of which was insufficient knowledge of soil chemistry, action of fertilizers, and nutrient requirements of tree species when the trials were initiated. Other causes listed, but of no less importance, include competition of weed vegetation which also responded to the fertilizer and deprived the trees of moisture, and adverse climatic conditions which not only annulled the benefit of the fertilizer treatment but made such treatments harmful.

Other Factors Affecting Tree Growth and Nutrition

Soil reaction

Very few studies have shown a significant, direct relation between soil pH and tree growth. On this subject, Wilde (1954) commented that too many attempts have been made to interpret soil fertility problems in terms of pH and to ignore the effect of other factors intimately associated with soil reaction. In an earlier paper, Wilde (1934) concluded that soil reaction affects the growth of tree seedlings primarily by influencing the availability of nutrients, potency of toxic agents, activity of useful and parasitic soil organisms, and physical conditions of the soil. Åslander (1952) also has concluded that it is a lack of plant nutrients and not an acid reaction that makes an acid soil unproductive.

The importance of considering the indirect effect of soil pH on the availability of nutrients is demonstrated in a study by Thomson and McComb (1962). The results of their experiment indicated a strong correlation between soil pH and site index, but regression analyses showed that this relation was coincident with exchangeable calcium or potassium. Thus, pH was an indicator but not the cause of site index variations. Further examination indicated that on the sites sampled, potassium and to a lesser extent calcium were the nutrient elements most limiting walnut growth.

Liming acid soils has become a standard agricultural practice to improve the fertility of such soils. The response of soils and plants to lime have been reviewed comprehensively by Coleman *et al.* (1958).

According to these workers many facets of the soil environment are changed when an acid soil is limed. Among these they include changes in the solubility and availability of the macro- and micro-nutrients.

Nitrogen mineralization usually increases when acid soils are limed (Allison and Sterling 1949). Bacteria which carry out nitrification are not active in soil with pH less than 5.5, and under these conditions liming can increase the rate of oxidation of ammonia to nitrate (Russell 1950). This will have the effect of supplying a different source of nitrogen to the plants. However, Thompson et al. (1954) were unable to find any significant change in nitrogen mineralization with pH at constant nitrogen content, which suggests that the previous view that liming stimulates mineralization reactions may be only partly correct.

The availability of soil phosphate to plants appears to increase as acid soils are limed to the vicinity of neutrality (Black 1957), although overliming has been found to decrease the availability of phosphorus temporarily on some soils (Pierre and Browning 1935). According to Black (1957), liming can activate two processes that releases soil phosphorus and one that locks it up. Phosphorus availability may be increased by hydrolysis of iron and aluminum phosphate and by mineralization of organic phosphorus. On the other hand, phosphorus may become non-available by the formation of relatively insoluble calcium phosphates.

The availability of soil potassium also may be increased when acid soils are limed but there is little agreement as to the magnitude or

even the direction of the effect, which usually is not large in any case (Reitemeier 1951).

Liming can modify the solubilities of a number of the micronutrients, leading to the alleviation of toxicities in some instances, and to the production of deficiencies in others (Coleman et al. 1958). The relation between the availability of the micronutrients and the lime content, however, may vary considerably under different soil conditions.

Manganese, which can be toxic under some soil conditions, often becomes deficient when acid soils are limed to pH 6.5 and above (Mulder and Gerretsen 1952). The solubilities and availabilities of copper, zinc, and iron generally decrease when soils are limed (Brown and Holmes 1956 and Peech 1941). Boron may become deficient on limed soils because of the fixation of the borate ion, and also because boron requirements of plants appear to be greater under conditions of abundant calcium supply (Berger 1949). Molybdenum reacts much like phosphorus, with the solubility and availability of the molybdate ion being rather low in acid soils and increasing considerably upon liming (Davies 1956).

Several investigators have reported significant growth responses after adding lime to forest tree seedlings growing on acid nursery and forest soils in Europe (Beltram 1950, Mayer-Krapoll 1956, Němec 1950 and Wittich 1952). However, little is known about the lime requirements of forest tree species in this country. More often than not, liming has proven to be detrimental to the growth of tree seedlings.

For example, Lunt (1947) found that liming of Cheshire loam produced marked growth response in hybrid poplars, sugar maple, and white

ash, but had an adverse effect on red pine, Norway and white spruce, and red oak. Wilde (1946) found that lime produced a significant response with American elm only if soluble nitrogen was added, indicating that the depressing effect of the limestone was due to stimulation of cellulose decomposition which consumed most of the available nitrogen.

McComb and Kapel (1942) measured the interaction of liming and fertilizer on growth of black locust and green ash on an infertile Lindley subsoil of pH 4.3. The soil was limed at varying rates to attain soil pH values of 6.6, 6.9, and 7.7. The seedlings grew very poorly when no fertilizer was added. Both species showed a response to NPK at all pH levels and no response to nitrogen and potassium, indicating that phosphorus was the element limiting growth. Both species developed best at pH 4.3 when phosphorus was added, and growth decreased as the pH values were increased. When phosphorus was omitted, growth of both species increased up to pH 6.9 and decreased again at pH 7.7. The results were interpreted largely in terms of phosphorus availability.

Light intensity

Light intensity can affect tree growth through its direct effects on photosynthesis, and indirectly through its effects on cell enlargement and differentiation, which affect height growth, leaf size, and the structure of leaves and stems (Kramer and Kozlowski 1960).

Tree seedlings growing under overtopping vegetation are often subjected to low light intensities. Several investigators have found that light intensities under forest canopies may vary from 0.1 to 20 percent of full daylight (Buell and Gordon 1945, Oosting and Kramer 1946 and

Shirley 1929a, 1929b).

The relation between light intensity and the growth of hardwood tree seedlings was studied extensively by Shirley (1929a, 1929b). His experiments show that light intensity under continuous forest canopies was almost always so low as to decrease seriously the rate of growth of shaded vegetation, and often was too low for survival. Light intensities as low as 1 percent of full sunlight supported growth temporarily, but none of the species tested made appreciable dry weight gains. Poor root development, failure to harden tissues, and inability to produce a food reserve were noted at these low light intensities.

The rate of growth as measured by increase in dry matter was almost directly proportional to the light intensity up to 20 to 30 percent of full summer sunlight. Above 50 percent intensity the amount of growth increased very little with further increases in light. While slight shading caused no marked deleterious effects, shading which cut out 80 percent or more of the light reduced the growth.

Height growth, on the other hand, tended to increase with decreasing light intensity. The height attained a maximum at about 20 percent of full summer sunlight, or 60 percent of late summer sunlight. Upon further decrease in light intensity the height fell off rapidly. From this he concluded that the light intensity cannot be reduced below the point at which maximum height growth occurs without causing incipient starvation of the plant. Plants under high light intensities tended to attain complete height growth earlier than shaded plants because they matured earlier.

Holch (1931), studying the growth of several hardwood tree species including northern red oak, found that the greatest growth was obtained in an open prairie site in full sunlight, and the least in the deep shade of a linden forest where the light intensity average 3.5 percent. Intermediate rates of growth were found in an oak forest where the light intensity averaged 10.4 percent.

Photosynthetic measurements at varying light intensities have supported, to some extent, the observed relations between growth and light intensity. Some of the experiments have included northern red oak (Bordeau 1954 and Kramer and Decker 1944).

Bordeau (1954) conducted a series of experiments that demonstrated the shade tolerance of northern red oak and the shade intolerance of blackjack oak seedlings. Under low light intensity and in a soil at field capacity, northern red oak seedlings were able to carry on photosynthesis, and thus accumulate dry matter, at a higher rate than blackjack oak seedlings. They reached their peak at a relatively low light intensity. Their photosynthetic rate decreased under strong light and with the high temperature associated with it.

The photosynthetic rates of blackjack oak seedlings increased continuously and significantly with increasing light intensity, while in northern red oak seedlings the maximum rate was reached at 1800 foot-candles. The decrease in rate of photosynthesis of northern red oak seedlings above 4000 foot-candles may be due not only to the effect of light but also to the effect of the higher temperatures at the high light intensities, or to the interaction of these two factors.

Kramer and Decker (1944) compared photosynthesis of red oak, white oak, dogwood, and loblolly pine at light intensities ranging from 300 to 10,000 foot-candles. All four species showed rapid increases in photosynthesis with increase in light intensity at the lower intensities. The hardwoods achieved maximum photosynthesis at one-third or less of full light, and any further increase in light intensity produced no further increase in photosynthesis.

There is some evidence in the literature that light intensity can affect greatly the response of tree seedlings to increased nutrient supplies. Because fertilizer trials may be established under conditions where light is deficient, knowledge of the relation between light intensity and mineral nutrition would be helpful in modifying the fertilization rate or the cutting practice.

Steinbauer (1932) carried out an experiment to determine the effect of concentration of mineral nutrients on green ash seedlings grown at or near the minimum light intensity required for growth. The seedlings were grown at light intensities of 130, 70, 48, and 31 foot-candles; previous experiments had indicated the minimum light intensity for growth was approximately 50 foot-candles under continuous illumination. The data obtained, relative to the effect of concentration of nutrients on light requirements of the seedlings, indicated that while a sufficient supply of nutrients must be present to satisfy the needs of the plant, the minimum light requirements cannot be lowered by increasing the available nutrients.

The greatest response to an increase in concentration of the

nutrient solution occurred at the higher light intensities, indicating a greater use of nutrients under these conditions. Thus, increasing the concentration of solution from 0.01 to 0.1 atmosphere at a light intensity of 48 foot-candles resulted in a dry weight increase of 11.7 percent. For seedlings grown under light intensities of 70 and 130 foot-candles the resulting increases were 16.0 and 34.5 percent respectively.

Mitchell (1934) grew Scots pine seedlings at "half light" and at "full light" with varying nitrogen supplies. Seedlings grown in both light intensities increased in size with the nitrogen concentration up to the optimum concentration of 300 ppm. Further additions depressed growth in each group. The rate of increase was approximately the same up to 55 ppm nitrogen, but above this point the growth at "full light" became greater and the difference between the yield of seedlings growth in the two light values increased with the nitrogen supply until the optimum was reached. The difference in yield became less above the optimum, since the "full light" yields tended to drop off more rapidly. These results indicated that only at relatively high nitrogen supplies is the full benefit of the high light intensities obtained.

Chemical analysis of the seedlings grown at the two light intensities indicated the seedlings at the lower light intensity extracted nitrogen from the nutrient media at approximately the same rate as at the higher light intensity. However, the concentration of the nitrogen in those grown under the lower light intensity was higher. This was explained on the basis that the same amount was extracted but it was

diluted through a smaller weight of seedling material. From these observations, Mitchell concluded that the nitrogen absorption of Scots pine seedlings may be said to be either dependent or independent--depending on how plant nitrogen is expressed--of solar radiation. Measured in terms of total nitrogen, the relation was independent, expressed as a percent the opposite was true.

Mycorhizae

The value of mycorhizae to forest trees has been known for many years. Early attempts to plant forest tree seedlings on grassland and other non-forest soils often failed because of the apparent lack or inactivity of mycorhizal fungi. The problems encountered have been discussed thoroughly by Hatch (1936), Kessell (1927), McComb (1943) and Rayner (1934).

Almost all of the research on mycorhizae has been associated with conifer tree species, while the mycorhizae of hardwood species remain essentially unknown. Except for some preliminary work by Clark (1964) and Doak (1955) the literature contains little more than mere mention of the presence of mycorhizae on hardwood forest tree species (Henry 1932, McComb 1949, McDougall 1914 and Trappe 1962).

The role of mycorhizal fungi in the mineral nutrition of forest tree seedlings has been the subject of much controversy, and detailed reviews have been published (Björkman 1949, Hatch 1937, Melin 1953, Rayner 1927, Rayner and Neilson-Jones 1944 and Slankis 1958).

There is little doubt that mycorhizae are beneficial in the mineral nutrition of forest tree seedlings. Frank (1885) first thought the

mycorhizae were important in transferring water and dissolved nutrients from the soil to the seedling, but later he proposed that the fungi particularly facilitated the absorption of nitrogen. Stahl (1900) concluded that the mycelium of the fungi is a more effective absorbing mechanism than the non-mycorhizal tree root in the competition for soil nutrients. Mycorhizal roots, therefore, are able to absorb nutrients from poor soils more effectively than non-mycorhizal.

It is now generally held that the mycorhizae aid in the over-all uptake of mineral nutrients from the soil, phosphorus in particular. Several experiments have shown that mycorhizal seedlings contain considerably more nitrogen, phosphorus, and potassium than seedlings without mycorhizae.

Hatch (1937) made quantitative chemical analyses of seedlings and found that the mycorhizal seedlings absorbed from the same substrate, 75 percent more potassium, 86 percent more nitrogen, and 234 percent more phosphorus than the non-mycorhizal seedlings.

From these experiments, Hatch proposed that: (1) ectotrophic mycorhizae are more efficient organs of absorption than non-mycorhizal roots because of enormously greater surface area; (2) they facilitate the absorption of any and all nutrients ordinarily absorbed by roots; and (3) they are invariably produced and are essential to tree growth in all but the most fertile of natural soils.

Mitchell et al. (1937) compared infected and uninfected conifer seedlings grown in the same nutrient material, and found that the mycorhizal seedlings absorbed significantly more nitrogen, phosphorus, and

potassium, and that their dry weight increase was significantly greater than that of non-mycorhizal seedlings. The latter seedlings showed symptoms of nutrient deficiency, made little or no growth and in some cases did not even survive the second growing season.

Harley (1952) also has concluded that mycotrophic tree species obtain most, if not all, of their nutrients by means of mycorhizal roots.

The increased concentration of mineral nutrients in mycorhizal seedlings could be interpreted as an indirect effect rather than a direct effect of the fungi. Recent work with labeled elements, however, indicates that the transfer of nutrients is of a direct nature, from the soil through the fungal hyphae into the roots (Harley and Brierly 1955, Harley and McCready 1950 and Melin and Nilsson 1950).

The mineral nutrients apparently can also become available and be absorbed by the seedlings from the presence of the fungi in the soil without infection of the roots (Levisohn 1954). Rayner (1934) also believed that trees are stimulated before mycorhizae are formed, and attributes this stimulation to growth promoting substances derived from fungal activity, and to liberation of nutrients needed by higher plants.

In addition to mineral nutrients, other substances also appear to move into the plant by way of mycorhizal roots. These include water (Cromer 1935), carbohydrates (Young 1940), and organic nitrogen in the form of glutamic acid (Melin and Nilsson 1953). The tree roots also appear to be favored by auxin excreted by the fungi (Slankis 1958).

The conditions necessary for the formation of mycorhizae on tree

roots are not fully understood. Hatch (1937) maintained that mycorhizae form when there is a deficiency of one or more of the mineral nutrients nitrogen, phosphorus, potassium, or calcium in the soil. Björkman (1942) reexamined the conditions necessary for the formation of mycorhizae more fully and found that their occurrence, to some extent, varied inversely with soil fertility, but the relationship was more complex than Hatch had proposed.

In these experiments, Björkman found that application of ammonium nitrate to tree seedlings on nitrogen deficient soils decreased the frequency of occurrence of mycorhizae but increased the growth of the plants. On the other hand, seedlings in a soil rich in nitrogen, but phosphorus deficient, were not affected either as regards growth or mycorhizal occurrence by the additions of rather large quantities of nitrogen. When phosphoric acid was added the frequency of occurrence of mycorhizae was increased in the soil initially poor in nitrogen but decreased in that which was originally rich in nitrogen.

Björkman also found that mycorhizae developed best in strong light, more than 25 percent of full daylight, and at a certain, but not too great deficiency of easily available nitrogen or phosphorus. From these investigations he concluded that the occurrence of mycorhizae conforms to the production of carbohydrates and the effects of nitrogen and phosphorus are of an indirect nature and due to their influence on carbohydrate production. Therefore, mycorhizae develop when the roots of the host plant contain a surplus of soluble carbohydrates.

Some investigators have obtained evidence that other soil condi-

tions beside fertility differences may also affect the occurrence of mycorhizae. For example, Dale et al. (1955) observed that jack pines were chlorotic and made poor growth on calcareous soils. Normal growth was obtained only in soils treated with unsterilized humus, when the seedlings were mycorhizal. They were not sure, however, that a satisfactory mycorhizal relationship could be maintained over the life span of the trees in such soils.

Richards and Wilson (1963) also studied mycorhizal occurrence under alkaline conditions and found that the direct effect of hydrogen ion concentration on the growth of the fungus probably plays a minor role. They believed the indirect effect of soil pH on the availability of soil nitrogen may be more important by altering the carbohydrate/total nitrogen ratio in the roots of the seedlings.

Goss (1960) observed that mycorhizae became established in virgin non-mycorhizal grassland soils with pH's ranging from 5.8 to 6.8 and of widely different physical and chemical structures. Mycorhizae were present in some nursery soils ranging up to pH 7.8. The addition of duff-soil inoculum to non-mycorhizal virgin grassland soils under conditions which permitted the development of the mycorhizal fungi usually resulted in a variable increase in the growth of tree seedlings on different soils, but the beneficial effect if any, was not in inverse ratio to the fertility of the soil. Severe chlorosis of seedlings in some virgin grassland soils was prevented or lessened in severity by inoculation which resulted in the formation of mycorhizae.

Diagnosis of Nutrient Deficiencies

Soil analysis

The use of soil analyses to evaluate mineral nutrient requirements has been explored by several investigators, both in this country and abroad (Baur 1959, Gessel 1962, Stoate 1950 and Wilde and Patzer 1940). For various reasons, the results of these investigations have provided only limited insight into the mineral nutrient requirements of forest tree species.

Mitchell (1939), Tarrant (1949), and Wilde (1958) believe a primary reason for uncertainty in soil nutrient values is that the chemical methods used to evaluate the fertility of the soil are not correlated with the ability of the plant to extract nutrients from the same soil. Wilde and Voigt (1955) recommend that special chemical tests be developed for evaluating fertility of sites for forest trees.

Soil analyses appear to have their greatest value when supplemented by other methods of evaluating nutrient status of the seedlings.

Heiberg and White (1951) have used soil analysis successfully in conjunction with fertilizer trials and foliar analysis to identify potassium deficiency in young coniferous plantings on potassium deficient sandy soils. They found a strong correlation between growth response and content of potassium in the needle tissue. The soil from the plots which supported trees with higher contents of potassium in the needle tissue also contained higher quantities of exchangeable potassium.

Thomson and McComb (1962), through the use of soil and foliage

analyses, observed that potassium and to a lesser extent calcium were the nutrient elements most limiting walnut growth on the sites sampled. Mitchell and Chandler (1939) established some definite and reproducible relationships between soil nitrogen supply, the concentration of this element in the foliage, and growth of several hardwood species.

Wilde and Patzer (1940) analyzed soils under productive stands of various hardwoods for various mineral nutrients, from which they have devised soil fertility standards for hardwood-nursery soils. The results indicated that the ideal $N:P_2O_5:K$ ratio is near 1:2:5 for yellow birch and 1:3:5 for the rest of the hardwood species studied.

Foliage analysis

The use of foliage analysis has proven to be one of the best methods of studying the mineral nutrient relationships of plants. Bould (1963) stated that many early workers used plant analysis as a biological method of assessing soil fertility, but the present trend is to use leaf analysis as a guide to the nutritional status of the plant, first to establish threshold levels for nutrients below which plants show deficiency symptoms, and second to establish nutrient values associated with optimum growth.

The basic principles of foliar analysis were presented by Macy (1936), who is credited with the concept of "critical nutrient percentages" in leaf dry matter. He proposed that for any given plant there exists a fixed "critical percentage" for each nutrient, subject only to slight modifications by other growth factors. Nutrient concentrations greater than the "critical percentage" represent luxury

consumption, and concentrations less than the "critical percentage" represent nutrient deficiency.

Other workers also have contributed significantly to the understanding of the relationship between foliar nutrient content and growth of plants. Shear et al. (1946) and Thomas (1937) maintained that plant growth is a function of two variables of nutrition, intensity and balance, as they are reflected in the composition of the leaves when the plants are in the same stages of growth or development. At any level of nutritional intensity, a multiplicity of ratios may exist between these elements. Maximum growth or yield occur only upon the coincidence of optimum intensity and balance.

Goodall and Gregory (1947) consider that plant growth is conditioned by two sets of factors; (1) the external factors such as light, temperature, water, and nutrient supply, and (2) internal factors mainly nutritive but also hormonal. For each factor there is an optimum intensity level. The optima are not fixed, but depend on all factors simultaneously.

Steenbjerg (1954) demonstrated that at low to moderate levels of deficiency an increase in mineral supply sometimes causes increased growth without any apparent increase in concentration. With the micronutrients an increased supply may cause such a large increase in growth that a decrease in concentration occurs.

Foresters have readily and successfully adapted the foliar analysis technique to forest trees. It has been used to relate certain deficiency symptoms exhibited in foliage color to mineral content in

the leaves for such elements as nitrogen (Fowells and Krauss 1959, Gessel and Walker 1956 and Lunt 1947), phosphorus (Fowells and Krauss 1959 and Mitchell 1939), potassium (Stone 1953 and Walker 1956), calcium (Lunt 1947 and Voigt et al. 1958), and magnesium (Heiberg and White 1951 and Stone 1953).

Mitchell and Chandler (1939) analyzed the foliage of hardwoods growing on sites of varying fertility which had been fertilized with nitrogen. For each species a curve of diminishing returns was established between growth and nitrogen concentration of leaves. For northern red oak the estimated optimum nitrogen percentage in the leaves was between 2.46 and 2.57 percent. They found also that the range of concentrations over which this relationship was linear varied on different sites.

Leyton (1957) found that for Sitka spruce growing on a nitrogen deficient site the nitrogen concentration in the needles was significantly correlated with needle dry weight, but the line relating these two quantities was displaced according to whether or not phosphate had been applied to the trees.

Leyton did not believe that specially designed fertilizer trials were always necessary to establish the nature of mineral deficiencies if a suitable range of material already existed covering the required variation in growth and concentration. Taking advantage of existing variation in the growth of Sitka spruce in an even aged plantation on a presumably heterogenous site, Leyton found a significantly positive correlation between height growth and nitrogen concentration in the

needles. Indications of a nitrogen deficiency were supported by a marked response in growth when the nitrogen status of the trees was improved, either by fertilizing or by other treatments, in which cases the linear correlations were no longer significant.

The use of foliar analysis requires certain precautions to obtain reliable results. Several investigators have studied the indirect factors affecting nutrient content in the foliage of forest trees. Kramer and Kozlowski (1960) have reviewed some of the research relating to these factors. Included among these factors are age of leaves (Leyton and Armson 1955, McHargue and Roy 1932 and Mitchell 1936), loss of nutrients by leaching (Mitchell 1936 and Tamm 1951), location of leaves on trees (Leyton and Armson 1955, Wallihan 1944 and White 1954), and handling of samples (Broyer 1939 and White 1954).

MATERIALS AND METHODS

Soils

General description

The four soils included in this study were: (1) Lindley, a forest soil, (2) Shelby, a prairie soil, (3) Clarksville, a forest soil, and (4) Clarksville, from an old field site. These soils were chosen on the basis of the recognized differences in fertility, parent material, and possible microbiological factors. All four soils are considered sub-marginal for agriculture purposes and cover extensive areas in the forested sections of Missouri and Iowa. Considerable forest tree planting already has been done on these soils.

The Lindley and Shelby soils were collected in Lucas County, Iowa. The sampling site for the Lindley soil was in Sec. 30, T. 71 N., R. 20 W., and for the Shelby soil the sampling site was in Sec. 31, T. 71 N., R. 20 W. These two soils have been described in detail in a recent soil survey report by Prill (1960).

The Lindley soil has developed under forest from Kansan till. These soils are rolling to steep and subject to erosion. A 40- to 60-year old oak-mixed hardwood stand now occupies the sampling site, which was on an upper slope of 13 to 20 percent. The subsoil is yellowish brown and has a medium texture. The A_1 horizon is 4 to 8 inches thick. The clay content of the subsoil ranges from 30 to 40 percent and permeability is slow. Iron-manganese concretions are common in the lower B and C horizons.

The Shelby soils have developed under prairie from weakly weathered Kansan till. The sampling site for this soil was on an upper slope of 13 to 20 percent that originally was cropped and pastured but was abandoned an unknown number of years ago. Mixed hardwood species are now encroaching this site. The Shelby soils are dark colored and moderately well drained. Erosion has removed all but 2 to 6 inches of the dark grayish-brown A_1 horizon. The subsoil is dark yellowish brown, contains 30 to 40 percent clay, and is slowly permeable. The B and C horizons have many dark yellow- and grayish-brown mottles.

The Clarksville soils were collected on the Sinkin Experimental Forest in Dent County, Missouri. The sampling site for the forest soil was in Sec. 16, T. 32 N., R. 3.W., and for the old field soil the sampling site was in Sec. 9, T. 32 N., R. 3 W.

The Clarksville soils are hilly to rolling, well drained soils, and have developed under predominately hardwood forest from cherty limestone and sandstone. There is a light colored stony silt loam surface and a friable, yellowish to light brown, stony, silty clay loam subsoil. Chert content grades from 10 to 15 percent in the A horizons to 60 to 70 percent in the B and C horizons. The soils are strongly weathered and leached. From an agriculture viewpoint, low natural fertility is a major problem with these soils.

The Clarksville forest soils was collected from an upper slope position that supported a well-stocked, 40- to 60-year old, mixed oak stand. The soil on this site is characterized by a solum 12 to 24 inches thick. Texture of the A horizon ranges from sandy loam to silt

loam. Surface chert and sandstone fragments increase in size and content with depth. This soil usually contains 50 to 80 percent chert and sandstone fragments at 18 inches or less. The A_2 horizon ranges from light brownish gray to pale brown.

The Clarksville old field site, also on an upper slope position, supports a broomsedge grass (Andropogon virginicus L.) cover. This site originally was covered by a mixed oak stand but was cleared for agriculture purposes and abandoned at least 50 years ago. The exact record of the past land use of this area is not available. The chert content of the soil ranges from 30 to 50 percent and 5 to 10 inches in size. The A horizon textures are usually loam or silt loam with frequent small areas of sandy loam. Subsoil textures are usually fine silt loam to clay loam. The structure and development ranges from very weakly to moderately well defined. Chert strata or bedrock occurs at 10 to 18 inches in depth. The A horizon color is pale brown to yellowish brown.

Collection and handling of soil samples

At each sampling site the litter layer was removed and soil samples were taken from the top 8 to 10 inches of the profile. This zone included the A horizons only in the forest soils, but with the Shelby and the Clarksville old field soils the upper part of the B horizon also was included. About 2 tons of soil was taken from each site in April and May 1962 and shipped to the Iowa Conservation Commission Nursery at Ames, Iowa, where the study was conducted.

Considerable care was exercised during all stages of the soil

sampling and handling to insure against accidental innoculation of non-forest soil with forest soil. The soil from each of the two sites in Missouri was placed in paper sacks and stored separately so that the sacks of forest soil never came in contact with the sacks of non-forest soil. The old field soil was sampled first and the digging equipment was cleaned thoroughly before collecting the forest soil. This same sampling plan was used for the Lindley and Shelby soils in Iowa except that these soils were transported in bulk to the nursery. The two soils were kept separated by use of plastic sheeting and canvas tarpaulins. At the nursery the soils were piled separately and covered until such time as the soil was placed in the pots for growing the tree seedlings.

When the study was initiated in May 1962, each soil was mixed thoroughly and was passed through a 1-inch mesh wire screen to remove rocks and roots and to insure uniformity. The soil was placed in 5-gallon polyethylene pots and allowed to settle for two weeks. After this settling period the soil in the pots had about the same volume weight as it had in the field. The pots then were brought to a fixed soil volume of 0.5 cubic feet of soil per pot by adding additional soil.

Soil chemical analyses

A sample was taken from each soil soon after digging, and air dried for future routine analysis to characterize some of the chemical and physical properties. These properties are listed in Table 1.

The soil pH determinations were made at the moisture saturation percentage, using glass electrodes, as outlined by Jackson (1958).

Table 1. Some chemical and physical properties of the four study soils

Soil	pH	O.M. %	Exch. Cap. m.e./ 100g	Exch. Bases m.e./ 100g	Base sat. %	Sand %	Silt %	Clay %	Text. class
Lindley (Forest)	5.8	5.7	20.9	13.8	66	40	44	16	L
Shelby (Prairie)	5.5	5.1	19.0	10.8	57	36	38	26	CL
Clarksville (Forest)	5.5	4.3	14.8	4.6	31	29	53	18	SiL
Clarksville (Old field)	5.5	2.8	15.8	4.7	30	37	45	18	L

Organic matter was estimated indirectly by the loss-on-ignition method outlined by Wilde and Voigt (1955), and expressed as a percent dry weight. The cation exchange capacity was determined by saturating the exchange positions with ammonia from neutral, 1 N ammonium acetate, leaching the ammonium with potassium sulfate, and assaying the ammonium by use of micro-diffusion cells, as outlined by Black (1954). Exchangeable bases were determined by taking up the bases in the leachate in 0.1 N hydrochloric acid and titrating with 0.1 N ammonium hydroxide. Base saturation represents the ratio of exchangeable bases to the total exchange capacity. Sand, silt, and clay contents of each soil were determined by the hydrometer method described by Wilde and Voigt (1955).

Soil analyses for nitrogen, phosphorus, and potassium were made at the beginning of the study and at the beginning of the second growing

season on fertilized and unfertilized soils. The results of these determinations are given in Table 2. All quantities are expressed as pounds per acre furrow slice, dry weight elemental basis.

The analytical methods employed in these determinations were those followed as routine analysis of agriculture soils by the Soil Testing Laboratory, Iowa State University. Nitrogen was determined colorimetrically as nitrifiable nitrate, using phenoldisulfonic acid as the reagent, after incubating the soil sample for 2 weeks at 35° C. Available phosphorus was extracted with 0.03 N ammonium fluoride in 0.025 N hydrochloric acid, and assayed colorimetrically as the molybdate in an ammonium molybdate-sulfuric acid system. Exchangeable potassium was extracted with neutral, 1 N ammonium acetate and assayed on a Perkin-Elmer flame photometer, using lithium as the internal standard.

Addition of fertilizer

The fertilizer was added at the beginning of the study in May 1962. The fertilizer application rates and source materials are summarized in Table 3. Nitrogen, potassium, and lime were added as finely ground solid powder. Phosphorus was added as liquid phosphoric acid after diluting to a 1:20 ratio with distilled water. No additional fertilizer was added to the soils in 1963. Any fertilizer response observed in 1963, therefore, was obtained from residual fertilizer in the soil from the previous year. It was hoped that by not refertilizing the soils in 1963 some additional information would be gained which would indicate how frequently to fertilize these soils to maintain improved tree seedling growth.

Table 2. Nitrogen, phosphorus, and potassium content of the study soils at the beginning of the 1962 and 1963 growing seasons

Soil	May 1962			May 1963					
	Unfertilized			Unfertilized			NPK fertilized		
	N	P	K	N	P	K	N	P	K
Lindley (Forest)	45	1.0	196	24	3.0	184	60	22	220
Shelby (Prairie)	33	1.0	184	36	0.5	140	48	21	172
Clarksville (Forest)	35	1.0	208	15	3.5	144	48	25	188
Clarksville (Old field)	27	0.5	155	36	0.5	136	45	18	172

[a]Nitrogen, phosphorus, and potassium were added to the soils in May 1962 at the rate of 90, 80, and 80 pounds per acre for each of the three elements, respectively.

Table 3. Source materials and basic rates of fertilization for each of the elements studied

Element	Source	Rate of application	
		per pot[a]	per acre[b]
Nitrogen	NH_4NO_3	2.41 g	90 lbs.
Phosphorus	H_3PO_4	1.65 ml	80 lbs.
Potassium	K_2CO_3	1.32 g	80 lbs.
Lime	$CaCO_3$	18.74 g	1 ton

[a]Chemical compound added per pot.

[b]On elemental basis, except for lime, and assuming the volume of an acre furrow slice is 24,200 cubic feet.

To add the fertilizer, the soil first was dumped out of each pot onto plastic sheeting. A small quantity of soil, about a quart, was separated out for mixing with the fertilizer. The phosphorus solution was sprinkled on the soil and along with the solid fertilizer was mixed into the smaller soil sample. This fertilizer-soil mixture then was thoroughly mixed with the remaining soil from each pot. After placing a 1 1/4-inch layer of 1/8- to 1/4-inch diameter washed river gravel in the bottom of each pot, and drilling three holes for drainage, the soil was replaced on top of the gravel.

Sterilization and inoculation of soils

The soil in a number of pots was sterilized to remove possible mycorhizal fungi. The soil was removed from the pots, spread out in a 4- to 6-inch layer on a plastic sheet, and covered with another plastic sheet. The edges of the cover were tightly sealed to the ground. Methyl bromide (Dowfume MC-2) was injected into the soil at the rate of 1 1/2 pounds of methyl bromide per 100 cubic feet of soil. The cover was left on for 72 hours to insure complete penetration of the gas. The cover was removed and the soil frequently mixed and aired for 4 days before replacing in the pots. The pots were not planted until 10 days after the application of the methyl bromide to eliminate toxic effects of the chemical.

The non-forest and sterilized soils in some cases were inoculated with mycorhizal fungi by thoroughly mixing a small sample (about 20 g) of the forest soils into these soils before replacing in the pots. The Shelby prairie soil was inoculated with the Lindley forest soil,

and the Clarksville old field soil was inoculated with the Clarksville forest soil. Inoculations were made in June 1962 and no additional soil was added during the course of the study.

Seedlings

Establishment and care

The pots were seeded in June 1962 with red oak, black walnut, and cottonwood. The seeds of all three species were of local seed source and collected from single seed trees. The acorns were washed in running water for several hours and then placed in cold storage. In March 1962, the red oak acorns and the black walnut seeds were stratified in sterile quartz sand. Because the study was not started as early as expected, the seeds had already started to germinate when they were sown in June. The radicles were about 1 to 2 inches long but the shoots had not begun to elongate. The acorns were washed again in running water to remove possible mycorhizal fungi. The cottonwood seed was sown directly in the pots without any prior treatment. All seeding was done during the first week of June 1962. Five acorns, 6 walnuts, and 30 to 50 cottonwood seeds were planted per pot.

It was originally planned to grow the seedlings for two years before harvesting for the final measurements. During April 1963, however, the 1-year old seedlings did not show any bud activity and closer examination indicated the cambium was turning brown and the seedlings were dying. Death was believed to have been the result of winter injury during February and March. The seedlings were harvested im-

mediately. No significant loss in dry weight appears to have occurred with these seedlings because the root and stem weights were comparable to that of healthy seedlings of the same height grown in 1963.

The pots were replanted in the second week of May 1963 with red oak, black walnut, and green ash. The green ash was substituted for the cottonwood which grew poorly the previous year. The red oak acorns and the black walnut seed were of local seed source and from single seed trees. The green ash seed, however, was collected from an unknown source in Ohio. All of the seed had been stratified in sterile moist sand. As in the previous year, the red oak and black walnut already had started to germinate when seeded in the pots. The same washing treatments were given to the red oak acorns to remove possible mycorhizal fungi as were used in 1962. Five acorns, 5 walnuts, and 20 to 30 green ash seed were sown per pot.

Each year, a layer of sphagnum was placed on top of the soil immediately after planting to reduce water loss through evaporation and to keep soil surface temperatures low. During mid-summer the seedlings were thinned, leaving the three tallest red oak and black walnut and the four tallest cottonwood or green ash seedlings. Sufficient water was added at frequent intervals during the growing season to keep the soil near field capacity.

Shading of seedlings

The light intensity at which the seedlings were grown was varied by use of shade frames constructed of woven plastic screening material of different mesh. Each shade frame was about 6 feet long, 3 feet

wide, and 4 feet high, and covered six pots. The top of the shade frame was sufficiently high to allow freedom in height growth of the seedlings, and also to allow free circulation of air. These shade frames are shown in Figure 1.

The shade frames were calibrated by taking measurements of light intensity with a Weston Illumination Meter (Model 756) at frequent intervals during the 1962 growing season. Observations were taken at mid-day under variable cloud conditions. The sensing element was placed about 10 inches above the soil surface in the pots. The light intensity measured under the shade frames was divided by the light intensity measured in the open to obtain the relative light intensity at which the seedlings were grown. Some slight variations were noted within a shade frame due to the placement of the sensing element. The relative light intensities cited in this thesis, therefore, are only approximations, but the error is not believed to be greater than 2 to 5 percent of each light intensity.

Foliage analyses

In September of 1962 and 1963 the leaves were cut from each seedling and their green weight recorded. The leaves then were oven-dried for 24 hours at 68° C. Because all leaves were fully expanded, the entire leaf sample from each seedling was ground in a Wiley micro-mill. The leaf material from the three replications of each treatment was combined into a single sample for the chemical analyses.

Chemical analyses were made by the Department of Horticulture, Michigan State University, to determine the N, P, K, Ca, Mg, Mn, Fe,

Figure 1. General view of the study area at the Iowa Conservation Commission Nursery showing location of shade frames and arrangement of pots.

B, Cu, Zn, Mo, Na, and Al content of the leaf sample. Nitrogen was determined by a modified Kjeldahl method, digesting the leaf material in sulfuric acid with catalysts, distilling off the ammonia into boric acid, and titrating with 0.07 N sulfuric acid. Potassium was extracted from the leaf material with distilled water, filtered, and the leachate assayed for potassium on a Beckman Model B Spectrophotometer. The nitrogen and potassium content in the 1963 leaf samples were determined by the Department of Agronomy, Iowa State University. Essentially the same method was used to determine nitrogen as in 1962, but potassium was extracted with nitric and perchloric acid and assayed on a flame photometer. All of the other elements were analyzed spectrographically. The leaf material was ashed for 12 hours at 550° C. The plant ash was dissolved in hydrochloric acid and 0.02 percent cobalt added as an internal standard. Lithium (0.5 percent) and potassium (1.0 percent) also were added to the solution. The final solution was placed in the spectrograph and the different elements assayed. Duplicate analyses were not made because the reproducibility of analysis of each element has been found to be very good, less than 10 percent variance of the mean mineral content.

Harvesting

When the seedlings were harvested at the end of April 1963, the roots were dug carefully from the soil, all loose dirt shaken back into the pot, and a stream of water then used to remove any remaining adhering soil. As in the other phases of the study, extreme care was taken to avoid contamination of the non-forest soils with forest soil.

The seedlings were oven dried for 24 hours at 68° C., and the dry weight of the roots and stem recorded separately.

In harvesting the seedlings grown during 1963, the entire soil mass in a pot was placed on a wire screen and the soil removed from the roots by a stream of water. The green weight of the roots and stem were obtained in addition to their dry weight. The same drying schedule as with the 1962 seedlings was followed.

Experimental Design and Statistical Analyses

With the exception of the light intensity experiment, the treatments were arranged in a randomized block design. Each treatment was replicated in three blocks. The blocks were oriented east to west, with the long rows of pots within a block oriented north and south. Each block contained 108 pots, arranged in 4 rows of 27 pots each. The pots were placed about 3 feet apart to minimize possible shading effects between pots.

The shade frames for the light intensity experiment were located at random within a block and individual treatments assigned at random to different positions within a shade frame. The light intensity experiment, therefore, was analyzed as a split-plot experiment, with the shade frames as main plots and the fertilizer-soil treatments as sub-plots as described by Cochran and Cox (1957).

All height and green and dry weight data were analyzed by analysis of variance. Treatments were evaluated by use of orthogonal comparisons as described by Snedecor (1956). Where varying levels of mineral

nutrients were added, the best form of the resulting relationship was evaluated by means of orthogonal polynomials. The analyses of variance were made using the total height and weight of all seedlings in a pot. The height and weight data cited in this thesis, however, are averages of the individual seedlings. This must be taken into account when applying the data in the tables of statistical analyses.

Because only one determination was made of the chemical content of each element in the leaves of the seedlings in a given treatment, there was no valid error term for testing the significance of the mineral composition data. Estimation of treatment effects on chemical content of the leaves, however, was obtained by assuming that the experiment was a single replication and testing treatment means by the interaction with most factors involved. That such a procedure was partly valid is supported by the fact that the interactions used as error terms were not significant for any of the growth data.

RESULTS

Basic Fertilizer Experiment

The red oak seedlings grew better on the two forest soils than on the two non-forest soils in both 1962 and 1963 (Tables 4 and 5). The growth differences were statistically significant at the 1-percent probability level in both years (Tables 6 and 7). In 1962, unfertilized red oak seedlings were 10 percent taller and 28 percent heavier on the Lindley forest soil than on the Shelby prairie soil, and 11 percent taller and 36 percent heavier on the Clarksville forest soil than on the Clarksville old field soil. Comparable differences in growth between forest and non-forest soils were observed with seedlings grown on these same soils in 1963. The average growth of the seedlings on the two Missouri soils was not significantly different from that on the two Iowa soils.

The application of fertilizers significantly increased the growth of the red oak seedlings in 1962 and 1963 on all four soils. The differences in growth between fertilized and unfertilized seedlings were evident in the field before they were harvested (Figure 2). The soil x fertilizer interaction was not significant for any measure of growth either year, which indicates that the fertilizer responses were similar on all four soils.

The main effects of nitrogen, phosphorus, and potassium were summarized separately for each soil (Tables 8 and 9). Although the statistical validity of this procedure may be open to question because

Table 5. Average height and green and dry weight per seedling of red oak from the basic fertilizer experiment, 1963

Soil	Fertilizer	Height, in.	Green weight, g	Dry weight, g			
				Leaves	Stem	Roots	Total
Lindley (Forest)	-	10.5	28.60	3.70	2.79	7.42	13.91
	N	9.5	26.21	2.77	2.64	7.06	12.47
	P	10.7	30.25	3.85	2.77	8.07	14.69
	K	10.4	30.60	3.70	2.71	8.14	14.55
	NP	11.8	31.34	3.53	2.82	8.22	14.57
	NK	9.3	26.06	3.18	2.10	6.93	12.21
	PK	9.9	31.71	3.47	2.89	8.57	14.93
	NPK	11.2	32.60	3.78	2.91	8.47	15.16
	Mean	10.4	29.67	3.50	2.70	7.86	14.06
Shelby (Prairie)	-	7.4	17.04	1.79	1.42	5.61	8.82
	N	7.1	16.61	1.90	1.43	5.26	8.49
	P	7.9	21.25	2.15	1.58	6.78	10.51
	K	7.6	15.31	1.81	1.25	4.20	7.26
	NP	8.2	21.51	3.05	1.83	5.81	10.69
	NK	7.5	17.62	2.10	1.25	5.60	8.95
	PK	8.4	21.57	2.69	1.91	5.89	10.49
	NPK	7.7	22.81	2.81	1.66	6.39	10.86
	Mean	7.7	19.21	2.29	1.54	5.68	9.51
Clarksville (Forest)	-	9.9	27.64	3.60	2.59	7.08	13.27
	N	8.8	21.79	2.90	1.94	5.08	9.92
	P	10.0	27.59	3.70	2.75	7.25	13.70
	K	9.1	27.45	3.37	2.29	7.11	12.77
	NP	11.5	37.06	4.77	3.16	9.93	17.86
	NK	10.0	30.05	3.84	2.98	7.60	14.42
	PK	11.2	33.90	4.29	2.65	8.83	15.77
	NPK	11.6	33.87	4.48	2.70	8.95	16.13
	Mean	10.3	29.92	3.87	2.63	7.73	14.23
Clarksville (Old field)	-	8.2	21.92	2.82	1.75	5.96	10.53
	N	7.9	14.28	1.88	1.44	3.79	7.11
	P	9.3	25.00	2.95	2.15	6.59	11.69
	K	7.8	15.15	2.05	1.37	4.26	7.68
	NP	9.0	27.94	3.30	2.16	7.81	13.27
	NK	8.5	16.44	2.00	1.43	4.41	7.84
	PK	8.5	23.08	2.52	1.84	6.71	11.07
	NPK	8.8	26.00	2.80	2.07	7.49	12.36
	Mean	8.5	21.22	2.54	1.78	5.88	10.20

Table 6. Mean squares from the analysis of variance of average height and dry weight per pot of red oak seedlings from the basic fertilizer experiment, 1962

Source of variation	Degrees of freedom	Height	Dry weight		
			Shoot	Roots	Total
Replication	2	5.50	6.35	23.38	40.56
Soil (S)	3	68.67**	133.16**	149.22**	544.89**
Iowa vs Missouri	(1)	6.10	0.00	39.50	39.40
Lindley vs Shelby	(1)	115.94**	186.20**	103.84**	568.15**
Cl.-F. vs Cl.-O.f.	(1)	84.27**	213.28**	304.32**	1027.12**
Fertilizer (F)	7	107.85**	124.30**	149.57**	521.90**
N	(1)	127.88**	154.94**	3.37	203.99**
P	(1)	557.77**	636.64**	890.24**	3032.55**
K	(1)	43.20*	19.78*	3.47	39.84
NP	(1)	21.28	32.50	30.99	126.96*
NK	(1)	0.70	2.52	42.37	65.54
PK	(1)	0.03	0.14	0.55	0.13
NPK	(1)	4.25	23.60*	76.01*	184.32**
S x F	21	8.19	6.00	5.92	18.32
Error	62	7.50	3.87	11.34	24.16

*Significant at the 5-percent probability level.

**Significant at the 1-percent probability level.

Table 7. Mean squares from the analysis of variance of average height and green and dry weight per pot of red oak seedlings from the basic fertilizer experiment, 1963

Source of variation	Degrees of freedom	Height	Total green weight	Dry weight		
				Shoot	Roots	Total
Replication	2	88.50**	60.15	19.20*	44.14*	10.63
Soil (S)	3	385.33**	6717.21**	385.47**	294.68**	1345.64**
Iowa vs Missouri	(1)	21.07	271.82	33.51*	0.25	39.55
Lindley vs Shelby	(1)	796.27**	11716.25**	606.77**	514.11**	2237.92**
Cl.-F. vs Cl.-O.f.	(1)	338.67**	8163.56**	516.14**	369.69**	1759.46**
Fertilizer (F)	7	38.57*	1317.87**	46.12**	101.87**	283.57**
N	(1)	2.10	15.31	0.17	0.03	0.35
P	(1)	214.80**	7549.79**	249.87**	586.18**	1601.48**
K	(1)	0.01	55.12	0.81	3.23	0.80
NP	(1)	32.20	937.88**	40.07*	61.31*	200.51**
NK	(1)	2.16	69.67	3.86	13.58	31.88
PK	(1)	2.87	0.63	1.03	0.05	1.53
NPK	(1)	15.20	596.70*	27.07*	48.74*	148.45*
S x F	21	7.24	150.96	6.33	16.66	34.96
Error	62	14.24	103.91	6.39	12.11	22.92

*Significant at the 5-percent probability level.

**Significant at the 1-percent probability level.

Figure 2. One-year-old red oak seedlings in 1962 on the four surface soils treated with different fertilizers.

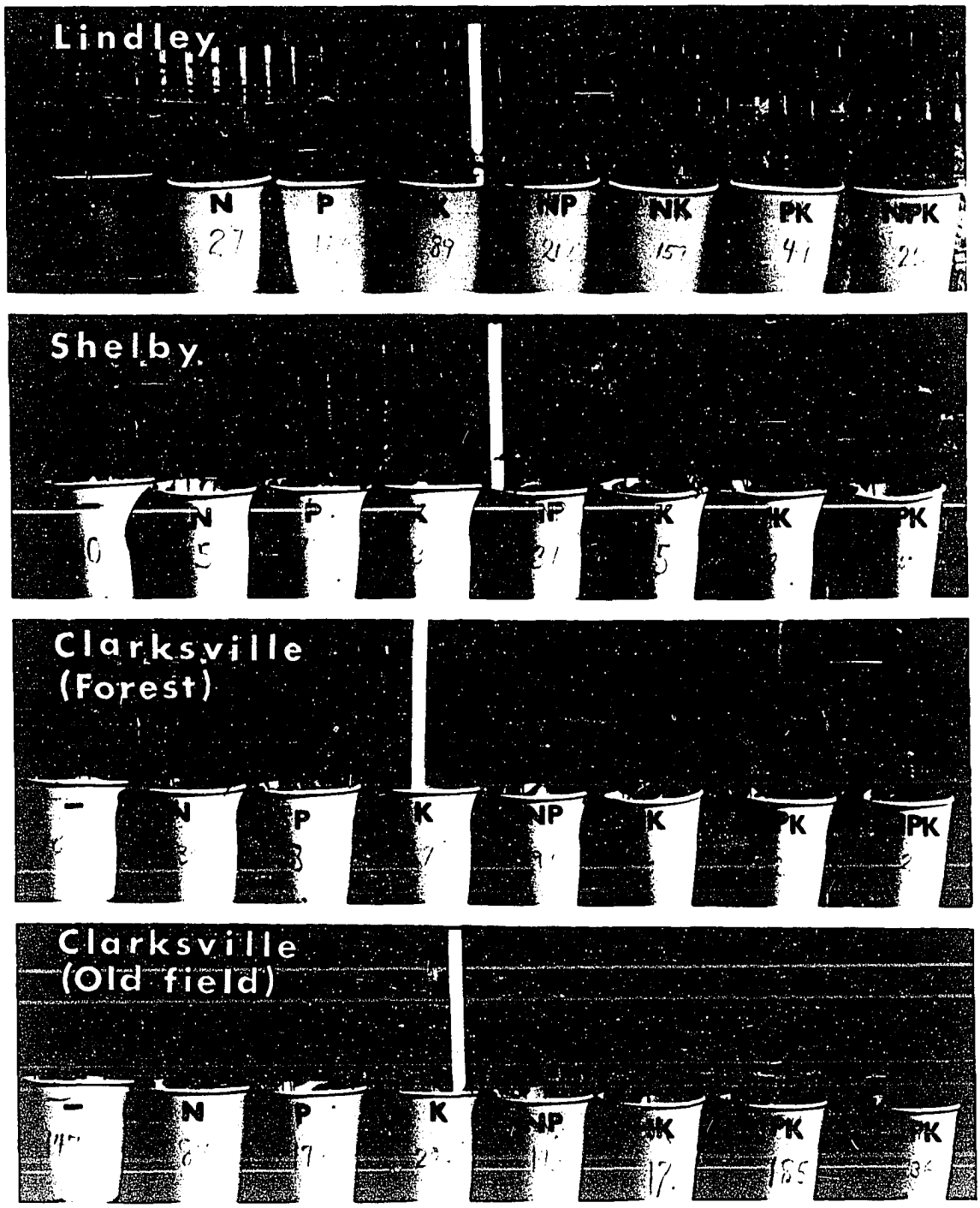

Lindley
N
P
K
NP
NK
PK
NPK
Shelby
Clarksville
(Forest)
Clarksville
(Old field)

Table 8. Main effects of nitrogen, phosphorus, and potassium on the average height and dry weight per seedling of red oak from the basic fertilizer experiment, 1962

Soil	Dependent variable	Nitrogen		%	Phosphorus		%	Potassium		%
		-N	+N	Diff.	-P	+P	Diff.	-K	+K	Diff.
Lindley (Forest)	Height	8.44	9.55	+13.2	8.46	9.52	+12.5	9.12	8.86	- 2.9
	Shoot dry weight	4.45	5.47	+22.9	4.45	5.46	+22.6	5.17	4.74	- 8.3
	Root dry weight	6.13	6.41	+ 4.4	5.55	6.99	+25.9	6.33	6.21	- 1.8
	Total dry weight	10.58	11.87	+12.2	10.00	12.45	+24.5	11.50	10.95	- 4.7
Shelby (Prairie)	Height	7.39	8.52	+15.4	7.29	8.62	+18.3	8.30	7.61	- 8.4
	Shoot dry weight	3.17	4.12	+30.0	2.94	4.35	+48.3	3.88	3.40	-12.3
	Root dry weight	5.24	5.34	+ 1.9	4.49	6.09	+35.7	5.43	5.15	- 5.1
	Total dry weight	8.41	9.46	+12.5	7.42	10.44	+40.7	9.31	8.55	- 8.1
Clarksville (Forest)	Height	8.42	9.07	+ 7.6	7.77	9.72	+25.1	8.97	8.52	- 5.0
	Shoot dry weight	4.47	5.54	+23.8	3.86	6.14	+59.0	5.17	4.84	- 6.2
	Root dry weight	6.16	6.22	+ 0.9	4.98	7.40	+48.7	6.10	6.28	+ 3.0
	Total dry weight	10.63	11.75	+10.5	8.84	13.55	+53.2	11.27	11.12	- 1.3
Clarksville (Old field)	Height	7.77	7.96	+ 2.4	6.82	8.91	+30.6	8.06	7.67	- 4.8
	Shoot dry weight	3.42	3.78	+10.3	2.52	4.68	+85.8	3.59	3.61	+ 0.6
	Root dry weight	4.48	4.55	+ 1.6	3.19	5.84	+83.3	4.66	4.36	- 6.3
	Total dry weight	7.90	8.32	+ 5.4	5.70	10.52	+84.4	8.25	7.97	- 3.3

Table 9. Main effects of nitrogen, phosphorus, and potassium on the average height and dry weight per seedling of red oak from the basic fertilizer experiment, 1963

Soil	Dependent variable	Nitrogen		%	Phosphorus		%	Potassium		%
		-N	+N	Diff.	-P	+P	Diff.	-K	+K	Diff.
Lindley (Forest)	Height	10.39	10.48	+ 0.8	9.96	10.90	+ 9.5	10.64	10.22	- 3.9
	Shoot dry weight	6.47	5.93	- 8.3	5.90	6.51	+10.3	6.22	6.18	- 0.6
	Root dry weight	8.05	7.67	- 4.7	7.39	8.33	+12.8	7.69	8.03	+ 4.4
	Total dry weight	14.52	13.60	- 6.3	13.28	14.84	+11.7	13.91	14.21	+ 2.2
Shelby (Prairie)	Height	7.81	7.62	- 2.4	7.40	8.03	+ 8.6	7.65	7.78	+ 1.7
	Shoot dry weight	3.65	4.01	+ 9.8	3.24	4.42	+36.5	3.79	3.87	+ 2.1
	Root dry weight	5.62	5.74	+ 2.1	5.14	6.22	+20.9	5.84	5.52	- 5.4
	Total dry weight	9.27	9.75	+ 5.1	8.38	10.64	+26.9	9.63	9.39	- 2.4
Clarksville (Forest)	Height	10.07	10.47	+ 4.0	9.47	11.07	+16.9	10.06	10.48	+ 4.2
	Shoot dry weight	6.31	6.69	+ 6.0	5.88	7.13	+21.2	6.36	6.65	+ 4.6
	Root dry weight	7.57	7.89	+ 4.3	6.72	8.74	+30.1	7.33	8.12	+10.8
	Total dry weight	13.88	14.58	+ 5.1	12.60	15.87	+26.0	13.69	14.77	+ 7.9
Clarksville (Old field)	Height	8.45	8.55	+ 1.1	8.09	8.91	+10.1	8.58	8.42	- 1.9
	Shoot dry weight	4.36	4.27	- 2.1	3.68	4.95	+34.3	4.61	4.02	-12.7
	Root dry weight	5.88	5.87	- 0.2	4.61	7.15	+55.3	6.04	5.72	- 5.3
	Total dry weight	10.24	10.15	- 1.0	8.29	12.10	+46.0	10.65	9.74	- 8.5

of the presence of certain significant nutrient element interactions, the main effects provide an estimate of the relative mineral nutrient deficiency of each soil for the three elements on the basis of the average response obtained from each element over all treatments. In observing the breakdown of fertilizer effects in the analysis of variance it should be remembered that the main effect of a given element is obtained from all treatments which contain that element. The various mineral combinations listed denote the interaction between the nutrient elements and do not refer to any particular treatment.

The greatest response in growth was from phosphorus and a smaller but statistically significant response from nitrogen. The nitrogen response was mainly in height growth and shoot weight, while root dry weight was not significantly affected. Phosphorus increased shoot and root weight proportionally. The phosphorus response was considerably greater on the two Missouri soils than on the two Iowa soils. In 1962, for example, the average phosphorus effect over all treatments amounted to an 84.4 percent increase in total dry weight per seedling on the Clarksville old field soil but the total dry weight increase from this element on the Lindley forest soil amounted to only 24.5 percent. In 1963, the increase in total dry weight per seedling from phosphorus was 46.0 and 11.7 percent on these same two soils respectively.

A comparison of the fertilizer responses in 1962 and in 1963 indicates that some residual fertilizer was available to the seedlings grown on these soils the second year. No additional fertilizer was added in 1963 but the seedlings grew significantly better on the soils

previously fertilized with phosphorus. As in 1962, the phosphorus response was greater on the two Missouri soils than on the two Iowa soils, but was about 20 to 30 percent less on all soils than was obtained with this element in 1962. There was no significant residual nitrogen effect on the seedlings in 1963.

The application of potassium did not significantly increase growth on any of the soils in either year. Generally, potassium fertilization had an adverse effect on the growth of the red oak seedlings, especially on height growth and shoot dry weight. Root growth was not significantly affected by potassium additions to these soils.

Certain interactions among nutrient elements in the fertilizers were apparent in the growth data and were confirmed by the statistical analyses. There was a significant nitrogen x phosphorus interaction on all soils in 1962, indicating that the effects of these two elements were not additive. Additions of nitrogen only had an adverse effect on the total dry weight of the red oak seedlings on all soils, brought about mainly by greatly reduced root growth, even though shoot growth was actually increased by this treatment on the two forest soils. Unlike nitrogen, phosphorus added alone increased the growth of the red oak seedlings on all soils. When nitrogen and phosphorus were added in combination as a fertilizer treatment, the growth of the seedlings was increased significantly over that obtained from these two elements added singly. The NP interaction was more significant in 1963 than in 1962. Possible explanations for this interaction may be that the available phosphorus had to be brought up to a certain level before there was

any significant nitrogen response. Also, the added nitrogen may have increased the ability of the red oak seedlings to absorb and utilize the fertilizer and soil phosphorus.

The NPK interaction also was significant in both years, and may partly have been due to the significant NP interaction. These results indicate that the main effects of the three elements were not independent and were not additive. Close examination of the 1962 growth data points out other possible sources of the significant NPK interaction. Both nitrogen and potassium added alone decreased the total dry weight of the red oak seedlings but when added in combination the two elements had a less adverse effect on growth. With added phosphorus, the nitrogen effect was almost independent of the level of potassium. It is interesting also to note that the NK fertilizer treatment increased seedling growth over the unfertilized seedlings only on the two forest soils, probably because available phosphorus was greater on these soils than on the non-forest soils. In 1963, the same general relationships were observed.

Due to the favorable interaction between nitrogen and phosphorus and the insignificant or detrimental effect of potassium, the NP fertilizer treatment generally was the best nutrient element combination tested with these soils and under these conditions. The NP fertilizer treatment increased the total dry weight of the red oak seedlings 28, 38, 67, and 59 percent in 1962, and 5, 21, 34, and 26 percent in 1963 on the Lindley, Shelby, Clarksville forest, and Clarksville old field soils, respectively.

Results of the foliage analyses indicated that the mineral content of the red oak seedlings varied greatly on the four soils (Tables 38 and 39, Appendix). The nitrogen and phosphorus concentrations were significantly higher in seedlings grown on the two Missouri soils than in seedlings grown on the two Iowa soils in 1962. Furthermore, the concentrations of these same two elements were significantly higher in the seedlings on the forest soils than in the seedlings on the non-forest soils. Potassium concentrations, on the other hand, were significantly higher in the seedlings grown on the non-forest soils.

In 1963, the nitrogen and potassium concentrations in the red oak leaves did not differ significantly over the four soils, although the foliar nitrogen percent appeared to be slightly higher in seedlings grown on the forest soils than on the non-forest soils. Phosphorus concentrations were significantly higher in the 1963 seedlings that were grown on the Missouri soils as compared to the seedlings grown on the Iowa soils and also higher in the seedlings grown on the Lindley soil as compared to the seedlings grown on the Shelby soils. The phosphorus concentration in seedlings grown on the Clarksville forest and on the old field soils did not differ significantly.

The application of nitrogen and phosphorus fertilizer significantly increased the concentrations of these two elements in the leaves of the 1962 seedlings. The nitrogen fertilizer also significantly increased the phosphorus content in the leaves of the red oak seedlings. On the other hand, phosphorus applications did not significantly affect the nitrogen concentrations in the leaves. There were certain

indications, however, that the nitrogen concentrations were greater after nitrogen fertilization if supplemented with phosphorus fertilizer.

The potassium concentration in the leaves of the red oak seedlings was not significantly affected by the addition of potassium in the fertilizers, a factor which may help explain the lack of growth response to this element on the soils studied. Both nitrogen and phosphorus applications, the latter element in particular, significantly reduced the concentration of potassium in the leaves of the seedlings. This effect probably was due to a dilution effect rather than ion antagonism. The 1963 seedlings also did not show any increase in potassium concentration in the leaves of seedlings on potassium fertilized soils. The effect of nitrogen and phosphorus fertilization on the potassium concentrations in the leaves was not significant in 1963, probably because the growth response to these two elements was smaller the second year and therefore the dilution effect was not as great.

The residual phosphorus fertilizer available to the 1963 seedlings was evident in the foliage analyses. The phosphorus concentrations in the leaves were significantly higher in the seedlings grown on the soils previously fertilized with this element. Most of the nitrogen, however, had either been utilized or lost by leaching by 1963 and consequently the concentrations of this element in the leaves of the red oak seedlings was not any higher on the soils fertilized with nitrogen the previous year.

The content of some of the micronutrients in the leaves of the

red oak seedlings also varied greatly over the various fertilizer treatments but the variations could not be related to any specific fertilizer effects or to growth rate. Some soil differences also were noted but the only obvious trend indicated during the two year study period was that the seedlings grown on the two Clarksville soils contained consistently higher concentrations of manganese in the foliage than seedlings grown on the Lindley and Shelby soils.

Nitrogen Experiment

Varying levels of nitrogen, supplemented by phosphorus and potassium at the basic rates of fertilization, were tested on all four study soils. The resulting growth data for the 1962 and 1963 seedlings are given in Tables 10 and 11. Statistical analyses relating to the growth data are given in Tables 12 and 13.

Significant growth responses were obtained in 1962 from nitrogen fertilization on all four soils. The growth response to the increasing nitrogen levels was mainly in height (Figure 3) and dry weight of the shoot (Figure 4). The quadratic relation between height growth and nitrogen supply was statistically significant at the 5-percent probability level. The quadratic relation between shoot dry weight and nitrogen supply was statistically significant at the 1-percent probability level. The quadratic relationships between these variables indicate that growth increased up to an optimum nitrogen application and then was suppressed by higher rates of nitrogen fertilization. For all soils that were studied, the greatest shoot growth was produced

Table 10. Average height and dry weight per seedling of red oak from the nitrogen experiment, 1962

Soil	Nitrogen level pounds/acre	Height, in.	Dry weight, g				Shoot/Root ratio
			Leaves	Stem	Roots	Total	
Lindley (Forest)	0	8.8	3.14	1.84	6.64	11.62	.75
	30	9.4	3.37	1.91	6.67	11.95	.80
	90	9.9	3.58	2.06	7.06	12.70	.81
	180	9.9	3.90	2.22	7.09	13.21	.86
	360	9.9	3.08	2.08	5.68	10.84	.90
Shelby (Prairie)	0	7.5	2.17	0.99	6.00	9.16	.53
	30	8.2	2.64	1.36	6.29	10.29	.67
	90	9.2	3.29	1.80	6.34	11.43	.81
	180	9.7	3.65	1:99	6.02	11.66	.94
	360	9.2	3.21	1.76	5.38	10.35	.92
Clarksville (Forest)	0	9.1	3.55	1.96	7.22	12.73	.76
	30	9.6	3.72	2.08	7.23	13.03	.81
	90	9.9	3.87	2.29	7.43	13.59	.83
	180	9.8	3.94	2.29	6.78	13.01	.93
	360	9.0	3.27	1.79	5.08	10.14	1.00
Clarksville (Old field)	0	8.4	2.90	1.41	5.60	9.91	.77
	30	8.7	3.02	1.55	5.93	10.50	.77
	90	8.9	3.46	1.65	6.04	11.15	.87
	180	8.7	3.41	1.73	5.36	10.50	.96
	360	8.6	3.17	1.43	3.82	8.42	1.02

Table 11. Average height and green and dry weight per seedling of red oak from the nitrogen experiment, 1963

Soil	Nitrogen level pounds/acre	Height, in.	Green weight, g	Dry weight, g				Root/Shoot ratio
				Leaves	Stem	Roots	Total	
Lindley (Forest)	0	9.9	31.71	3.47	2.89	8.47	14.93	.75
	30	9.6	34.11	4.11	2.83	8.74	15.68	.80
	90	11.2	32.60	3.78	2.91	8.47	15.16	.79
	180	10.3	31.54	3.85	2.52	8.14	14.51	.79
	360	9.4	30.98	3.66	2.49	7.76	13.91	.79
Shelby (Prairie)	0	8.4	21.57	2.69	1.91	5.89	10.49	.79
	30	7.6	21.30	2.38	1.67	6.68	10.73	.60
	90	7.7	22.81	2.81	1.66	6.39	10.86	.70
	180	8.4	22.53	2.46	1.85	7.01	11.32	.63
	360	8.9	21.41	2.73	1.92	6.05	10.70	.80
Clarksville (Forest)	0	11.2	33.90	4.29	2.65	8.83	15.77	.80
	30	10.4	32.88	4.30	2.71	8.70	15.71	.83
	90	11.6	33.87	4.48	2.70	8.95	16.13	.81
	180	10.1	30.12	3.32	2.31	8.51	14.14	.66
	360	9.9	26.07	3.26	2.26	6.65	12.17	.83
Clarksville (Old field)	0	8.5	23.08	2.52	1.84	6.71	11.07	.66
	30	9.4	24.82	2.74	2.06	5.90	10.70	.90
	90	8.8	26.00	2.80	2.07	7.49	12.36	.67
	180	7.9	23.22	2.51	1.99	6.47	10.97	.71
	360	9.1	22.03	2.75	1.86	5.75	10.36	.81

Table 12. Mean squares from analysis of variance of average height and dry weight per pot and shoot/root ratio per seedling of red oak from the nitrogen experiment, 1962

Source of variation	Degrees of freedom	Height	Dry weight			Shoot/Root ratio
			Shoot	Root	Total	
Replication	2	0.50	3.45	16.88	31.72	.033
Soil (S)	3	30.00*	42.22**	56.11**	180.13**	.180**
Iowa vs Missouri	(1)	1.60	7.98	9.58	0.07	.134**
Lindley vs Shelby	(1)	45.14*	50.65**	26.36	150.08**	.018
Cl.-F. vs Cl.-O.f.	(1)	42.72*	68.04**	132.38**	390.24**	.027
Nitrogen level (N)	4	19.25	28.45**	50.81**	95.82**	.747**
Linear	(1)	15.06	8.53	155.73**	91.35*	.708**
Quadratic	(1)	54.46*	104.57**	44.42*	285.32**	.037
Cubic	(1)	7.45	0.69	2.82	6.30	.000
Remainder	(1)	0.03	0.00	0.25	0.56	.001
S x N	12	4.33	4.40	2.90	11.07	.019
Error	38	7.76	3.61	8.86	18.53	.014

*Significant at the 5-percent probability level.

**Significant at the 1-percent probability level.

Table 13. Mean squares from analysis of variance of average height and green and dry weight per pot and shoot/root ratio per seedling of red oak from the nitrogen experiment, 1963

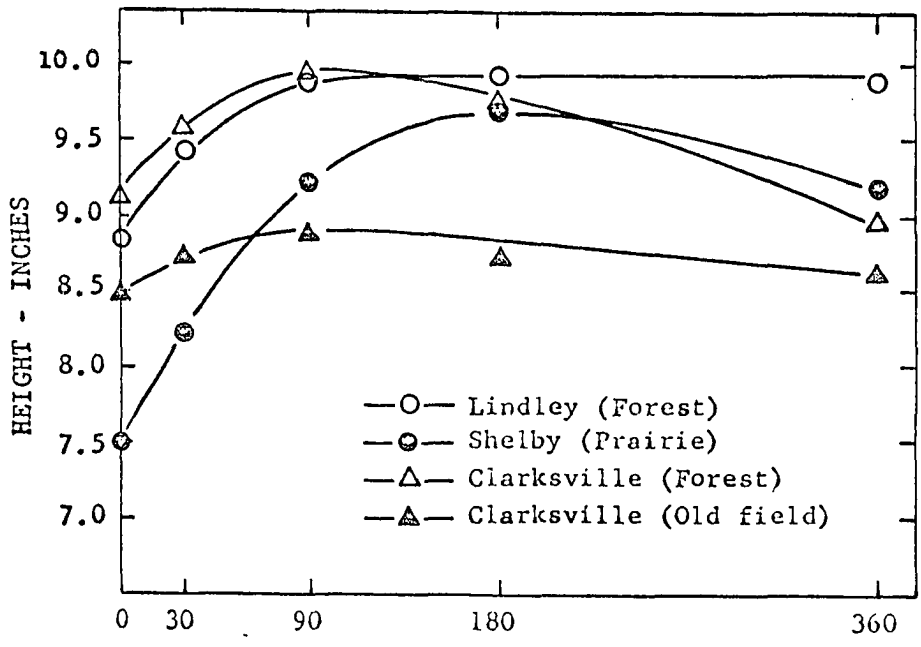
Source of variation	Degrees of freedom	Height	Total green weight	Dry weight			Shoot/Root ratio
				Shoot	Root	Total	
Replication	2	2.50	444.88*	1.15	90.48**	106.99**	.112**
Soil (S)	3	173.33**	3663.11**	173.04**	160.38**	669.51**	.023
Iowa vs Missouri	(1)	40.51	40.03	0.96	0.18	1.66	.008
Lindley vs Shelby	(1)	238.57**	7112.95**	293.53**	246.59**	1089.02**	.051
Cl.-F. vs Cl.-O.f.	(1)	240.27**	3836.35**	224.63**	234.36**	917.87**	.009
Nitrogen level (N)	4	7.25	223.15	8.10	25.01*	52.05*	.021
Linear	(1)	2.36	659.88**	18.10*	65.44*	155.05**	.007
Quadratic	(1)	0.00	87.37	0.12	31.42	26.35	.051
Cubic	(1)	9.52	141.56	13.73	1.14	21.65	.019
Remainder	(1)	17.12	3.79	1.46	2.06	5.16	.005
S x N	12	11.75	65.86	5.04	7.33	17.29	.018
Error	38	10.50	88.91	4.45	8.87	18.92	.015

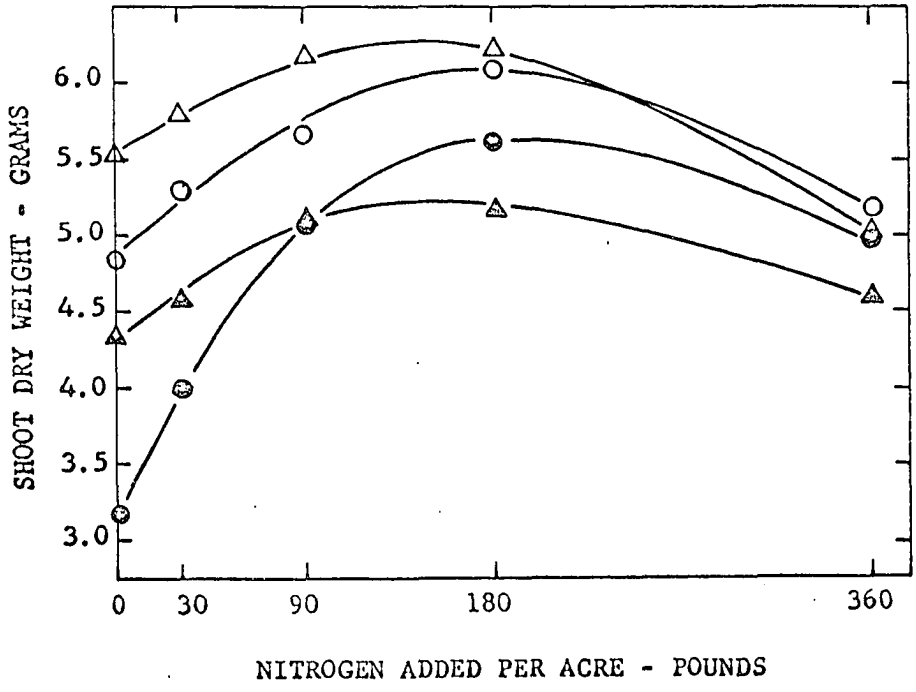
*Significant at the 5-percent probability level.

**Significant at the 1-percent probability level.

Figure 3. Height growth of red oak seedlings in relation to nitrogen fertilization, 1962

Figure 4. Shoot dry weight of red oak seedlings in relation to nitrogen fertilization, 1962


HEIGHT - INCHES
10.0
9.5
9.0
8.5
8.0
7.5
7.0
0
30
90
180
360
—O— Lindley (Forest)
—⊖— Shelby (Prairie)
—△— Clarksville (Forest)
—▲— Clarksville (Old field)


SHOOT DRY WEIGHT - GRAMS
6.0
5.5
5.0
4.5
4.0
3.5
3.0
0
30
90
180
360
NITROGEN ADDED PER ACRE - POUNDS

with 180 pounds of nitrogen per acre, although the shape of the growth curves suggests that the optimum application rates may be about 200 pounds of nitrogen per acre on the Lindley and the Shelby soils and about 150 pounds per acre on the two Clarksville soils. The 360-pound rate of nitrogen application depressed shoot dry weight on all soils.

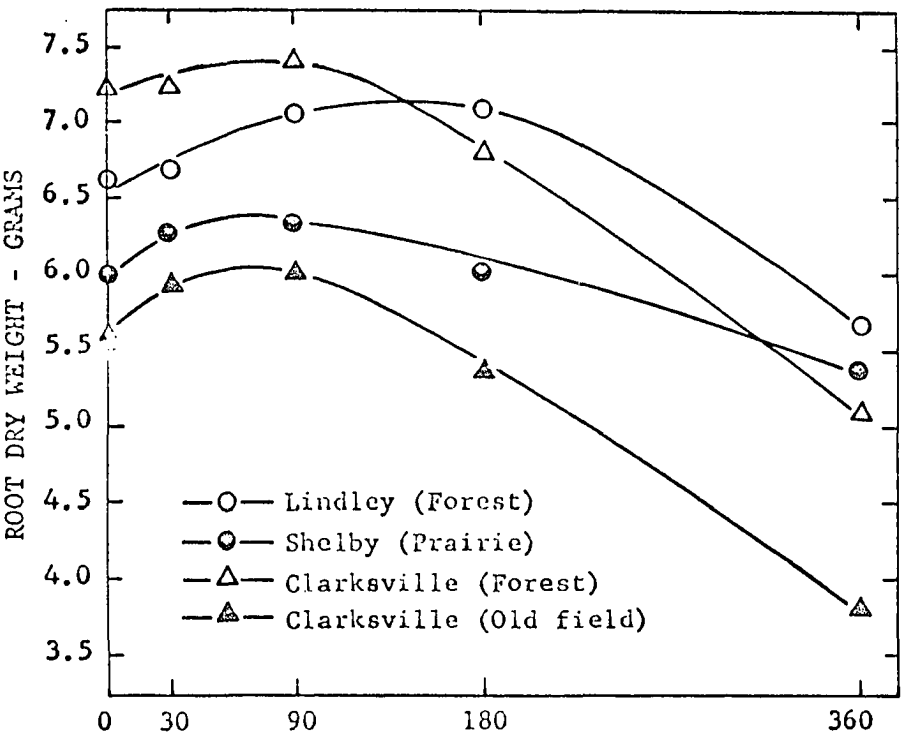
Root growth was more sensitive to nitrogen supply than shoot growth (Figure 5). The application of 180 pounds of nitrogen per acre, which was optimum for shoot growth, was detrimental to root growth on all but the Lindley soil. The greatest root growth on the other soils was attained by seedlings fertilized with 90 pounds of nitrogen per acre. The reduction in root growth from the heavy applications of nitrogen was most apparent on the two Clarksville soils.

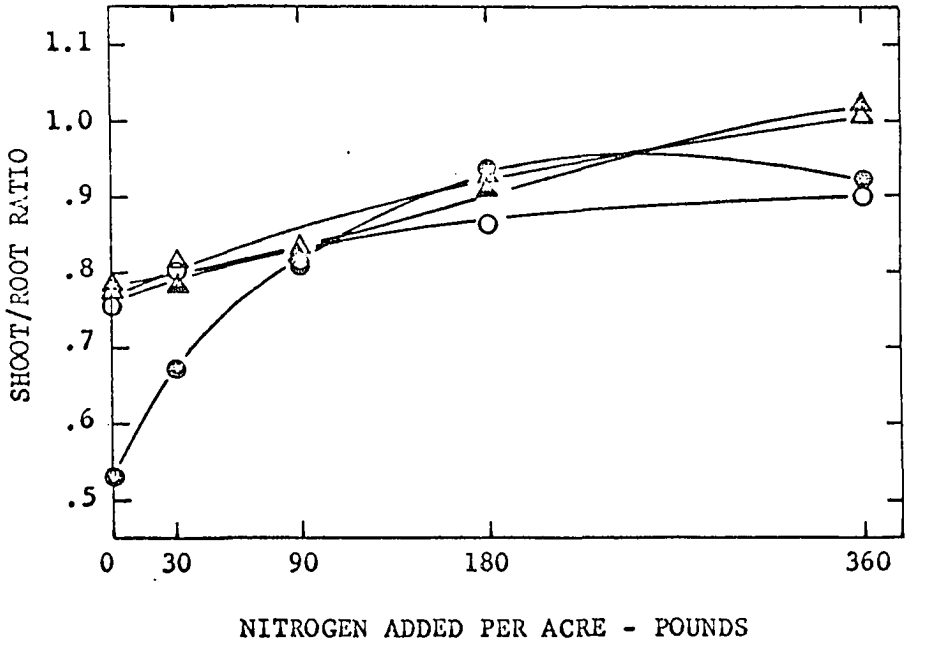
Because of the difference in response of shoots and roots to the varying levels of nitrogen, the shoot/root ratio increased significantly with increasing applications of nitrogen fertilizer on all of the soils (Figure 6). The relation was essentially linear over the rates of nitrogen fertilization tested, although a curvilinear trend appeared to be indicated on the Shelby soils. The seedlings on the two Clarksville soils had significantly higher shoot/root ratios than seedlings on the Lindley and Shelby soils. This was due mainly to the greater reduction in root growth following heavy nitrogen fertilization on the two Clarksville soils.

The greatest total dry weight of the red oak seedlings on the Lindley and Shelby soils was obtained with the application of 180 pounds

Figure 5. Root dry weight of the red oak seedlings in relation to nitrogen fertilization, 1962

Figure 6. Shoot/root ratio of the red oak seedlings in relation to nitrogen fertilization, 1962


ROOT DRY WEIGHT - GRAMS
7.5
7.0
6.5
6.0
5.5
5.0
4.5
4.0
3.5
0
30
90
180
360
Lindley (Forest)
Shelby (Prairie)
Clarksville (Forest)
Clarksville (Old field)


SHOOT/ROOT RATIO
1.1
1.0
.9
.8
.7
.6
.5
0
30
90
180
360
NITROGEN ADDED PER ACRE - POUNDS

of nitrogen per acre, whereas 90 pounds of nitrogen per acre appeared to be sufficient for maximum growth on the two Clarksville soils (Figure 7). Considering all data, nitrogen was not seriously limiting because the total nitrogen responses were not large on any of the four soils, even though the responses were statistically significant. There were no apparent symptoms of nitrogen deficiency on the foliage of the unfertilized seedlings, but the application of nitrogen did produce a definitely darker green color in the leaves.

There was no significant shoot growth response with seedlings grown in 1963 on the soils fertilized with the different levels of nitrogen, indicating that there was little residual nitrogen in the soils from the previous year. Root growth, however, was significantly lower on the soils that had received the heavier applications of nitrogen the previous year, and therefore the total dry weight of these seedlings was significantly lower than the seedlings grown on the soils that had received lighter applications of nitrogen. Significance was expressed at the 5-percent probability level. The reduced root growth probably was associated with acid residues from the heavy nitrogen applications which had reduced the soil pH by about 0.5 units.

The concentration of nitrogen in the leaves of the red oak seedlings was significantly increased by the application of nitrogen fertilizers on all soils in 1962 (Table 40, Appendix). A quadratic relation was found between nitrogen supply and nitrogen concentration in the leaves, which was significant at the 1-percent probability level. This relation is shown in Figure 8 for the 1962 seedlings.

Figure 7. Total dry weight of the red oak seedlings in relation to nitrogen fertilization, 1962

Figure 8. Foliar nitrogen concentration of the red oak seedlings in relation to nitrogen fertilization, 1962

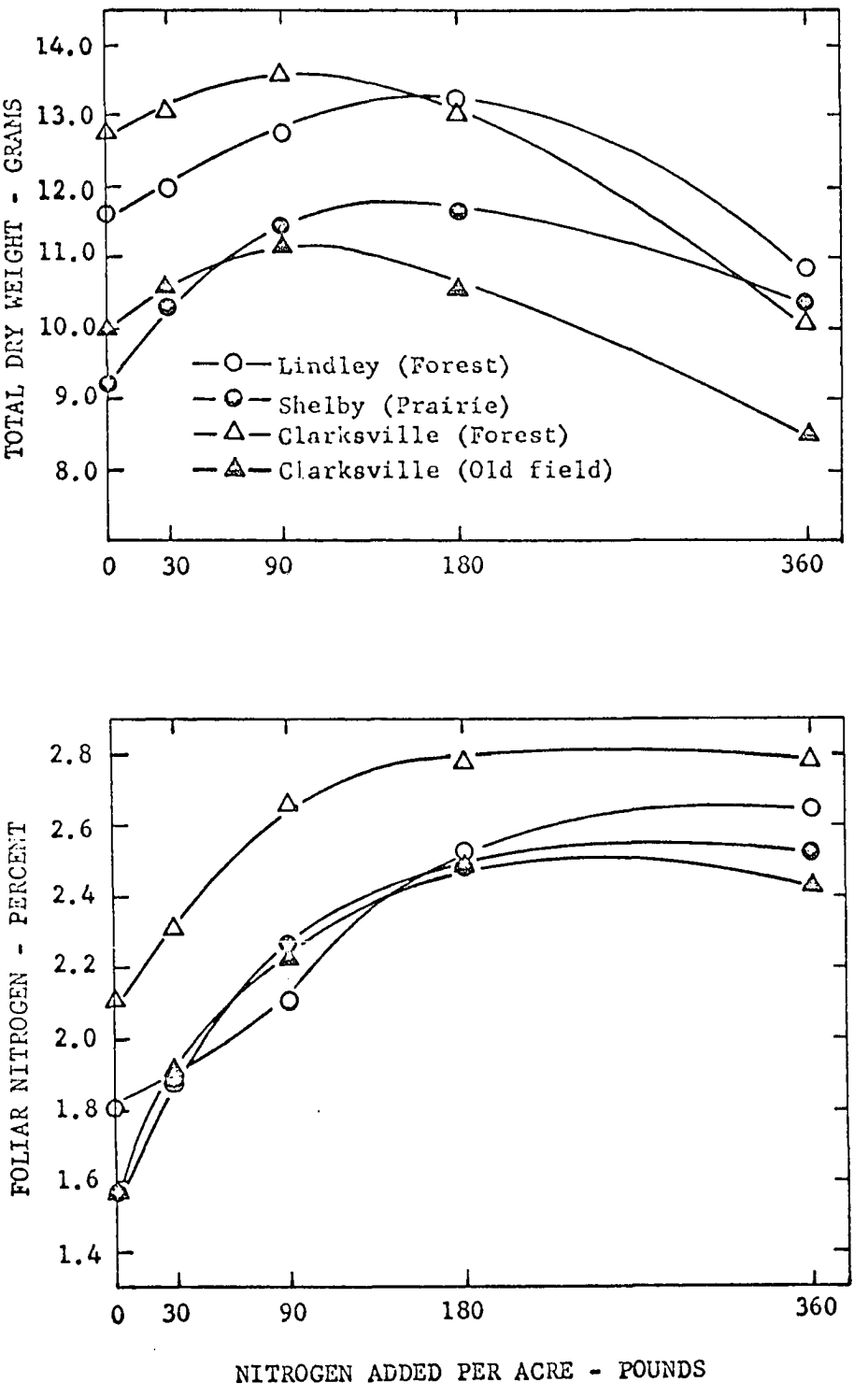
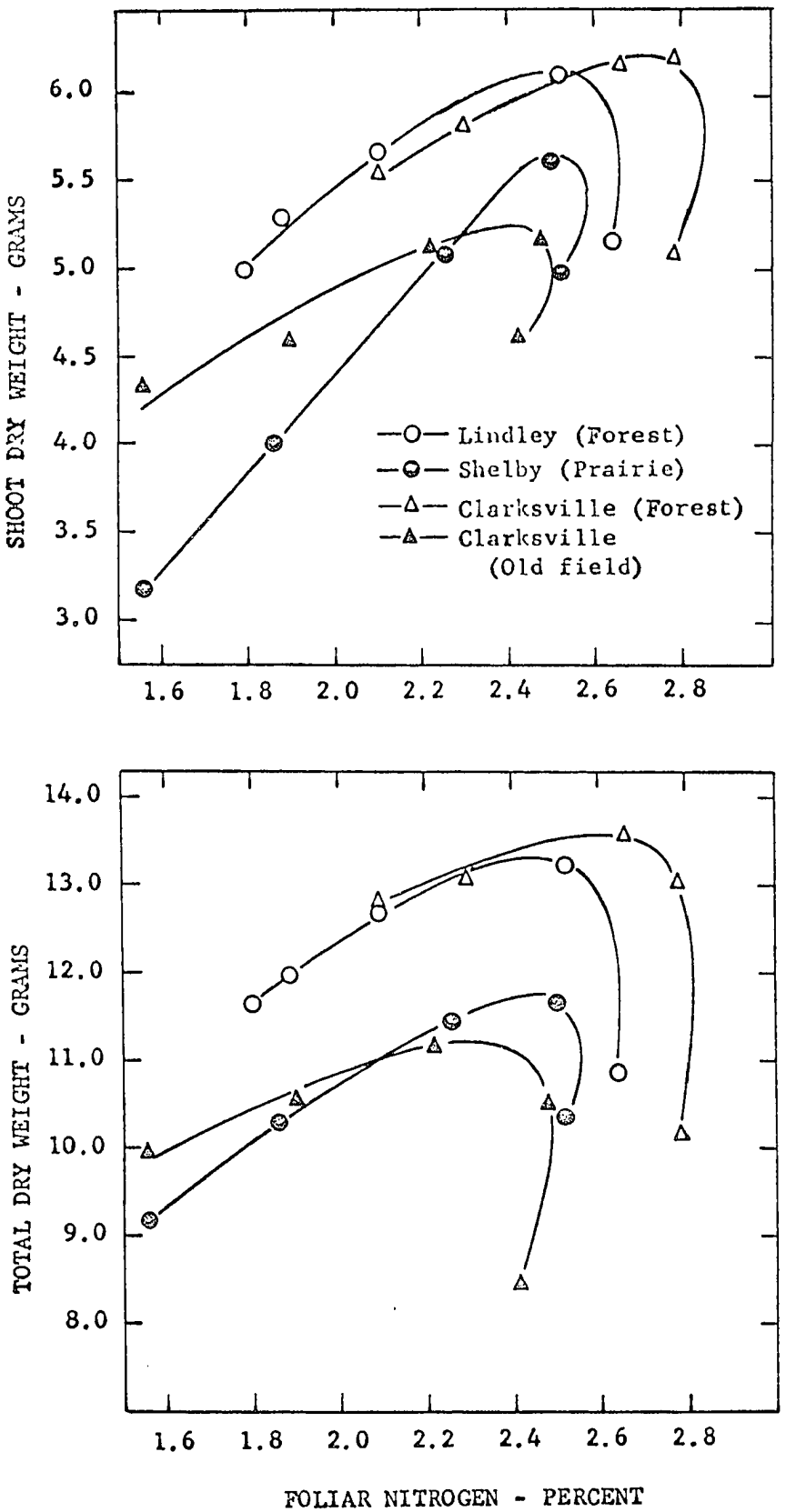

TOTAL DRY WEIGHT - GRAMS
14.0
13.0
12.0
11.0
10.0
9.0
8.0
0
30
90
180
360
Lindley (Forest)
Shelby (Prairie)
Clarksville (Forest)
Clarksville (Old field)
FOLIAR NITROGEN - PERCENT
2.8
2.6
2.4
2.2
2.0
1.8
1.6
1.4
0
30
90
180
360
NITROGEN ADDED PER ACRE - POUNDS

Figure 9. Shoot dry weight of the red oak seedlings in relation to foliar nitrogen concentration, 1962

Figure 10. Total dry weight of the red oak seedlings in relation to foliar nitrogen concentration, 1962


SHOOT DRY WEIGHT - GRAMS
6.0
5.5
5.0
4.5
4.0
3.5
3.0
1.6
1.8
2.0
2.2
2.4
2.6
2.8
—O— Lindley (Forest)
—⊖— Shelby (Prairie)
—Δ— Clarksville (Forest)
—▲— Clarksville (Old field)
TOTAL DRY WEIGHT - GRAMS
14.0
13.0
12.0
11.0
10.0
9.0
8.0
1.6
1.8
2.0
2.2
2.4
2.6
2.8
FOLIAR NITROGEN - PERCENT

The application of varying levels of nitrogen to the four soils in 1962 also affected the uptake of some of the other elements by the red oak seedlings. Nitrogen fertilization greatly increased the concentration of phosphorus in the leaves of the red oak seedlings in 1962. The greatest phosphorus concentrations, however, were obtained at the nitrogen fertilization rate at which the maximum growth was produced. The highest rate of nitrogen fertilization generally reduced the phosphorus concentration in the leaves of the seedlings, probably because of the reduced root growth which decreased the ability of the seedlings to absorb mineral nutrients from the soil. The 1963 seedlings growing on the soils that had received heavy nitrogen applications in 1962 also appeared to contain greater concentrations of phosphorus but the relationship was not as apparent as in the previous year.

The application of nitrogen to the four soils also tended to increase the concentration of aluminum and manganese in the leaves of the 1962 seedlings. The manganese trend, however, was only apparent on the Lindley and the Shelby soils because the content of this element in the seedlings grown on the two Clarksville soils was too high to be measured on the spectrograph. The concentration of boron in the leaves, on the other hand, tended to decrease upon application of nitrogen to the soils. In the 1963 seedlings, boron and manganese concentrations followed the same trend as was observed in 1962, but aluminum was more variable. The concentrations of the other elements also were too variable to establish any relationship with nitrogen level in either year.

Liming Experiment

Applications of varying levels of lime to the Lindley and the Clarksville forest soils were detrimental rather than beneficial to the growth of the red oak seedlings in 1962 (Table 14). All measures of growth--height and shoot, root, and total dry weight--were significantly decreased by the application of lime to these two soils. The significance of the lime effect generally was expressed at the 1-percent probability level (Table 15). Height growth was less variable than dry weight of the seedlings. The 2-ton rate of liming decreased growth more on the Clarksville soil than on the Lindley soil.

In 1963, the seedlings on the limed Lindley soil grew better than the seedlings on the unlimed soil (Tables 16 and 17). The growth of the seedlings on the limed Clarksville soil was adversely affected as in the previous year. The different response of the red oak seedlings to lime on the two soils was reflected in the significant lime x soil interaction in the statistical analysis of the 1963 growth data.

Liming also greatly conditioned the response of the red oak seedlings to the application of fertilizer and to the elements they contained. The lime x fertilizer interaction was significant at the 1-percent probability level both years. This interaction was most apparent with dry and green weight growth of the seedlings.

To establish the source of the lime x fertilizer interaction, individual mean squares were calculated for the interactions between lime and the added effects of nitrogen, phosphorus, and potassium. The added effects of these elements were obtained by comparing the

Table 14. Average height and dry weight per seedling of red oak from the lime experiment, 1962

Soil	Lime level, tons/acre	Fertilizer	Height, in.	Dry weight, g			
				Leaves	Stem	Roots	Total
Lindley (Forest)	0	-	8.1	3.02	1.45	6.33	10.80
		N	9.0	3.23	1.77	4.72	9.72
		NP	10.1	4.16	2.22	7.48	13.86
		NPK	9.9	3.58	2.06	7.06	12.70
	1	-	7.5	2.35	1.33	5.29	8.97
		N	7.3	2.08	1.10	4.84	8.02
		NP	9.1	3.32	1.81	6.91	12.04
		NPK	8.8	3.26	1.71	6.98	11.95
	2	-	7.6	2.54	1.38	5.78	9.70
		N	8.3	2.52	1.42	5.40	9.34
		NP	9.2	2.58	1.83	5.70	10.12
		NPK	8.7	3.19	1.66	6.22	11.06
Clarksville (Forest)	0	-	8.0	2.36	1.28	5.69	9.33
		N	8.0	2.74	1.39	3.74	7.87
		NP	10.9	4.93	2.61	8.06	15.60
		NPK	9.9	3.87	2.29	7.43	13.59
	1	-	7.9	2.56	1.37	5.14	9.07
		N	6.9	2.15	1.16	5.21	8.52
		NP	8.5	3.94	1.86	7.42	13.22
		NPK	8.9	3.65	1.83	6.79	12.27
	2	-	8.2	2.55	1.48	4.90	8.93
		N	8.2	2.59	1.56	5.26	9.42
		NP	7.6	2.58	1.40	5.32	9.30
		NPK	8.8	3.72	1.70	5.39	10.81

Table 15. Average height and green and dry weight per seedling of red oak from the lime experiment, 1963

Soil	Lime level, t./a.	Fertilizer	Height in.	Total green weight, g	Dry weight, g			
					Leaves	Stem	Roots	Total
Lindley (Forest)	0	-	10.5	28.60	3.70	2.79	7.42	13.91
		N	9.5	26.21	2.77	2.64	7.06	12.47
		NP	11.8	31.34	3.53	2.82	8.22	14.57
		NPK	11.2	32.60	3.78	2.91	8.47	15.16
	1	-	10.0	34.21	3.90	2.92	9.29	16.11
		N	10.9	32.92	4.84	2.73	7.96	15.53
		NP	10.4	35.69	4.24	3.20	9.28	16.72
		NPK	9.7	32.46	3.61	2.74	8.79	15.14
	2	-	12.0	33.65	4.21	3.23	9.16	16.60
		N	12.3	36.40	4.98	3.71	8.67	17.36
		NP	11.2	34.86	4.39	3.37	9.24	17.00
		NPK	11.6	31.50	3.68	3.22	7.98	14.88
Clarksville (Forest)	0	-	9.9	27.64	3.60	2.59	7.08	13.27
		N	8.8	21.79	2.90	1.94	5.08	9.92
		NP	11.5	37.06	4.77	3.16	9.93	17.86
		NPK	11.6	33.87	4.48	2.70	8.95	16.13
	1	-	9.2	23.45	2.82	2.09	6.69	11.60
		N	8.7	27.16	3.10	2.16	7.72	12.98
		NP	9.4	29.32	3.53	2.15	7.96	13.64
		NPK	9.7	26.70	3.14	2.38	6.94	12.46
	2	-	7.6	22.76	2.21	1.60	6.75	10.56
		N	10.2	29.78	3.59	2.48	8.50	14.57
		NP	8.4	27.67	3.39	2.16	7.30	12.85
		NPK	9.5	25.89	3.43	2.36	6.43	12.22

Table 16. Mean squares from the analysis of variance of average height and dry weight per pot of red oak seedlings from the lime experiment, 1962

Source of variation	Degrees of freedom	Height	Dry weight		
			Shoot	Root	Total
Replication	2	16.00	5.42	2.78	1.39
Soil (S)	1	3.00	4.39	6.19	0.40
Lime (L)	2	79.00**	69.90**	38.29**	188.16**
Fertilizer (F)	3	90.00**	127.04**	140.27**	515.07**
L x S	2	0.50	2.22	6.50	11.69
F x S	3	6.67	6.04	4.30	18.12
L x F	6	14.50	22.46**	30.98**	83.48**
L x F x S	6	7.83	5.51	3.49	14.74
Error	46	8.56	4.50	11.69	22.86

*Significant at the 5-percent probability level.

**Significant at the 1-percent probability level.

Table 17. Mean squares from the analysis of variance of average height and green and dry weight per pot of red oak seedlings from the lime experiment, 1963

Source of variation	Degrees of freedom	Height	Total green weight	Dry weight		
				Shoot	Root	Total
Replication	2	16.50	244.33	0.98	106.32	94.07
Soil (S)	1	311.00**	3684.39**	277.81**	170.82**	842.76**
Lime (L)	2	43.50	11.84	5.09	3.06	6.62
Fertilizer (F)	3	16.33	583.18*	15.51	36.28	104.74*
L x S	2	89.50**	1096.59**	94.24**	37.75	269.84*
F x S	3	15.33	201.07	19.71	11.80	51.79
L x F	6	40.33**	532.19**	28.73*	38.57*	135.28**
L x F x S	6	8.17	94.08	3.65	24.25	37.69
Error	46	17.41	156.06	10.57	16.80	36.43

*Significant at the 5-percent probability level.

**Significant at the 1-percent probability level.

treatments differing only in the element being studied. For example, the dry weight of the seedlings fertilized with NP fertilizer minus the dry weight of the seedlings fertilized with N fertilizer provides an estimate of the added effects of phosphorus. The added effects of nitrogen and potassium were obtained by the same technique. Only the N effect is free from possible interactions with other fertilizer nutrients. The total sum of squares of these individual interactions is larger than the sum of squares of the lime x fertilizer interaction and therefore does not meet the requirements for orthogonality. However, the difference in total sum of squares is not large.

A lime x nitrogen interaction was indicated in the growth data for the 1962 seedlings but was not statistically significant by the above analysis. In 1963, the lime x nitrogen interaction was significant at the 1-percent probability level. This interaction was due to the fact that nitrogen alone as a treatment increased growth of the red oak seedlings over the unfertilized seedlings only on the limed soils. On the unlimed soils the N fertilizer treatment actually depressed the dry weight growth of the seedlings. The favorable effect of the N fertilizer treatment on the limed soils was brought about mainly by increased shoot growth. These results do not suggest necessarily that lime and nitrogen form a suitable combination for fertilizing red oak seedlings; the detrimental effect of the lime also must be considered. On the Lindley soil where a lime response was obtained the lime-nitrogen combination did appear to improve growth but this was not true on Clarksville soils where lime adversely affected growth.

The lime x phosphorus interaction also was significant and brought about greater differences in growth than the lime-nitrogen interaction. Significance was at the 1-percent probability level in both years and for all measures of growth. The response to phosphorus as an individual nutrient was greatly depressed by the addition of lime to these soils. For example, the total dry weight of the NP fertilized seedlings was 98 percent greater than the dry weight of the N fertilized seedlings on the unlimed Clarksville forest soil in 1962 but there essentially was no difference in growth of the NP and N fertilized seedlings on this same soil limed with the 2-ton rate.

The lime x potassium interaction on total dry weight was significant at the 5-percent probability level in 1962 but was not significant in 1963. The adverse effect of potassium on seedling growth in 1962 was reduced by liming. With the application of 2 tons of lime per acre the potassium fertilizer had a slight beneficial effect on total dry weight of the red oak seedlings. The response was due mainly to increased shoot growth.

Considering all growth data, none of the lime-fertilizer combinations produced seedlings as large as the unlimed, NP fertilized seedlings on the two soils in 1962. This also was true on the Clarksville soil in 1963, but a slightly beneficial effect of lime was observed on the Lindley soil.

Results of the foliage analyses showed that liming did not significantly affect the nitrogen concentration in the leaves of the red oak seedlings on either soil in 1962 or 1963 (Tables 42 and 43, Appendix).

The phosphorus concentration in the red oak leaves, however, was significantly decreased by liming on the Clarksville forest soil in 1962 and 1963. The reduction in phosphorus concentration in the leaves of the red oak seedlings was most apparent on the soils to which phosphorus had been added as a fertilizer. On the Lindley soil the phosphorus concentrations in the red oak leaves appeared to increase on the unfertilized soil but on the phosphorus fertilized soil the concentration of this element in the leaves tended to decrease with lime additions as on the Clarksville soil. The increased phosphorus concentrations in the seedlings on unfertilized Lindley soil may partly explain the response observed to liming on this soil in 1963. On the phosphorus fertilized soils the presence of excess lime in the soil apparently inhibited the uptake of the phosphorus by the red oak seedlings.

The calcium concentration in the red oak leaves was increased significantly by liming on both soils in 1962 and 1963. The other macronutrients were not significantly affected by the application of lime to these soils, although magnesium showed a rather consistent decrease in concentration in leaves of seedlings growing on the limed soils in 1963.

The micronutrients were particularly affected by liming. Although a statistical analysis of the manganese content of the seedlings was not made because the concentrations of this element were too high to be measured on the Clarksville soil, there is little reason to believe that the effect of lime on the concentration of manganese in the leaves

of the red oak seedlings was not significant. There was almost an 8- to 10-fold decrease in manganese concentration in the leaves of the red oak seedlings with the application of 2 tons of lime per acre.

The boron content in the leaves also was significantly reduced in seedlings grown on the limed soils in both years. The lime x soil interaction in the statistical analysis of boron concentration was significant at the 1-percent probability level in 1963, and was due to the fact that the reduction of foliar boron was much greater in the seedlings on the Lindley soil than in seedlings on the Clarksville soil, although the reduction was significant on both soils.

The molybdenum concentration in the leaves was increased by liming in 1962, and most markedly so in the seedlings on the Clarksville soil. This element was not analyzed in the 1963 seedlings. Sodium and aluminum, although not essential elements, were found in greater concentrations in the leaves of seedlings on limed soils in 1962, but in 1963 the opposite trend was true. The relationships were significant at the 1-percent probability level in both years.

Light Intensity Experiment

The growth of the red oak seedlings on the Lindley and Clarksville forest soils was greatly affected by the light intensity at which the seedlings were grown (Figure 11). The growth data obtained in 1962 and 1963 are presented in Tables 18 and 19. The results of the statistical analyses relating to these growth data are presented in Tables 20 and 21.

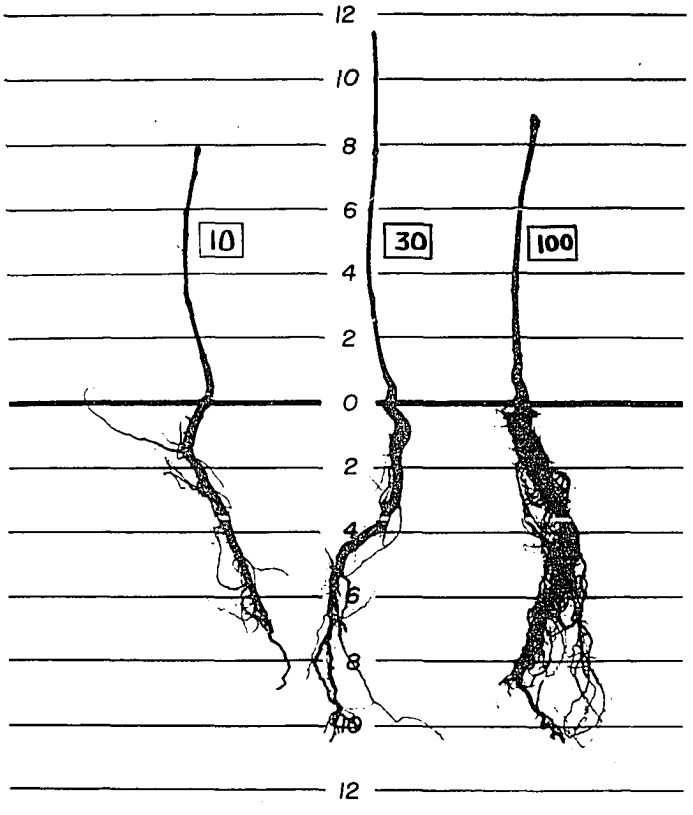


Figure 11. One-year-old red oak seedlings grown at 10-, 30-, and 100-percent light intensities, 1963

Table 18. Average height and dry weight per seedling of red oak from the light intensity experiment, 1962

Soil	Light intensity, percent	Fertilizer	Height, in.	Dry weight, g				Shoot/Root ratio
				Leaves	Stem	Roots	Total	
Lindley (Forest)	10	-	9.1	1.00	0.70	1.11	2.81	1.63
		NPK	8.4	0.96	0.64	1.14	2.74	1.49
		N_4PK	9.2	1.05	0.74	1.16	2.95	1.56
	30	-	9.3	2.21	1.41	5.08	8.70	0.72
		NPK	15.9	4.09	2.51	5.71	12.31	1.23
		N_4PK	15.2	3.19	2.33	4.29	9.81	1.29
	100	-	8.1	3.02	1.45	6.33	10.80	0.70
		NPK	9.9	3.58	2.06	7.06	12.70	0.81
		N_4PK	9.9	3.08	2.08	5.68	10.84	0.90
Clarksville (Forest)	10	-	9.0	0.78	0.57	0.98	2.33	1.39
		NPK	9.7	1.15	0.79	1.35	3.29	1.46
		N_4PK	9.5	1.14	0.71	0.80	2.65	2.37
	30	-	11.5	2.62	1.64	4.30	8.56	1.00
		NPK	14.3	3.80	2.44	6.11	12.35	1.04
		N_4PK	14.5	3.66	2.29	4.24	10.19	1.41
	100	-	8.0	2.36	1.28	5.69	9.33	0.66
		NPK	9.9	3.87	2.29	7.43	13.59	0.83
		N_4PK	9.0	3.27	1.79	5.08	10.14	1.00

Table 19. Average height and green and dry weight per seedling of red oak from the light intensity experiment, 1963

Soil	Light intensity, percent	Fertilizer	Height, in.	Total green weight, g	Dry weight, g				Shoot/Root ratio
					Leaves	Stem	Roots	Total	
Lindley (Forest)	10	-	8.7	7.52	1.17	0.79	1.40	3.36	1.66
		NPK	8.7	8.65	1.33	0.88	1.62	3.83	1.42
		N_4PK	8.6	7.91	1.36	0.83	1.47	3.66	1.55
	30	-	11.8	21.95	2.89	2.39	5.48	10.76	1.00
		NPK	13.6	24.79	3.29	2.58	5.69	11.56	1.05
		N_4PK	11.8	22.56	3.04	2.43	5.17	10.64	1.07
	100	-	10.5	28.60	3.70	2.79	7.42	13.91	0.89
		NPK	11.2	32.60	3.78	2.91	8.47	15.16	0.79
		N_4PK	9.4	30.98	3.66	2.49	7.76	13.91	0.79
Clarksville (Forest)	10	-	8.3	8.17	1.32	0.83	1.60	3.75	1.02
		NPK	8.2	7.89	1.26	0.83	1.54	3.63	1.44
		N_4PK	8.9	7.68	1.17	0.84	1.37	3.38	1.54
	30	-	10.3	19.54	2.50	1.90	4.78	9.18	0.92
		NPK	14.2	24.56	3.36	2.67	6.43	12.46	0.95
		N_4PK	12.0	23.29	2.85	2.25	5.40	10.51	0.97
	100	-	9.9	27.64	3.60	2.59	7.08	13.27	0.90
		NPK	11.6	33.87	4.48	2.70	8.95	16.13	0.81
		N_4PK	9.9	26.07	3.26	2.26	6.65	12.17	0.83

Table 20. Mean squares from the analysis of variance of average height and dry weight per pot and average shoot/root ratio per seedling of red oak from the light intensity experiment, 1962

Source of variation	Degrees of freedom	Height	Dry weight			Shoot/Root ratio
			Shoot	Roots	Total	
Replication	2	0.50	2.03	3.15	1.98	.131
Light intensity (L)	2	1015.00**	663.05**	1153.00**	3474.37**	3.211**
Error A	4	33.00	8.79	3.52	22.06	.098
Soil (S)	1	1.00	0.16	3.67	2.28	.119
Fertilizer (F)	2	237.50**	98.39**	67.51**	250.10**	.774**
F x L	4	95.50**	18.93**	10.67	46.08*	.074
L x S	2	6.50	1.49	0.41	2.91	.030
F x S	2	13.00	1.44	8.14	14.54	.216*
F x L x S	4	25.50*	5.13	1.18	5.08	.168*
Error B	30	6.40	3.43	6.44	14.06	.042

*Significant at the 5-percent probability level.

**Significant at the 1-percent probability level.

Table 21. Mean squares from the analysis of variance of average height and green and dry weight per pot, and average shoot/root ratio per seedling of red oak from the light intensity experiment, 1963

Source of variation	Degrees of freedom	Height	Total green weight	Dry weight			Shoot/Root ratio
				Shoot	Roots	Total	
Replication	2	98.5	228.52	16.96	14.39	39.83	.077
Light intensity (L)	2	558.5**	20376.21**	807.41**	1609.67**	4677.01**	2.132**
Error A	4	4.5	99.83	2.45	9.71	17.79	.066
Soil (S)	1	2.0	70.59	4.02	0.71	8.11	.048
Fertilizer (F)	2	82.5*	432.78**	19.59*	36.27*	109.16**	.012
F x L	4	15.5	108.51	6.89	8.59	26.43	.015
L x S	2	1.0	20.91	1.08	1.90	1.96	.022
F x S	2	37.8	25.29	3.92	6.36	20.25	.016
F x L x S	4	4.0	74.40	2.37	4.89	13.80	.017
Error B	30	18.3	63.00	4.10	6.93	14.70	.082

*Significant at the 5-percent probability level.

**Significant at the 1-percent probability level.

There was no significant difference in height growth of the red oak seedlings on the two soils and therefore the data have been combined to show the relations between height growth and the different fertilizer-light treatments. These relations are presented in Figures 12 and 13.

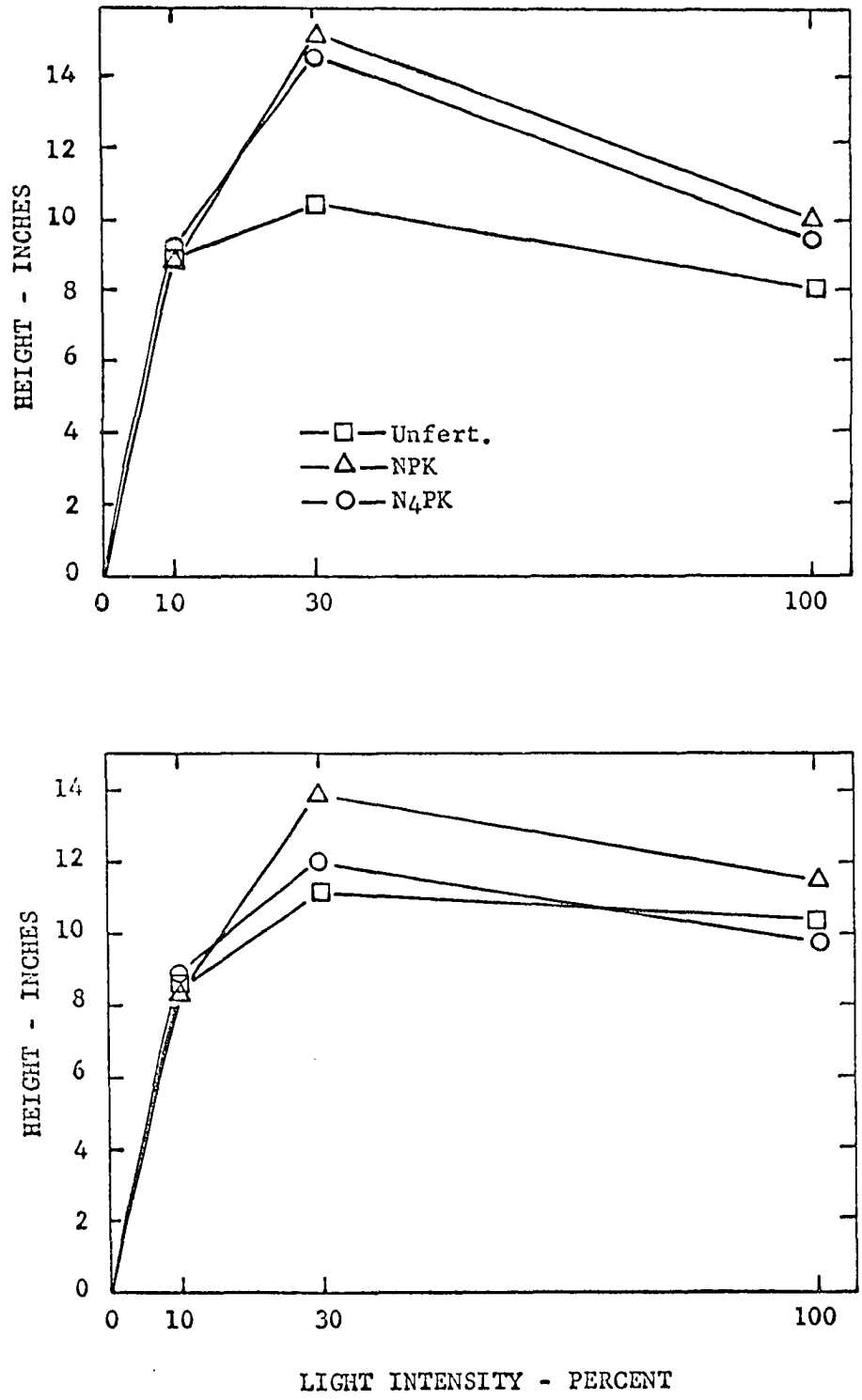
The tallest seedlings were produced at 30-percent light intensity in both years. On the unfertilized soils, the seedlings grown at 30-percent light intensity were 29 percent taller in 1962 and 8 percent taller in 1963 than seedlings grown at full light intensity. These height growth differences were significant in 1962 but not in 1963. The seedlings grown at 30-percent light intensity were 15 percent taller in 1962 and 32 percent taller in 1963 as compared to seedlings grown at 10-percent light intensity.

The fertilizers influenced height growth of the red oak seedlings grown only at full and at 30-percent light intensity. The height of seedlings grown at 10-percent light intensity was not affected by the fertilizers in either year. At this light intensity, the unfertilized seedlings were as tall as the fertilized seedlings.

The effects of the fertilizers on height growth were more pronounced at 30-percent light intensity than at full light intensity. The NPK fertilizer increased height growth at 30-percent light about 45 percent in 1962 and about 25 percent in 1963. The N_4PK (360 pounds of nitrogen per acre) fertilized seedlings were about the same height as the NPK fertilized seedlings at 30-percent and at full light intensity in 1962, but were significantly shorter than the NPK fertilized

Figure 12. Average height of red oak seedlings in relation to light intensity and fertilization, 1962

Figure 13. Average height of red oak seedlings in relation to light intensity and fertilization, 1963


HEIGHT - INCHES
14
12
10
8
6
4
2
0
0
10
30
100
Unfert.
NPK
N4PK
HEIGHT - INCHES
14
12
10
8
6
4
2
0
0
10
30
100
LIGHT INTENSITY - PERCENT

seedlings at both light intensities in 1963. Seedlings grown at full light intensity and fertilized with NPK were 23 percent taller in 1962 and 11 percent taller in 1963 compared to unfertilized seedlings.

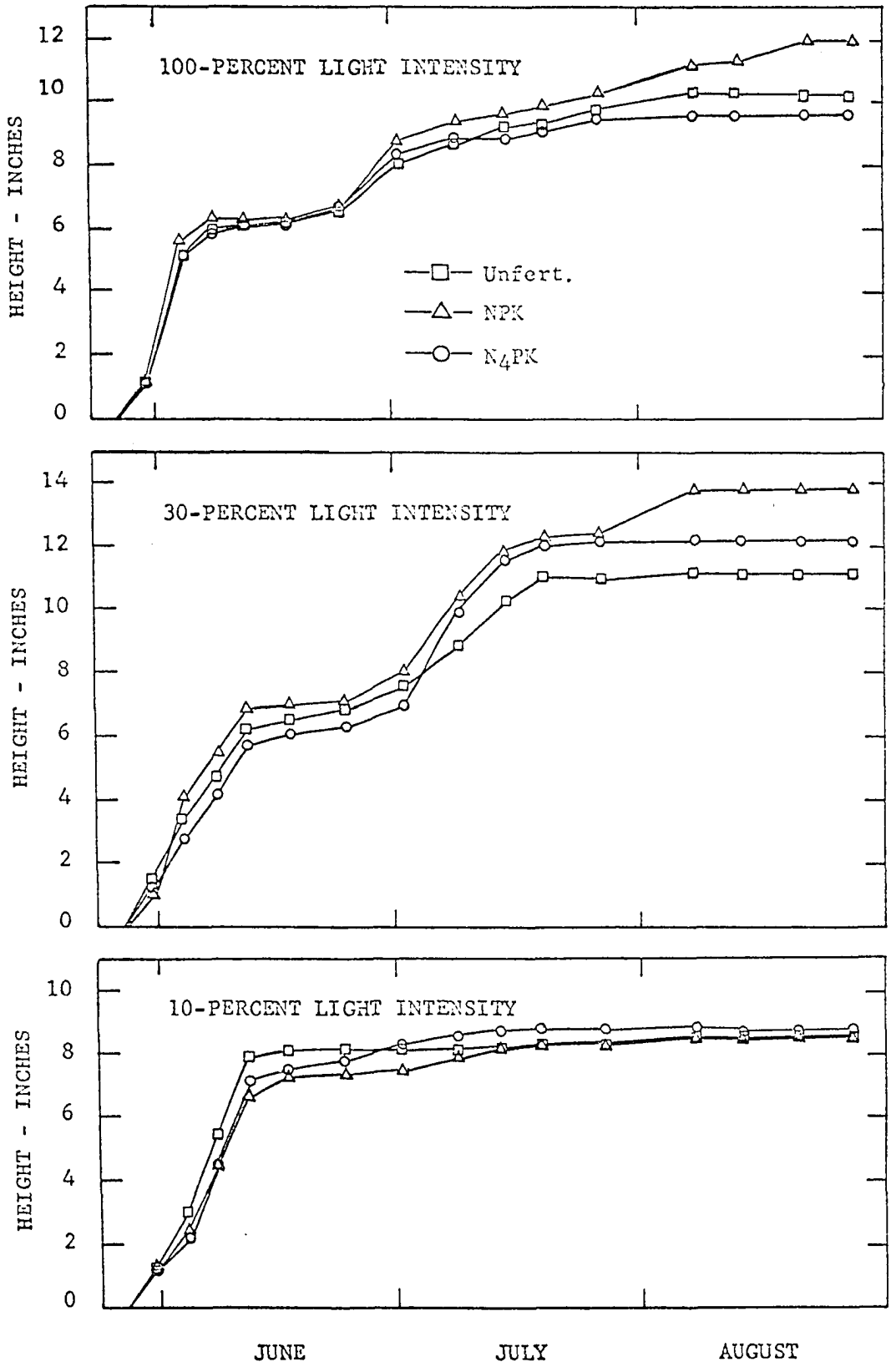
The height growth of the red oak seedlings was measured weekly during the 1963 growing season. The results are shown in Figure 14.

Height growth of the red oak seedlings was not accumulated at a uniform rate during the growing season but exhibited a pattern of intermittent growth, even when fertilized. The shoots elongated for a few weeks, ceased growth for a time, and then, depending upon the external conditions, resumed growth one or more times during the remainder of the growing season. Although the fertilizer and light treatments did not prevent this flushing habit, the treatments did have a significant effect on the number of growth flushes that occurred during the growing season.

The height growth of the red oak seedlings during the first growth period after germination was not influenced much by the fertilizers, but did vary inversely with the light intensity. The seedlings grown at 10-percent light intensity were about 25 percent taller than the seedlings grown at full light at the end of the first growth period. The growth during this period probably was almost entirely at the expense of foods stored in the acorns.

The seedlings grown at 30-percent light and at full light had one to two additional flushes of growth. Seedlings at 10-percent light, however, had only one growth period, which partly explains the lack of a fertilizer response at the lower light intensity. The fact that

Figure 14. Seasonal height growth pattern of red oak seedlings in relation to light intensity and fertilization, 1963


100-PERCENT LIGHT INTENSITY
30-PERCENT LIGHT INTENSITY
10-PERCENT LIGHT INTENSITY
HEIGHT - INCHES
Unfert.
NPK
N4PK
JUNE
JULY
AUGUST

the NPK fertilized seedlings were taller than the unfertilized seedlings at the two higher light intensities is due mainly to an additional flush of growth by these seedlings in August. The N_4PK fertilized seedlings did not produce this third flush of growth.

The dry weight of the roots and shoot of the red oak seedlings also did not differ significantly on the two soils and the data were combined. The relation between shoot dry weight and light intensity is shown in Figures 15 and 16. The relation between root dry weight and light intensity is shown in Figures 17 and 18.

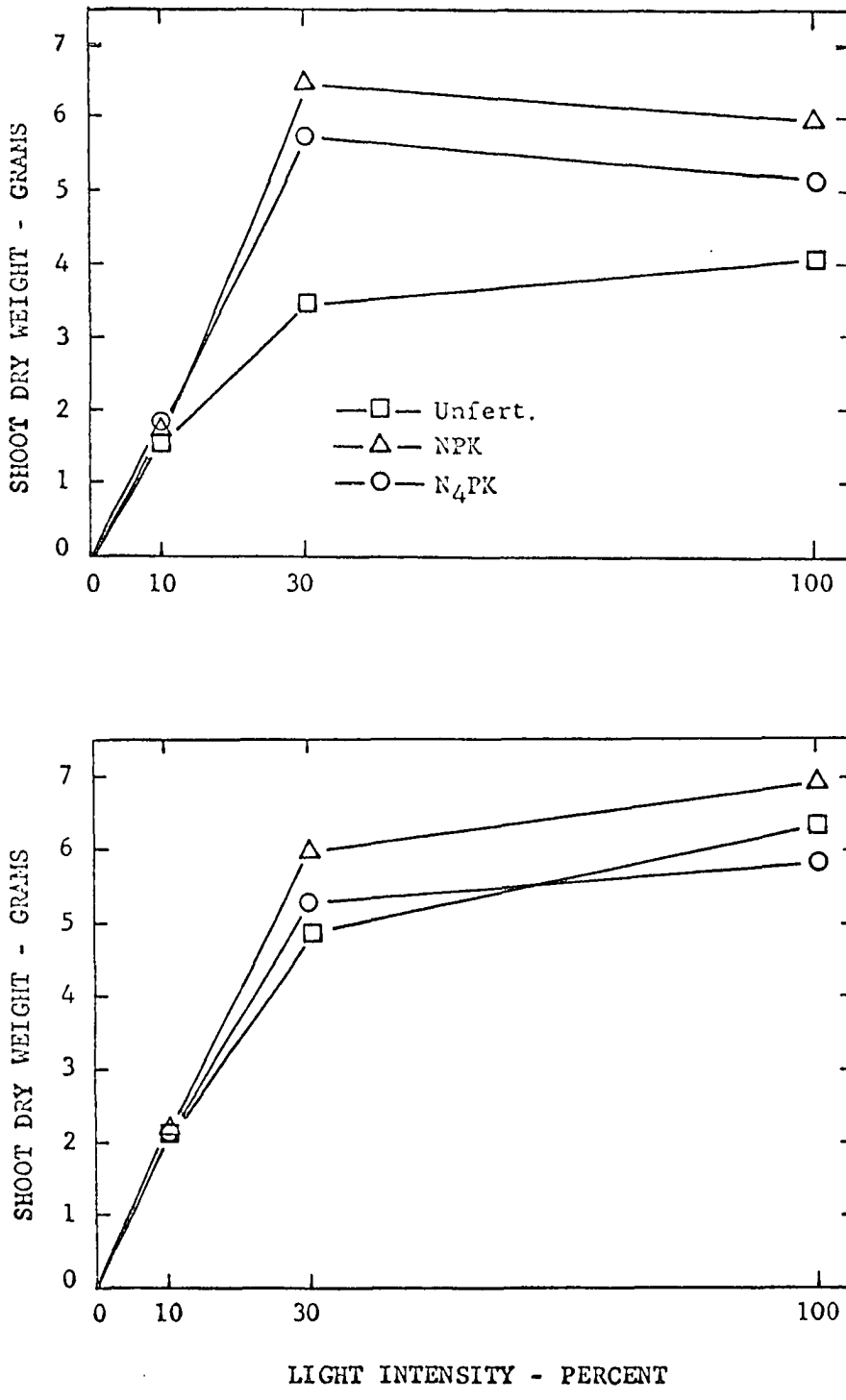
The shoot dry weight of the red oak seedlings increased significantly up to 30-percent light. There was no significant increase in shoot weight above 30-percent light in either 1962 or 1963. The effects of fertilizers on shoot weight were most pronounced at 30-percent light intensity in 1962. In 1963, fertilizer effects on shoot dry weight were small over all light intensities.

Root growth increased significantly over all light intensities. The differences in root dry weight of seedlings grown at 30-percent light and at full light intensity were significant at the 1-percent probability level both years. Unlike shoot growth, root growth appeared to be influenced by fertilizers at full light more than under reduced light intensities.

Because of the difference in relative response of shoot and roots to decreasing light intensities the shoot/root ratio of the red oak seedlings increased with decreasing light intensity (Figures 19 and 20). The largest increase in shoot/root ratio occurred between 30-

Figure 15. Shoot dry weight of red oak seedlings in relation to light intensity and fertilization, 1962

Figure 16. Shoot dry weight of red oak seedlings in relation to light intensity and fertilization, 1963


SHOOT DRY WEIGHT - GRAMS
0
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2
3
4
5
6
7
0
10
30
100
Unfert.
NPK
N4PK
SHOOT DRY WEIGHT - GRAMS
0
1
2
3
4
5
6
7
0
10
30
100
LIGHT INTENSITY - PERCENT

Figure 17. Root dry weight of red oak seedlings in relation to light intensity and fertilization, 1962

Figure 18. Root dry weight of red oak seedlings in relation to light intensity and fertilization, 1963

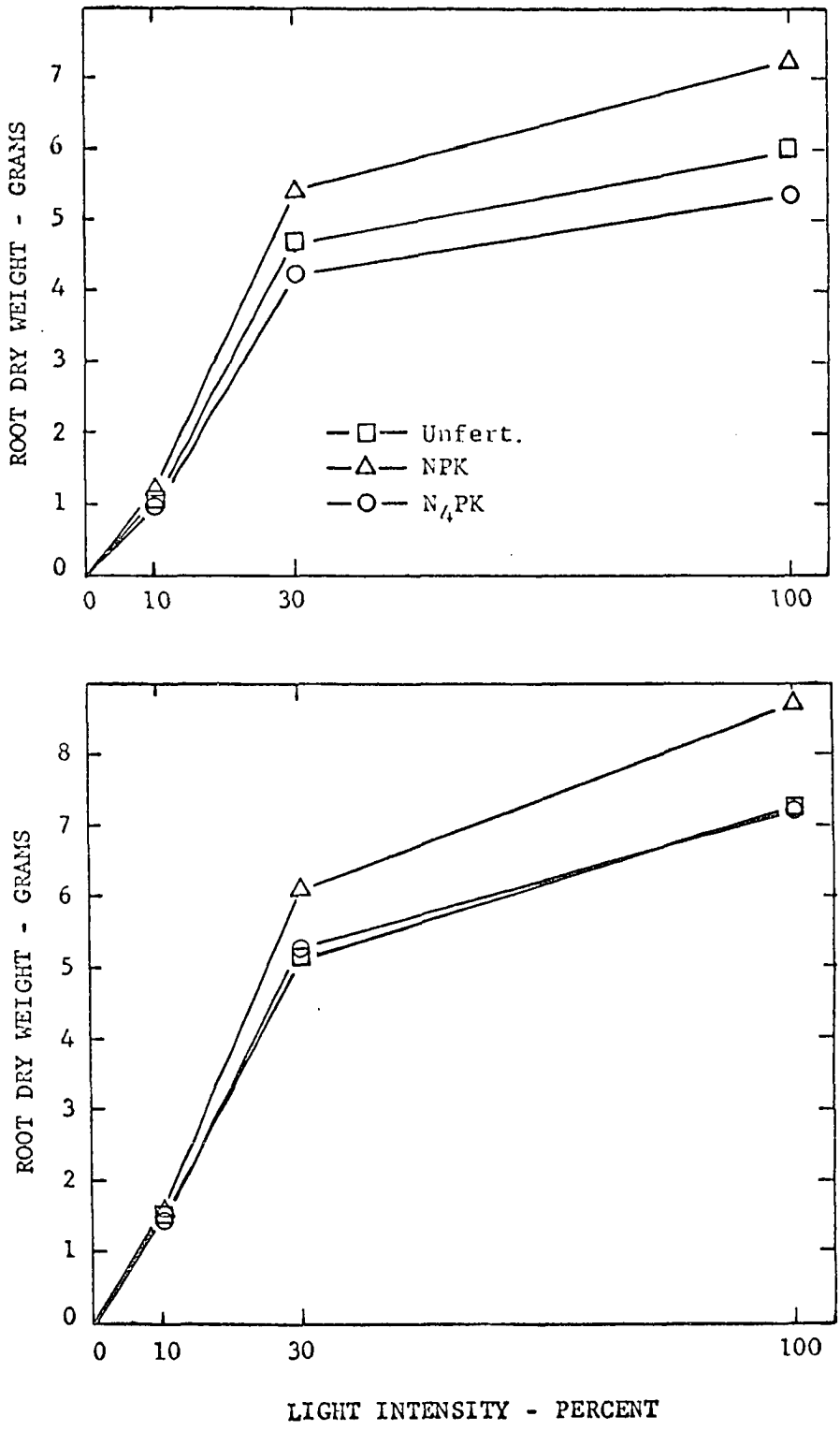

ROOT DRY WEIGHT - GRAMS
0
1
2
3
4
5
6
7
0
10
30
100
Unfert.
NPK
N¼PK
ROOT DRY WEIGHT - GRAMS
0
1
2
3
4
5
6
7
8
0
10
30
100
LIGHT INTENSITY - PERCENT

Figure 19. Shoot/root ratio of red oak seedlings in relation to light intensity and fertilization, 1962

Figure 20. Shoot/root ratio of red oak seedlings in relation to light intensity and fertilization, 1963

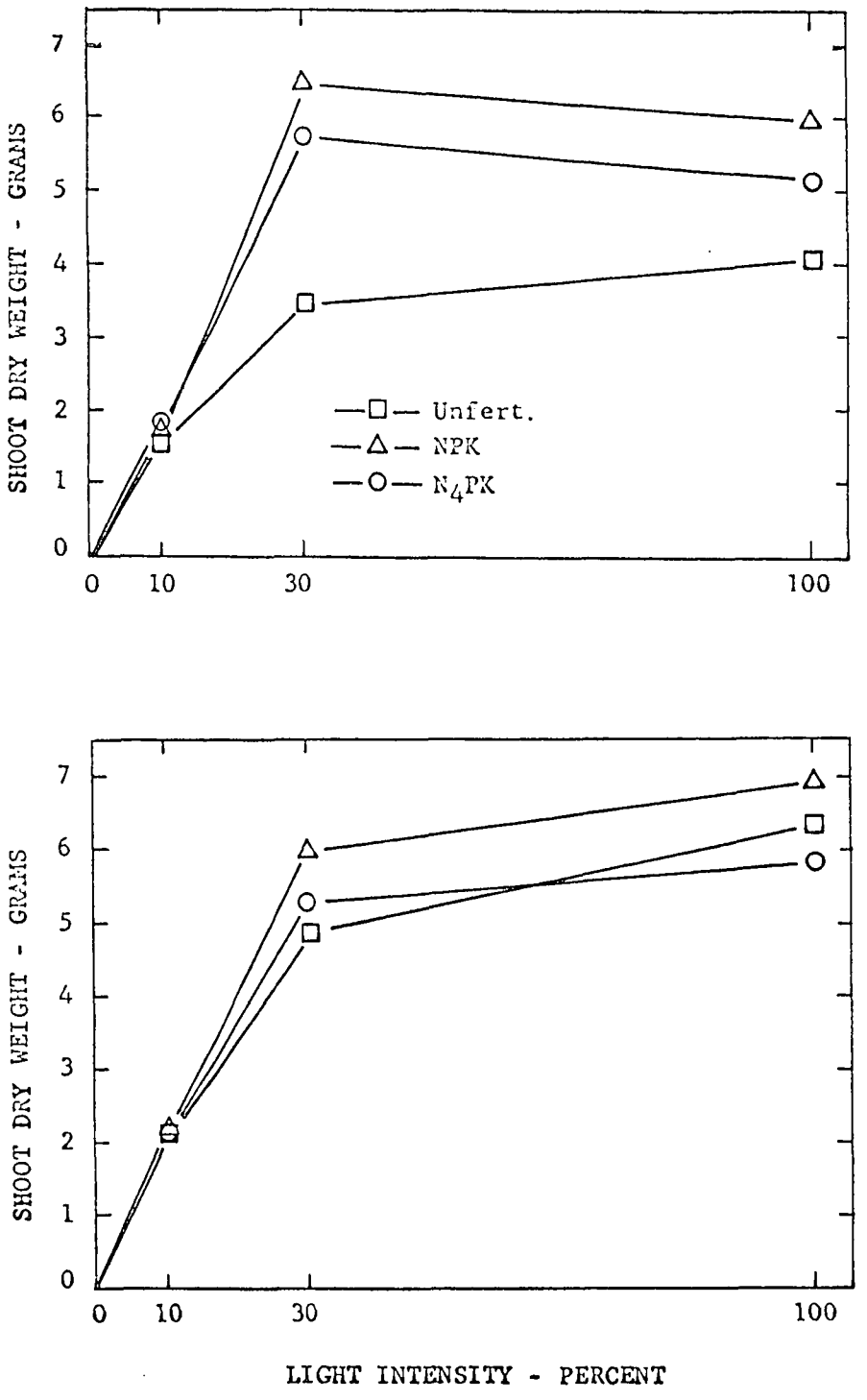

SHOOT DRY WEIGHT - GRAMS
0
1
2
3
4
5
6
7
0
10
30
100
—□— Unfert.
—△— NPK
—○— N4PK
SHOOT DRY WEIGHT - GRAMS
LIGHT INTENSITY - PERCENT

Figure 17. Root dry weight of red oak seedlings in relation to light intensity and fertilization, 1962

Figure 18. Root dry weight of red oak seedlings in relation to light intensity and fertilization, 1963

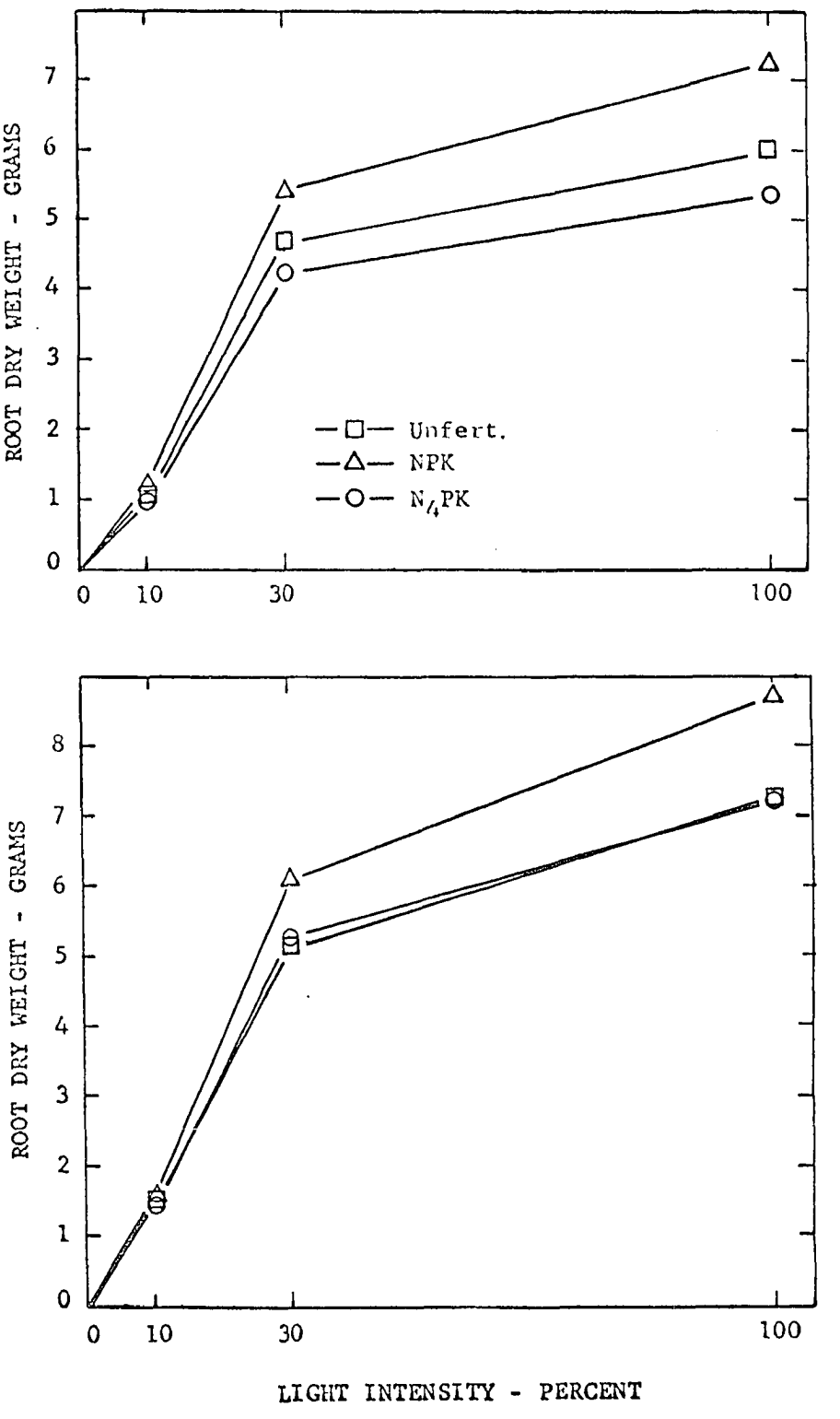
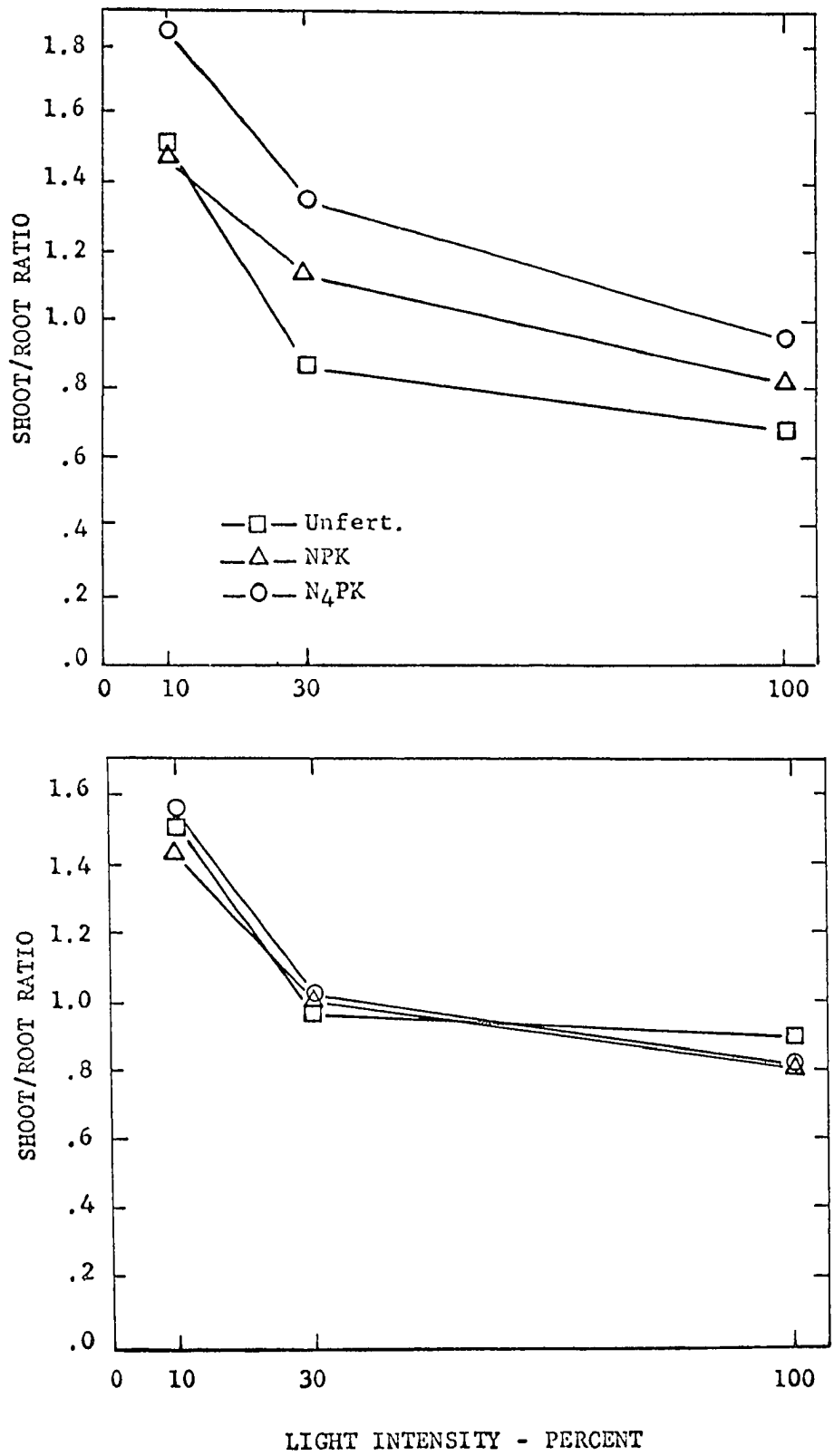

ROOT DRY WEIGHT - GRAMS
0
1
2
3
4
5
6
7
0
10
30
100
Unfert.
NPK
N4PK
ROOT DRY WEIGHT - GRAMS
0
1
2
3
4
5
6
7
8
0
10
30
100
LIGHT INTENSITY - PERCENT

Figure 19. Shoot/root ratio of red oak seedlings in relation to light intensity and fertilization, 1962

Figure 20. Shoot/root ratio of red oak seedlings in relation to light intensity and fertilization, 1963


SHOOT/ROOT RATIO
1.8
1.6
1.4
1.2
1.0
.8
.6
.4
.2
.0
0
10
30
100
—□— Unfert.
—△— NPK
—○— N4PK
SHOOT/ROOT RATIO
1.6
1.4
1.2
1.0
.8
.6
.4
.2
.0
0
10
30
100
LIGHT INTENSITY - PERCENT

and 10-percent light intensity in both years. The shoot/root ratio of unfertilized seedlings was about twice as great at 10-percent light as at full light intensity.

The application of N_4PK fertilizer increased the shoot/root ratio of the seedlings at all light intensities in 1962. The NPK fertilizer increased the shoot/root ratio of the seedlings at 30-percent light and at full light intensity but not at 10-percent light intensity. In 1963, there was no apparent influence of the fertilizers on the shoot/root ratio of the seedlings on either soil.

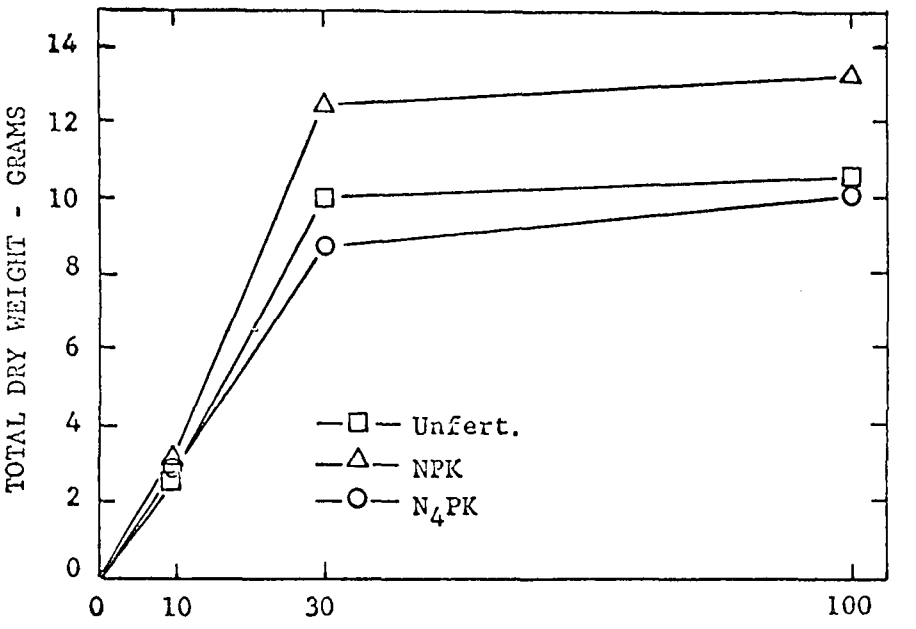
The fertilizers increased the shoot/root ratios much more on the Clarksville soil than on the Lindley soil in 1962. This result was due in part to somewhat greater shoot growth from the fertilizer on the Clarksville soil, but was due mainly to reduced root growth following heavy nitrogen fertilization on this soil. Root growth was not affected as much on the Lindley soil by the N_4PK fertilizer.

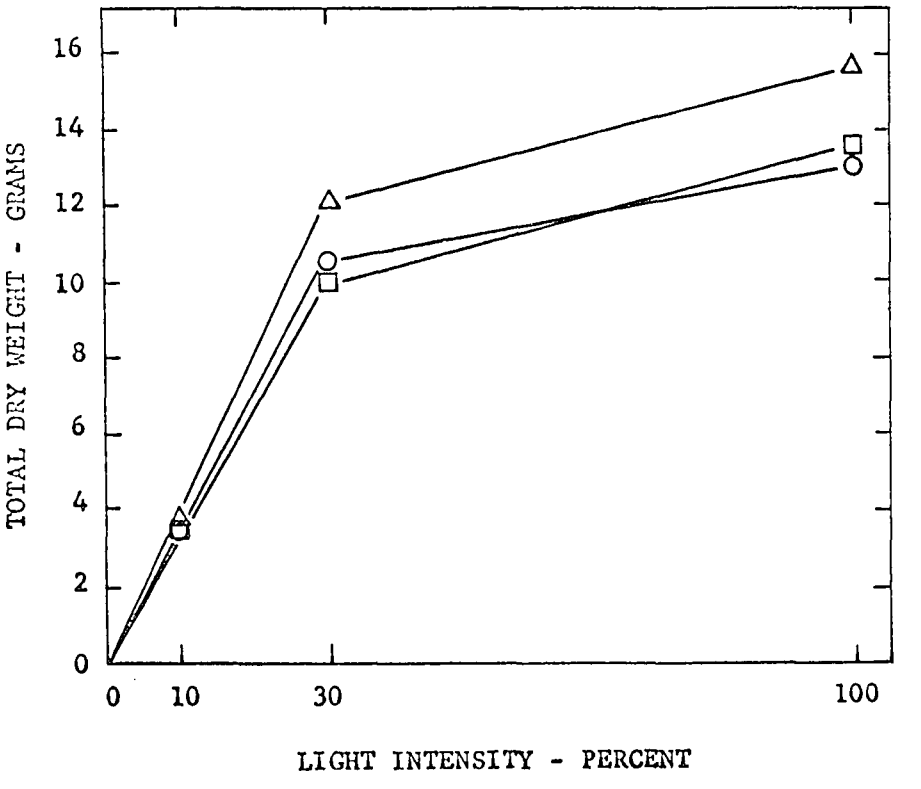
The greatest total dry weight of the red oak seedlings was attained at full light intensity (Figures 21 and 22). The total dry weight increase was almost linear up to 30-percent light intensity in both years. The greatest increase in total dry weight occurred between 10- and 30-percent light intensity and above this the total dry weight increase was much less.

The total dry weight of unfertilized seedlings grown at full light intensity in 1962 was 17 percent and 291 percent greater than that of seedlings grown at 30- and at 10-percent light intensity, respectively. In 1963, the dry weight increases were 36 and 283 percent for the same

Figure 21. Total dry weight of red oak seedlings in relation to light intensity and fertilization, 1962

Figure 22. Total dry weight of red oak seedlings in relation to light intensity and fertilization, 1963


TOTAL DRY WEIGHT - GRAMS
14
12
10
8
6
4
2
0
0
10
30
100
Unfert.
NPK
N4PK


TOTAL DRY WEIGHT - GRAMS
16
14
12
10
8
6
4
2
0
0
10
30
100
LIGHT INTENSITY - PERCENT

corresponding light intensity comparisons. The dry weight increases between 10- and 30-percent light intensity and between 10- and 100-percent light intensity were significant at the 1-percent probability level both years. The dry weight increase between 30- and 100-percent light intensity was not significant in 1962, but was significant at the 1-percent probability level in 1963.

The total dry weight of the seedlings was increased by the NPK fertilizer at the 30- and the 100-percent light intensity but not at the 10-percent light intensity. The dry weight increase from the NPK fertilizer amounted to 43 percent and 31 percent at the 30- and the 100-percent light intensity levels in 1962, and 20 and 15 percent at these same two light intensity levels in 1963. The N_4PK fertilizer treatment decreased total dry weight of the seedlings as compared to the NPK fertilized seedlings in both years.

The total fresh weight of the seedlings in 1963 followed almost the same trend as total dry weight over the varying light intensity levels. The moisture content of the seedlings grown at 10-percent light intensity was about 10 percent greater than of the seedlings grown at 30- and 100-percent light intensity. The moisture content of the seedlings grown at the two higher light intensities did not differ to any great extent. The relationship between seedling weight at 30-percent and at 100-percent light intensity was not altered by the use of green weight rather than dry weight.

The concentration of minerals in the leaves of the seedlings grown at 10-percent light intensity was greater, for practically all of the

elements analyzed, than in leaves of seedlings grown at full light intensity (Tables 44 and 45, Appendix). Some of the elements showed large relative increases in concentration in seedlings grown at the low light intensity. The increased concentration of the elements between 100- and 30-percent light intensity partly can be explained on the basis that about the same absolute amount of mineral nutrients was absorbed but was diluted to a greater extent in seedlings grown at full light intensity by the additional dry matter in the leaves.

The application of fertilizers was effective in increasing the concentrations of nitrogen and phosphorus in the leaves of the seedlings grown at all light intensities. Potassium concentrations in the leaves, however, were not greatly affected by fertilizer. Because nitrogen was the major element varied in the fertilizers, the relations between the concentrations of this element in the leaves and light intensity were explored more fully. The milligrams of nitrogen in the leaves was calculated for each of the treatments. The data for the two soils were averaged and the results are presented in Table 22.

The quantity of nitrogen in the leaves of the red oak seedlings was almost the same at 30- and at 100-percent light intensity in 1962, but the concentration on a percent basis was somewhat greater in seedlings grown at the lower light intensity. In 1963, the seedlings grown at 100-percent light intensity contained about 15 percent more nitrogen than seedlings grown at 30-percent light intensity, but because duplicate samples were not analyzed this difference in nitrogen content could not be evaluated statistically.

Table 22. Nitrogen content in leaves of red oak seedlings from the light intensity experiment, milligrams per seedling

Year	Fertilizer	Light intensity, percent		
		10	30	100
1962	-	21.2	53.7	53.2
	NPK	27.1	86.6	89.2
	N_4PK	29.7	87.1	86.1
	Mean	26.0	75.8	76.2
1963	-	28.1	53.3	64.2
	NPK	30.2	61.3	72.8
	N_4PK	31.6	61.2	67.4
	Mean	28.3	58.6	67.8

Seedlings grown at the 10-percent light intensity contained much less foliar nitrogen than seedlings at the two higher light intensities. The seedlings had poorly developed root systems at the 10-percent light intensity and apparently were unable to absorb the same quantities of nitrogen from the soil as at the higher light intensities. The results also show that the application of nitrogen fertilizer did not increase greatly the amount of nitrogen in the leaves of the seedlings at 10-percent light intensity, but at the higher light intensities there was almost a 60 percent increase in the amount of nitrogen in the leaves of nitrogen fertilized seedlings. The N_4PK fertilizer did not greatly increase the amount of foliar nitrogen over NPK fertilized seedlings at any of the light intensities, probably because the high nitrogen application adversely affected the root growth and the ability of the red oak seedlings to absorb nitrogen from the soil.

Mycorhizae Experiment

A number of sterilization and inoculation treatments were tested on the Lindley, Shelby, and Clarksville surface soils to determine the relative importance of mycorhizae to the growth and nutrition of the red oak seedlings. These treatments are given in Tables 23 and 24 with the growth data for the 1962 and 1963 seedlings. Statistical analyses were made separately for the forest soils and the non-forest soils. The results are given in Tables 25 and 26.

The red oak seedlings grew better on the unsterilized forest soils than on the sterilized in 1962. The total dry weight of the seedlings was about 12 percent less on the sterilized Lindley soils and about 25 percent less on the sterilized Clarksville soils than on the unsterilized soils. These differences were significant at the 1-percent probability level. The seedlings grown on the sterilized forest soils in 1963 also had significantly less total dry weight than seedlings on unsterilized soils. There were no significant interactions between sterilization and soil or fertilizer, indicating that the adverse effect of this treatment was rather uniform over all soil conditions.

Statistical analyses were not made separately for root and shoot dry weight, but the 1962 growth data indicated that sterilization of the forest soils affected root growth more than shoot growth. The average dry weight of the red oak roots was reduced about 29 percent while the shoot dry weight was reduced only about 5 percent by the sterilization treatments on the two forest soils. Conversely, these treatments reduced shoot growth 22 percent and root growth 12 percent in 1963.

Table 23. Average height and dry weight per seedling of red oak from the mycorhizae experiment, 1962

Soil	Fertilizer	Soil treatment	Height, in.	Dry weight, g			
				Leaves	Stem	Roots	Total
Lindley (Forest)	-	Untreated	8.1	3.02	1.45	6.33	10.80
		Sterilized	9.3	2.80	1.43	3.99	8.23
		+forest inoculum	9.6	3.15	1.54	4.56	9.24
	NPK	Untreated	9.9	3.58	2.06	7.06	12.70
		Sterilized	10.8	3.83	2.08	6.52	12.43
Shelby (Prairie)	-	Untreated	7.4	2.09	1.11	5.24	8.45
		+forest inoculum	7.3	2.05	1.17	5.36	8.58
		Sterilized	7.2	1.71	0.88	3.36	5.96
		+forest inoculum	8.6	2.32	1.13	3.70	7.93
		+prairie inoculum	8.1	2.07	0.96	4.22	7.25
	NPK	Untreated	9.2	3.29	1.80	6.34	11.43
		+forest inoculum	9.1	3.06	1.52	6.43	11.01
		Sterilized	9.0	3.13	1.56	6.30	10.99
		+forest inoculum	10.4	3.27	1.79	5.96	11.02
Clarksville (Forest)	-	Untreated	8.0	2.35	1.28	5.70	9.33
		Sterilized	7.8	2.34	1.24	3.74	7.32
		+forest inoculum	7.9	2.63	1.42	3.82	7.87
	NPK	Untreated	9.9	3.88	2.29	7.43	13.59
		Sterilized	9.5	3.45	1.81	4.60	9.86

Table 23. (Continued)

Soil	Fertilizer	Soil treatment	Height, in.	Dry weight, g			
				Leaves	Stem	Roots	Total
Clarksville (Old field)	-	Untreated	7.2	1.91	1.07	3.86	6.84
		+forest inoculum	7.4	2.03	1.06	3.91	7.01
		Sterilized	7.6	2.16	1.07	3.27	6.50
		+forest inoculum	8.3	2.54	1.14	3.63	7.31
		+old field inoculum	8.1	2.18	1.31	3.58	7.07
	NPK	Untreated	8.9	3.46	1.65	6.04	11.15
		+forest inoculum	9.5	3.78	1.89	7.09	12.76
		Sterilized	11.4	4.04	2.08	5.02	11.14
		+forest inoculum	9.1	4.09	1.95	6.24	12.28

Table 24. Average height and green and dry weight per seedling of red oak from the mycorhizae experiment, 1963

Soil	Fertilizer	Soil treatment	Height, in.	Green weight, g	Dry weight, g			
					Leaves	Stem	Roots	Total
Lindley (Forest)	-	Untreated	10.5	28.60	3.70	2.79	7.42	13.91
		Sterilized	9.0	25.15	3.24	2.18	7.03	12.45
		+forest inoculum	9.3	28.61	3.33	2.29	8.34	13.96
	NPK	Untreated	11.2	32.60	3.78	2.91	8.47	15.16
		Sterilized	10.8	29.13	3.40	2.61	8.15	14.16
Shelby (Prairie)	-	Untreated	7.4	17.04	1.79	1.42	5.61	8.82
		+forest inoculum	8.3	20.10	2.06	1.56	6.16	9.78
		Sterilized	7.9	18.96	2.26	1.42	5.50	9.18
		+forest inoculum	8.6	20.62	2.34	1.63	5.84	9.81
		+prairie inoculum	7.7	19.78	2.21	1.41	5.81	9.43
	NPK	Untreated	7.7	22.81	2.81	1.66	6.39	10.86
		+forest inoculum	9.2	24.18	2.68	1.86	6.89	11.43
		Sterilized	7.6	22.10	2.69	1.56	6.36	10.61
		±forest inoculum	9.2	22.66	2.48	1.76	6.45	10.69
Clarksville (Forest)	-	Untreated	9.9	27.64	3.60	2.59	7.08	13.27
		Sterilized	9.1	20.94	2.79	1.99	5.55	10.33
		+forest inoculum	9.0	21.77	2.85	1.79	5.90	10.54
	NPK	Untreated	11.6	33.87	4.48	2.70	8.95	16.13
		Sterilized	8.1	24.07	2.76	1.73	7.43	11.92

Table 24. (Continued)

Soil	Fertilizer	Soil treatment	Height, in.	Green weight, g	Dry weight, g			
					Leaves	Stem	Roots	Total
Clarksville (Old field)	-	Untreated	8.2	21.92	2.82	1.75	5.96	10.53
		+forest inoculum	8.5	22.41	3.02	1.84	6.31	11.17
		Sterilized	7.8	16.78	2.08	1.34	4.71	8.13
		+forest inoculum	10.0	24.30	3.23	2.17	6.43	11.83
		+old field inoculum	8.0	17.63	1.99	1.60	4.71	8.30
	NPK	Untreated	8.8	26.00	2.80	2.07	7.49	12.36
		+forest inoculum	8.9	27.80	3.04	2.22	7.80	13.06
		Sterilized	8.1	24.33	2.50	2.11	7.27	11.88
		+forest inoculum	9.2	26.79	3.15	2.19	7.33	12.67

Table 25. Mean squares from the analysis of variance of total dry weight per pot of red oak seedlings on the two forest soil, 1962 and 1963

Source of variation	Degrees of freedom	1962	1963
Replication	2	0.25	6.66
Soil (S)	1	55.51	54.72
Fertilizer (F)	1	562.21**	184.93**
Sterilization (St)	1	249.10**	312.34**
F x S	1	1.70	7.44
St x S	1	28.12	74.20
F x St	1	1.11	2.16
F x St x S	1	54.54	10.09
Error	14	16.85	22.81

*Significant at the 5-percent probability level.

**Significant at the 1-percent probability level.

Sterilization of the two non-forest soils, however, did not significantly affect the total dry weight of the red oak seedlings as it did on the two forest soils. The seedlings on the sterilized non-forest soils had slightly less total dry weight than seedlings on unsterilized but the differences were not statistically significant either year.

Inoculation of the two non-forest soils with forest inoculum increased the growth of the red oak seedlings about 7 percent in 1962 and about 11 percent in 1963. The increase was not significant in 1962 but was significant at the 1-percent probability level in 1963. There were no significant interactions between inoculation and the other factors tested. The response to the inoculation, however, was not as great as to the addition of fertilizer on either soil.

Table 26. Mean squares from the analysis of variance of total dry weight per pot of red oak seedlings on the two non-forest soils, 1962 and 1963

Source of variation	Degrees of freedom	1962	1963
Replication	2	5.03	39.72
Soil (S)	1	0.26	184.44**
Fertilizer (F)	1	1860.66**	346.21**
Sterilization (St)	1	28.11	17.64
Inoculation (I)	1	49.79	109.73**
F x S	1	63.54	9.13
St x S	1	15.60	6.74
I x S	1	6.80	21.63
F x St	1	8.65	0.44
I x F	1	0.87	24.39
I x St	1	10.19	9.00
F x St x S	1	16.99	8.40
I x F x S	1	30.84	6.26
I x St x S	1	7.51	26.64
I x F x St	1	10.36	16.58
I x F x St x S	1	0.13	13.49
Error	30	22.83	13.88

*Significant at the 5-percent probability level.

**Significant at the 1-percent probability level.

As a matter of interest, the sterilized forest and non-forest soils were re-inoculated with unsterilized portions of the same soils. This treatment was not included in the statistical analyses because it was tested only on the unfertilized soils. The seedlings generally responded to this treatment, but on the forest soils re-inoculated seedlings did not grow as well as seedlings on untreated soils and on the non-forest soils the response was less than to inoculation with forest soil. The results are inconclusive but suggest: (1) sterilization may have pro-

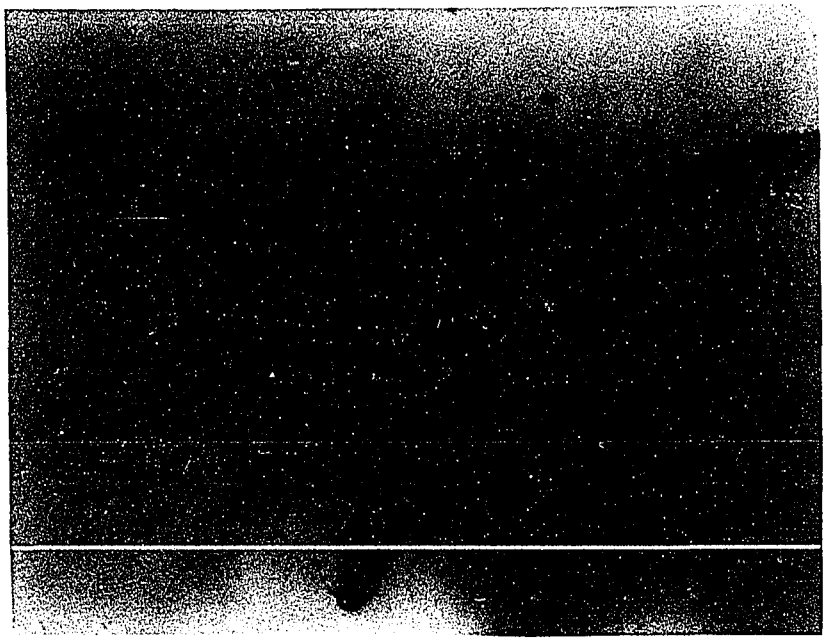
duced adverse effects other than the elimination of mycorhizae, and (2) the forest inoculum provided some biological factor not present or active in the prairie or old field inoculum, pointing possibly to mycorhizae.

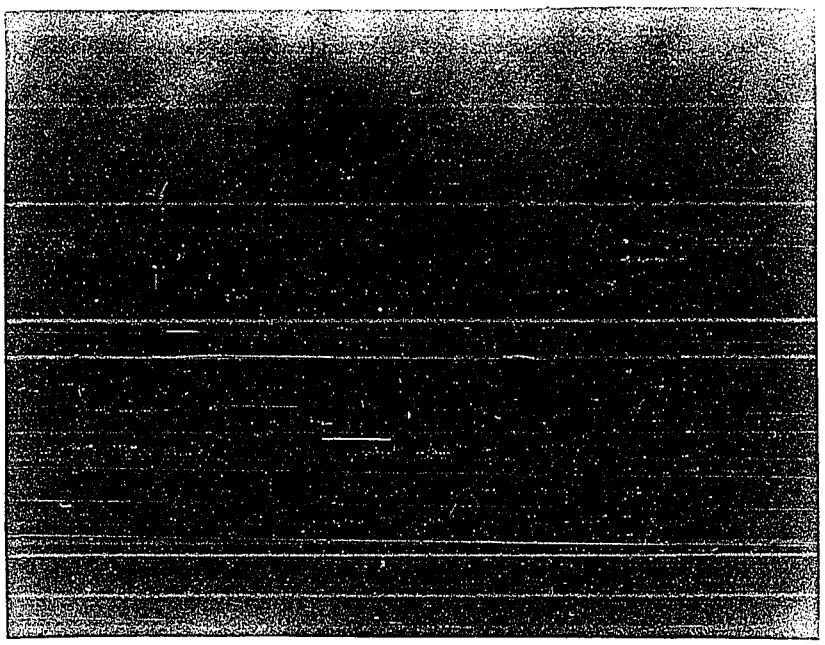
The red oak seedlings were examined closely when harvested at the end of the 1963 growing season and were found to be definitely mycorhizal. Unfortunately, similar observations were not made on the 1962 seedlings. Microtome sections of mycorhizal short roots indicated a well developed fungal mantle whose characteristics depended somewhat upon the soil. The Hartig network of hyphae in the roots, which is considered positive evidence of a mycorhizal relationship, was found in several root sections but usually was restricted to the outer two or three layers of cortical cells. There was no evidence of intracellular infection by the hyphae which characterize the ectendotrophic mycorhizae. Photomicrographs were made of the root sections infected with the major types of mycorhizal fungi found on the red oak seedlings and are shown in Figures 23 and 24.

The seedlings grown on unsterilized Lindley soil possessed mycorhizal roots covered by a white to dull grey mantle. This type of mycorhizae was not found in any other soil, except where the Lindley soil was used as the source of inoculum. Numerous white hyphal strands were found in the surrounding soil. The hyphae were very fine and formed a rather compact mantle. The short roots were swollen and dicotomously branched. The sites of infection, however, were infrequent on the root and at each only two or three short roots were mycorhizal.

Figure 23. Typical white mycorhizae observed on red oak seedlings on the Lindley soil, 1963

Figure 24. Typical black mycorhizae observed on red oak seedlings on the Clarksville soils, 1963





The rootlet tips of seedlings on the Clarksville forest soil possessed a fungal mantle characterized by thick black hyphae. The same type of mycorhizae was found on seedlings on the Clarksville old field soil but were, in general, not as numerous as on seedlings on the forest soil. The fungal mantle was restricted to the tip 1 to 2 millimeters of the rootlets, which usually were digitate (unbranched). The hyphae protruded at right angles from the black mantle, but there was no obvious network of hyphae in the soil.

A third type of mycorhizae, characterized by an olive-brown mantle, was found on seedlings on all soils. Seedlings grown in a nearby seedbed also possessed this same type of mycorhizae. It is believed, therefore, that their presence in the pots resulted from wind-blown inoculum. The short roots were strongly hypertrophied and numerous densely-packed mycorhizal clusters were found on the upper half of the root system. The olive-brown hyphae formed a visible network through the soil, terminating at a rather compact mantle covering the short roots. Dicotomous branching of the short roots was very apparent. This type of mycorhizae was not believed to have been present on the seedlings grown the previous year in these soils.

A subjective measurement of mycorhizal occurrence was attempted in order to establish possible relationships with soil treatments. The results are shown in Table 27, and indicate that the sterilization treatment effectively killed or inactivated the natural mycorhizal fungi in each of the forest soils. For example, the white mycorhizae were not found on any seedlings grown on sterilized Lindley soil unless

Table 27. Occurrence of mycorhizae on the red oak seedlings from the mycorhizae experiment, 1963

Soil	Fertilizer	Soil treatment	Pots[a]	Relative Frequency[b]	Color[c]
Lindley (Forest)	-	Untreated	3	++	A
		Sterilized	2	++	C
		+forest inoculum	3	+++	AC
	NPK	Untreated	2	+	A
		Sterilized	2	+	C
Shelby (Prairie)	-	Untreated	1	+	C
		+forest inoculum	1	+	A
		Sterilized	2	++	C
		+forest inoculum	2	++	CA
		+prairie inoculum	1	+	C
	NPK	Untreated	1	++	C
		+forest inoculum	1	+	C
		Sterilized	3	+	C
		+forest inoculum	3	+++	CA
Clarksville (Forest)	-	Untreated	3	++	B
		Sterilized	3	+++	C
		+forest inoculum	3	+++	BC
	NPK	Untreated	2	+	B
		Sterilized	3	+++	C
Clarksville (Old field)	-	Untreated	3	+	B
		+forest inoculum	3	++	BC
		Sterilized	3	+	C
		+forest inoculum	3	+	B
		+old field inoculum	3	+	CB
	NPK	Untreated	2	+	BC
		+forest inoculum	3	++	B
		Sterilized	1	++	C
		+forest inoculum	2	++	B

[a]Each treatment replicated in three pots.

[b]+ = present, ++ = several, and +++ = abundant.

[c]A = white, B = black, and C = olive-brown.

the soil was re-inoculated with forest inoculum. The black mycorhizae were absent on seedlings on sterilized Clarksville soils but inoculation brought about re-infection of the roots of the seedlings by this same type of mycorhizal fungi. The olive-brown mycorhizae appeared to develop especially well on seedlings on the sterilized soils, probably because of the absence of the natural fungi.

The results of the foliage analyses were quite variable and definite treatment effects were difficult to establish. The chemical analyses are given in Tables 46 and 47 in the Appendix.

Sterilization had a tendency to increase the concentration of nitrogen in the leaves of the 1962 seedlings on all soils, but in 1963 the opposite trend appeared to be true. These results, however, corroborate the adverse effect of this treatment observed with root growth in 1962 and with shoot growth in 1963, since other experiments showed that shoot growth was promoted more by nitrogen than root growth. The lower nitrogen concentrations in the 1963 seedlings possibly were due to the increased utilization of soil and fertilizer nitrogen the previous year. Phosphorus concentrations followed almost the same trend as nitrogen but some of the other elements, such as manganese, appeared to be consistently higher in seedlings on sterilized soils. The significance of the increased concentrations of these elements is not clear in view of the poorer growth of seedlings on the sterilized soils.

Because inoculation of the non-forest soils did not significantly improve growth of the red oak seedlings in 1962 the foliage analyses were not examined very closely with regard to this treatment. In 1963,

when a significant effect of inoculation was observed, the foliage analyses indicated that the concentration of some of the elements was somewhat greater in the inoculated seedlings than in the uninoculated. On an absolute basis, the inoculated seedlings on the two non-forest soils contained 14 percent more nitrogen, 30 percent more phosphorus, and 5 percent more potassium than uninoculated. However, the fact that the seedlings on the uninoculated soils also possessed mycorhizae makes such data questionable as evidence of a beneficial influence of mycorhizae on mineral nutrient uptake.

As a separate part of the mycorhiza investigations, the seedlings from the other experiments also were examined closely for mycorhizae when harvested in 1963. These observations failed to show any definite relation between mycorhizal occurrence and fertilization in the basic fertilizer experiment and in the nitrogen experiment. In the liming experiment, however, mycorhizal occurrence was found to be greater on unlimed soils than on limed (Table 28). On the Lindley soils that had been limed with 2 tons of lime the previous year, only 4 of the 12 pots contained mycorhizal seedlings. On the unlimed Lindley soil, 11 of the 12 pots contained mycorhizal seedlings. On the Clarksville soil limed at the 2-ton rate mycorhizal formation was completely suppressed, but on the unlimed soil 9 of the 12 pots contained mycorhizal seedlings.

Mycorhizal occurrence also was found to vary inversely with light intensity when the seedlings from the light intensity experiment were examined (Table 29). Almost all of the pots in full light, about three-fourths of those in 30-percent light, but only about one-tenth of those

Mycorhizae Experiment

A number of sterilization and inoculation treatments were tested on the Lindley, Shelby, and Clarksville surface soils to determine the relative importance of mycorhizae to the growth and nutrition of the red oak seedlings. These treatments are given in Tables 23 and 24 with the growth data for the 1962 and 1963 seedlings. Statistical analyses were made separately for the forest soils and the non-forest soils. The results are given in Tables 25 and 26.

The red oak seedlings grew better on the unsterilized forest soils than on the sterilized in 1962. The total dry weight of the seedlings was about 12 percent less on the sterilized Lindley soils and about 25 percent less on the sterilized Clarksville soils than on the unsterilized soils. These differences were significant at the 1-percent probability level. The seedlings grown on the sterilized forest soils in 1963 also had significantly less total dry weight than seedlings on unsterilized soils. There were no significant interactions between sterilization and soil or fertilizer, indicating that the adverse effect of this treatment was rather uniform over all soil conditions.

Statistical analyses were not made separately for root and shoot dry weight, but the 1962 growth data indicated that sterilization of the forest soils affected root growth more than shoot growth. The average dry weight of the red oak roots was reduced about 29 percent while the shoot dry weight was reduced only about 5 percent by the sterilization treatments on the two forest soils. Conversely, these treatments reduced shoot growth 22 percent and root growth 12 percent in 1963.

Table 23. Average height and dry weight per seedling of red oak from the mycorhizae experiment, 1962

Soil	Fertilizer	Soil treatment	Height, in.	Dry weight, g			
				Leaves	Stem	Roots	Total
Lindley (Forest)	-	Untreated	8.1	3.02	1.45	6.33	10.80
		Sterilized	9.3	2.80	1.43	3.99	8.23
		+forest inoculum	9.6	3.15	1.54	4.56	9.24
	NPK	Untreated	9.9	3.58	2.06	7.06	12.70
		Sterilized	10.8	3.83	2.08	6.52	12.43
Shelby (Prairie)	-	Untreated	7.4	2.09	1.11	5.24	8.45
		+forest inoculum	7.3	2.05	1.17	5.36	8.58
		Sterilized	7.2	1.71	0.88	3.36	5.96
		+forest inoculum	8.6	2.32	1.13	3.70	7.93
		+prairie inoculum	8.1	2.07	0.96	4.22	7.25
	NPK	Untreated	9.2	3.29	1.80	6.34	11.43
		+forest inoculum	9.1	3.06	1.52	6.43	11.01
		Sterilized	9.0	3.13	1.56	6.30	10.99
		+forest inoculum	10.4	3.27	1.79	5.96	11.02
Clarksville (Forest)	-	Untreated	8.0	2.35	1.28	5.70	9.33
		Sterilized	7.8	2.34	1.24	3.74	7.32
		+forest inoculum	7.9	2.63	1.42	3.82	7.87
	NPK	Untreated	9.9	3.88	2.29	7.43	13.59
		Sterilized	9.5	3.45	1.81	4.60	9.86

Table 23. (Continued)

Soil	Fertilizer	Soil treatment	Height, in.	Dry weight, g			
				Leaves	Stem	Roots	Total
Clarksville (Old field)	-	Untreated	7.2	1.91	1.07	3.86	6.84
		+forest inoculum	7.4	2.03	1.06	3.91	7.01
		Sterilized	7.6	2.16	1.07	3.27	6.50
		+forest inoculum	8.3	2.54	1.14	3.63	7.31
		+old field inoculum	8.1	2.18	1.31	3.58	7.07
	NPK	Untreated	8.9	3.46	1.65	6.04	11.15
		+forest inoculum	9.5	3.78	1.89	7.09	12.76
		Sterilized	11.4	4.04	2.08	5.02	11.14
		+forest inoculum	9.1	4.09	1.95	6.24	12.28

Table 24. Average height and green and dry weight per seedling of red oak from the mycorhizae experiment, 1963

Soil	Fertilizer	Soil treatment	Height, in.	Green weight, g	Dry weight, g			
					Leaves	Stem	Roots	Total
Lindley (Forest)	-	Untreated	10.5	28.60	3.70	2.79	7.42	13.91
		Sterilized	9.0	25.15	3.24	2.18	7.03	12.45
		+forest inoculum	9.3	28.61	3.33	2.29	8.34	13.96
	NPK	Untreated	11.2	32.60	3.78	2.91	8.47	15.16
		Sterilized	10.8	29.13	3.40	2.61	8.15	14.16
Shelby (Prairie)	-	Untreated	7.4	17.04	1.79	1.42	5.61	8.82
		+forest inoculum	8.3	20.10	2.06	1.56	6.16	9.78
		Sterilized	7.9	18.96	2.26	1.42	5.50	9.18
		+forest inoculum	8.6	20.62	2.34	1.63	5.84	9.81
		+prairie inoculum	7.7	19.78	2.21	1.41	5.81	9.43
	NPK	Untreated	7.7	22.81	2.81	1.66	6.39	10.86
		+forest inoculum	9.2	24.18	2.68	1.86	6.89	11.43
		Sterilized	7.6	22.10	2.69	1.56	6.36	10.61
		+forest inoculum	9.2	22.66	2.48	1.76	6.45	10.69
Clarksville (Forest)	-	Untreated	9.9	27.64	3.60	2.59	7.08	13.27
		Sterilized	9.1	20.94	2.79	1.99	5.55	10.33
		+forest inoculum	9.0	21.77	2.85	1.79	5.90	10.54
	NPK	Untreated	11.6	33.87	4.48	2.70	8.95	16.13
		Sterilized	8.1	24.07	2.76	1.73	7.43	11.92

Table 24. (Continued)

Soil	Fertilizer	Soil treatment	Height, in.	Green weight, g	Dry weight, g			
					Leaves	Stem	Roots	Total
Clarksville (Old field)	-	Untreated	8.2	21.92	2.82	1.75	5.96	10.53
		+forest inoculum	8.5	22.41	3.02	1.84	6.31	11.17
		Sterilized	7.8	16.78	2.08	1.34	4.71	8.13
		+forest inoculum	10.0	24.30	3.23	2.17	6.43	11.83
		+old field inoculum	8.0	17.63	1.99	1.60	4.71	8.30
	NPK	Untreated	8.8	26.00	2.80	2.07	7.49	12.36
		+forest inoculum	8.9	27.80	3.04	2.22	7.80	13.06
		Sterilized	8.1	24.33	2.50	2.11	7.27	11.88
		+forest inoculum	9.2	26.79	3.15	2.19	7.33	12.67

Table 25. Mean squares from the analysis of variance of total dry weight per pot of red oak seedlings on the two forest soil, 1962 and 1963

Source of variation	Degrees of freedom	1962	1963
Replication	2	0.25	6.66
Soil (S)	1	55.51	54.72
Fertilizer (F)	1	562.21**	184.93**
Sterilization (St)	1	249.10**	312.34**
F x S	1	1.70	7.44
St x S	1	28.12	74.20
F x St	1	1.11	2.16
F x St x S	1	54.54	10.09
Error	14	16.85	22.81

*Significant at the 5-percent probability level.

**Significant at the 1-percent probability level.

Sterilization of the two non-forest soils, however, did not significantly affect the total dry weight of the red oak seedlings as it did on the two forest soils. The seedlings on the sterilized non-forest soils had slightly less total dry weight than seedlings on unsterilized but the differences were not statistically significant either year.

Inoculation of the two non-forest soils with forest inoculum increased the growth of the red oak seedlings about 7 percent in 1962 and about 11 percent in 1963. The increase was not significant in 1962 but was significant at the 1-percent probability level in 1963. There were no significant interactions between inoculation and the other factors tested. The response to the inoculation, however, was not as great as to the addition of fertilizer on either soil.

Table 26. Mean squares from the analysis of variance of total dry weight per pot of red oak seedlings on the two non-forest soils, 1962 and 1963

Source of variation	Degrees of freedom	1962	1963
Replication	2	5.03	39.72
Soil (S)	1	0.26	184.44**
Fertilizer (F)	1	1860.66**	346.21**
Sterilization (St)	1	28.11	17.64
Inoculation (I)	1	49.79	109.73**
F x S	1	63.54	9.13
St x S	1	15.60	6.74
I x S	1	6.80	21.63
F x St	1	8.65	0.44
I x F	1	0.87	24.39
I x St	1	10.19	9.00
F x St x S	1	16.99	8.40
I x F x S	1	30.84	6.26
I x St x S	1	7.51	26.64
I x F x St	1	10.36	16.58
I x F x St x S	1	0.13	13.49
Error	30	22.83	13.88

*Significant at the 5-percent probability level.

**Significant at the 1-percent probability level.

As a matter of interest, the sterilized forest and non-forest soils were re-inoculated with unsterilized portions of the same soils. This treatment was not included in the statistical analyses because it was tested only on the unfertilized soils. The seedlings generally responded to this treatment, but on the forest soils re-inoculated seedlings did not grow as well as seedlings on untreated soils and on the non-forest soils the response was less than to inoculation with forest soil. The results are inconclusive but suggest: (1) sterilization may have pro-

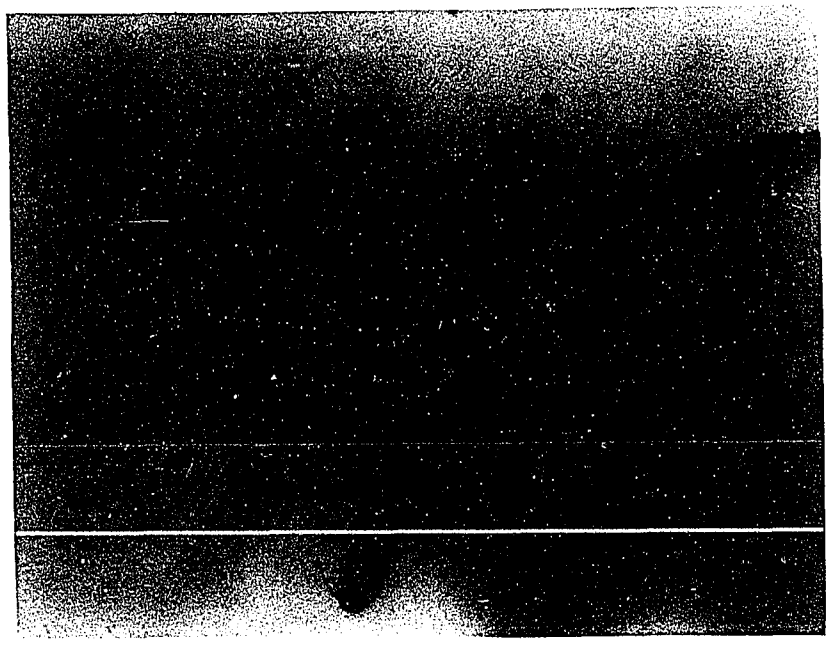
duced adverse effects other than the elimination of mycorhizae, and (2) the forest inoculum provided some biological factor not present or active in the prairie or old field inoculum, pointing possibly to mycorhizae.

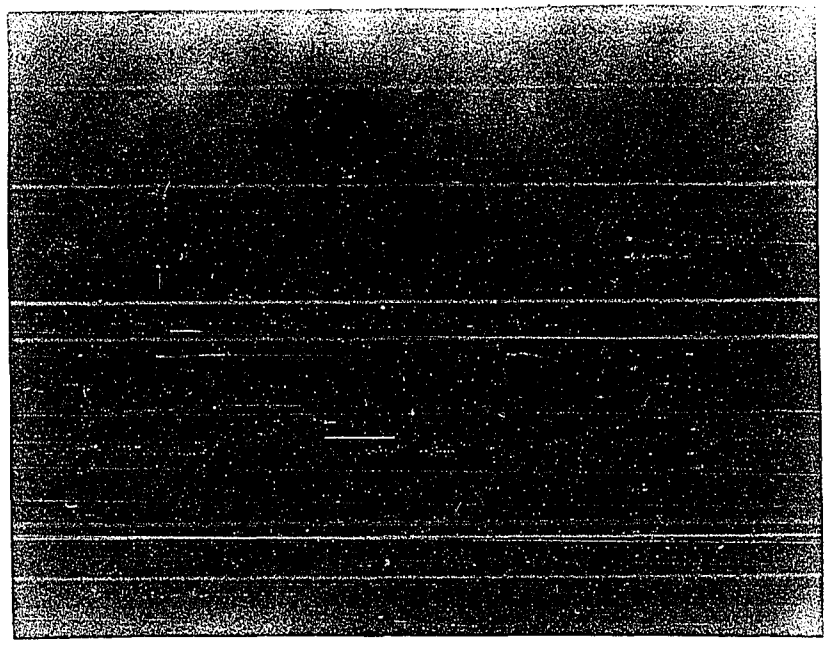
The red oak seedlings were examined closely when harvested at the end of the 1963 growing season and were found to be definitely mycorhizal. Unfortunately, similar observations were not made on the 1962 seedlings. Microtome sections of mycorhizal short roots indicated a well developed fungal mantle whose characteristics depended somewhat upon the soil. The Hartig network of hyphae in the roots, which is considered positive evidence of a mycorhizal relationship, was found in several root sections but usually was restricted to the outer two or three layers of cortical cells. There was no evidence of intracellular infection by the hyphae which characterize the ectendotrophic mycorhizae. Photomicrographs were made of the root sections infected with the major types of mycorhizal fungi found on the red oak seedlings and are shown in Figures 23 and 24.

The seedlings grown on unsterilized Lindley soil possessed mycorhizal roots covered by a white to dull grey mantle. This type of mycorhizae was not found in any other soil, except where the Lindley soil was used as the source of inoculum. Numerous white hyphal strands were found in the surrounding soil. The hyphae were very fine and formed a rather compact mantle. The short roots were swollen and dicotomously branched. The sites of infection, however, were infrequent on the root and at each only two or three short roots were mycorhizal.

Figure 23. Typical white mycorhizae observed on red oak seedlings on the Lindley soil, 1963

Figure 24. Typical black mycorhizae observed on red oak seedlings on the Clarksville soils, 1963





The rootlet tips of seedlings on the Clarksville forest soil possessed a fungal mantle characterized by thick black hyphae. The same type of mycorhizae was found on seedlings on the Clarksville old field soil but were, in general, not as numerous as on seedlings on the forest soil. The fungal mantle was restricted to the tip 1 to 2 millimeters of the rootlets, which usually were digitate (unbranched). The hyphae protruded at right angles from the black mantle, but there was no obvious network of hyphae in the soil.

A third type of mycorhizae, characterized by an olive-brown mantle, was found on seedlings on all soils. Seedlings grown in a nearby seedbed also possessed this same type of mycorhizae. It is believed, therefore, that their presence in the pots resulted from wind-blown inoculum. The short roots were strongly hypertrophied and numerous densely-packed mycorhizal clusters were found on the upper half of the root system. The olive-brown hyphae formed a visible network through the soil, terminating at a rather compact mantle covering the short roots. Dicotomous branching of the short roots was very apparent. This type of mycorhizae was not believed to have been present on the seedlings grown the previous year in these soils.

A subjective measurement of mycorhizal occurrence was attempted in order to establish possible relationships with soil treatments. The results are shown in Table 27, and indicate that the sterilization treatment effectively killed or inactivated the natural mycorhizal fungi in each of the forest soils. For example, the white mycorhizae were not found on any seedlings grown on sterilized Lindley soil unless

Table 27. Occurrence of mycorhizae on the red oak seedlings from the mycorhizae experiment, 1963

Soil	Fertilizer	Soil treatment	Pots[a]	Relative Frequency[b]	Color[c]
Lindley (Forest)	-	Untreated	3	++	A
		Sterilized	2	++	C
		+forest inoculum	3	+++	AC
	NPK	Untreated	2	+	A
		Sterilized	2	+	C
Shelby (Prairie)	-	Untreated	1	+	C
		+forest inoculum	1	+	A
		Sterilized	2	++	C
		+forest inoculum	2	++	CA
		+prairie inoculum	1	+	C
	NPK	Untreated	1	++	C
		+forest inoculum	1	+	C
		Sterilized	3	+	C
		+forest inoculum	3	+++	CA
Clarksville (Forest)	-	Untreated	3	++	B
		Sterilized	3	+++	C
		+forest inoculum	3	+++	BC
	NPK	Untreated	2	+	B
		Sterilized	3	+++	C
Clarksville (Old field)	-	Untreated	3	+	B
		+forest inoculum	3	++	BC
		Sterilized	3	+	C
		+forest inoculum	3	+	B
		+old field inoculum	3	+	CB
	NPK	Untreated	2	+	BC
		+forest inoculum	3	++	B
		Sterilized	1	++	C
		+forest inoculum	2	++	B

[a]Each treatment replicated in three pots.

[b]+ = present, ++ = several, and +++ = abundant.

[c]A = white, B = black, and C = olive-brown.

the soil was re-inoculated with forest inoculum. The black mycorhizae were absent on seedlings on sterilized Clarksville soils but inoculation brought about re-infection of the roots of the seedlings by this same type of mycorhizal fungi. The olive-brown mycorhizae appeared to develop especially well on seedlings on the sterilized soils, probably because of the absence of the natural fungi.

The results of the foliage analyses were quite variable and definite treatment effects were difficult to establish. The chemical analyses are given in Tables 46 and 47 in the Appendix.

Sterilization had a tendency to increase the concentration of nitrogen in the leaves of the 1962 seedlings on all soils, but in 1963 the opposite trend appeared to be true. These results, however, corroborate the adverse effect of this treatment observed with root growth in 1962 and with shoot growth in 1963, since other experiments showed that shoot growth was promoted more by nitrogen than root growth. The lower nitrogen concentrations in the 1963 seedlings possibly were due to the increased utilization of soil and fertilizer nitrogen the previous year. Phosphorus concentrations followed almost the same trend as nitrogen but some of the other elements, such as manganese, appeared to be consistently higher in seedlings on sterilized soils. The significance of the increased concentrations of these elements is not clear in view of the poorer growth of seedlings on the sterilized soils.

Because inoculation of the non-forest soils did not significantly improve growth of the red oak seedlings in 1962 the foliage analyses were not examined very closely with regard to this treatment. In 1963,

when a significant effect of inoculation was observed, the foliage analyses indicated that the concentration of some of the elements was somewhat greater in the inoculated seedlings than in the uninoculated. On an absolute basis, the inoculated seedlings on the two non-forest soils contained 14 percent more nitrogen, 30 percent more phosphorus, and 5 percent more potassium than uninoculated. However, the fact that the seedlings on the uninoculated soils also possessed mycorhizae makes such data questionable as evidence of a beneficial influence of mycorhizae on mineral nutrient uptake.

As a separate part of the mycorhiza investigations, the seedlings from the other experiments also were examined closely for mycorhizae when harvested in 1963. These observations failed to show any definite relation between mycorhizal occurrence and fertilization in the basic fertilizer experiment and in the nitrogen experiment. In the liming experiment, however, mycorhizal occurrence was found to be greater on unlimed soils than on limed (Table 28). On the Lindley soils that had been limed with 2 tons of lime the previous year, only 4 of the 12 pots contained mycorhizal seedlings. On the unlimed Lindley soil, 11 of the 12 pots contained mycorhizal seedlings. On the Clarksville soil limed at the 2-ton rate mycorhizal formation was completely suppressed, but on the unlimed soil 9 of the 12 pots contained mycorhizal seedlings.

Mycorhizal occurrence also was found to vary inversely with light intensity when the seedlings from the light intensity experiment were examined (Table 29). Almost all of the pots in full light, about three-fourths of those in 30-percent light, but only about one-tenth of those

Table 28. Occurrence of mycorhizae on the 1963 red oak seedlings from the liming experiment, number of pots with mycorhizal seedlings[a]

Soil	Lime level, tons/acre	Fertilizer				Total
		-	N	NP	NPK	
Lindley (Forest)	0	3	3	3	2	11
	1	2	2	2	2	8
	2	0	1	3	0	4
Clarksville (Forest)	0	3	2	2	2	9
	1	0	1	1	1	3
	2	0	0	0	0	0

[a]Each treatment replicated in three pots.

Table 29. Occurrence of mycorhizae on the 1963 red oak seedlings from the light intensity experiment, number of pots with mycorhizal seedlings[a]

Soil	Light intensity, percent	Fertilizer			Total
		-	NPK	N_4PK	
Lindley (Forest)	10	0	0	0	0
	30	2	1	3	6
	100	3	2	3	8
Clarksville (Forest)	10	1	1	0	2
	30	2	3	1	6
	100	3	2	3	8

[a]Each treatment replicated in three pots.

at 10-percent light contained mycorhizal seedlings. The seedlings that were mycorhizal at 10-percent light intensity were found only on the Clarksville soils. There was no apparent fertilizer effect or fertilizer x light interaction in the occurrence of mycorhizae on seedlings on these soils.

Species Experiment

The growth data for the other hardwood tree species planted on the four soils are given in Tables 30, 31, 32, and 33. Statistical analyses of the growth data are presented in Tables 34, 35, 36, and 37.

Black walnut seedlings responded to the differences in fertility among the four soils in much the same manner as red oak. In 1962 and 1963 the average height and dry weight of the black walnut seedlings was significantly greater on the forest soils than on the prairie and old field soils. Green weight differences among the four soils were more significant than dry weight in 1963.

The application of NPK fertilizer significantly increased all measures of growth of the black walnut seedlings in 1962 and all except height growth in 1963. The increase in dry weight in 1962 from the NPK fertilizer ranged from 44 percent on the Clarksville old field soil to 57 percent on the Lindley soil. In 1963, the increase in total dry weight on fertilized soils ranged from 14 percent on the Lindley soil to 42 percent on the Clarksville old field soil.

Cottonwood grew poorly on all four soils in 1962 because of poor germination and an unknown foliage disease in mid-summer. Nevertheless,

Table 30. Average height and dry weight per seedling of black walnut from the species experiment, 1962

Soil	Fertilizer	Height, in.	Dry weight, g			
			Leaves[a]	Stem	Roots	Total
Lindley	-	7.4	--	2.13	14.00	16.13
(Forest)	NPK	10.6	--	3.07	22.20	25.27
Shelby	-	7.2	--	1.26	12.13	13.39
(Prairie)	NPK	7.7	--	2.87	18.03	20.90
Clarksville	-	7.8	--	2.17	15.02	17.19
(Forest)	NPK	8.3	--	3.02	23.69	26.71
Clarksville	-	7.8	--	1.58	13.11	14.69
(Old field)	NPK	8.4	--	2.49	18.62	21.21

[a]No data taken.

Table 31. Average height and dry weight per seedling of cottonwood from the species experiment, 1962

Soil	Fertilizer	Height, in.	Dry weight, g			
			Leaves[a]	Stem	Roots	Total
Lindley	-	4.1	--	0.48	1.58	2.06
(Forest)	NPK	8.0	--	1.07	3.50	4.57
Shelby	-	1.4	--	0.20	0.73	0.93
(Prairie)	NPK	2.4	--	0.43	1.21	1.64
Clarksville	-	3.4	--	0.59	1.30	1.89
(Forest)	NPK	7.1	--	0.97	3.11	4.08
Clarksville	-	2.4	--	0.39	0.87	1.26
(Old field)	NPK	5.6	--	0.61	2.13	2.74

[a]No data taken.

Table 32. Average height and green and dry weight per seedling of black walnut from the species experiment, 1963

Soil	Fertilizer	Height, in.	Green weight, g	Dry weight, g			
				Leaves	Stem	Roots	Total
Lindley	-	11.2	62.38	3.89	3.73	23.18	30.80
(Forest)	NPK	12.6	67.81	4.75	4.43	25.83	35.01
Shelby	-	10.4	41.26	1.44	2.82	15.43	19.69
(Prairie)	NPK	11.1	50.58	2.11	3.07	19.69	24.87
Clarksville	-	10.6	54.61	2.79	3.35	20.40	26.54
(Forest)	NPK	10.8	64.73	3.75	3.84	25.31	32.90
Clarksville	-	9.6	41.39	1.61	3.07	14.59	19.27
(Old field)	NPK	10.7	55.66	3.34	3.73	20.34	27.41

Table 33. Average height and green and dry weight per seedling of green ash from the species experiment, 1963

Soil	Fertilizer	Height, in.	Green weight, g	Dry weight, g			
				Leaves	Stem	Roots	Total
Lindley	-	6.3	8.32	0.61	0.68	1.79	3.08
(Forest)	NPK	6.9	12.32	0.81	0.84	2.66	4.31
Shelby	-	4.8	4.29	0.26	0.28	0.82	1.36
(Prairie)	NPK	6.4	8.04	0.44	0.56	1.71	2.71
Clarksville	-	4.9	5.14	0.36	0.37	1.01	1.74
(Forest)	NPK	6.4	8.53	0.48	0.60	1.64	2.72
Clarksville	-	4.8	3.61	0.22	0.28	0.82	1.32
(Old field)	NPK	6.5	5.75	0.36	0.45	1.14	1.95

Table 34. Mean squares from the analysis of variance of average height and dry weight per pot of black walnut seedlings from the species experiment, 1962

Source of variation	Degrees of freedom	Height	Dry weight		
			Shoot	Roots	Total
Replication	2	10.47	0.43	106.5	119.0
Soil (S)	3	16.45	5.42*	210.3*	279.3*
Iowa vs Missouri	(1)	0.12	0.01	55.9	54.2
Lindley vs Shelby	(1)	49.21	7.78*	245.6	340.8*
Cl.-F. vs Cl.-O.f.	(1)	0.03	8.47*	329.0	443.0*
Fertilizer (F)	1	96.40*	62.73**	2700.0**	3585.0**
F x S	3	31.40	1.71	34.3	28.3
Error	14	16.56	1.52	59.0	73.8

*Significant at the 5-percent probability level.

**Significant at the 1-percent probability level.

Table 35. Mean squares from the analysis of variance of average height and dry weight per pot of cottonwood seedlings from the species experiment, 1962

Source of variation	Degrees of freedom	Height	Dry weight		
			Shoot	Roots	Total
Replication	2	6.21	0.11	1.43	2.02
Soil (S)	3	176.06**	2.76**	26.88**	46.49**
Iowa vs Missouri	(1)	22.23	0.48	0.52	2.00
Lindley vs Shelby	(1)	463.76**	5.68**	66.69**	111.26**
Cl.-F. vs Cl.-O.f.	(1)	42.19	2.12*	13.42	26.20
Fertilizer	1	476.15**	6.77**	101.11**	160.21**
F x S	3	23.80	0.41	5.85	8.68
Error	14	18.29	0.34	4.08	6.27

*Significant at the 5-percent probability level.

**Significant at the 1-percent probability level.

Table 36. Mean squares from the analysis of variance of average height and green and dry weight per pot of black walnut seedlings from the species experiment, 1963

Source of variation	Degrees of freedom	Height	Total green weight	Dry weight		
				Shoot	Roots	Total
Replication	2	4.54	10.0	0.5	216.0	204.0
Soil (S)	3	28.37	4463.0**	131.7	708.3	1402.3*
Iowa vs Missouri	(1)	45.38	107.4	1.9	41.3	60.9
Lindley vs Shelby	(1)	32.67	9928.5**	366.1**	1299.8*	3045.5**
Cl.-F. vs Cl.-O.f.	(1)	7.05	3344.3*	26.7	783.8	1099.8
Fertilizer (F)	1	40.56	5170.0*	135.0*	1042.0*	1926.0*
F x S	3	3.81	177.3	5.0	23.0	38.7
Error	14	11.67	592.6	20.6	213.6	323.5

*Significant at the 5-percent probability level.

**Significant at the 1-percent probability level.

Table 37. Mean squares from the analysis of variance of average height and green and dry weight per pot of green ash seedlings from the species experiment, 1963

Source of variation	Degrees of freedom	Height	Total green weight	Dry weight		
				Shoot	Roots	Total
Replication	2	33.00	102.5	1.02	18.12**	27.74*
Soil (S)	3	22.32	548.0**	12.39**	28.30**	77.91**
Iowa vs Missouri	(1)	17.34	594.1**	11.04*	34.34**	84.34**
Lindley vs Shelby	(1)	49.61	827.0**	23.32**	44.51**	132.27**
Cl.-F. vs Cl.-O.f.	(1)	0.01	222.8	2.81	6.05	17.11
Fertilizer (F)	1	173.88**	1060.0**	13.11*	44.74**	106.30**
F x S	3	5.99	16.0	0.09	1.63	2.33
Error	14	17.61	56.6	1.59	2.18	7.06

*Significant at the 5-percent probability level.

**Significant at the 1-percent probability level.

significant growth differences were observed on the four soils. The greatest growth was attained on the forest soils, with the greatest difference occurring between the Lindley and Shelby soils.

The relative response of cottonwood seedlings to fertilizer was rather large in comparison to red oak and black walnut, but this may have been because the seedlings were initially much smaller. The increase in total dry weight of stem and roots ranged from 76 percent on the Shelby soil to 122 percent on the Lindley soil. Fertilizer increased total dry weight of the cottonwood seedlings on the two Clarksville soils about 117 percent.

Green ash was used in place of cottonwood when the pots were replanted in 1963 because of the poor development of the cottonwood the previous year. The total dry weight and total green weight of the green ash seedlings were significantly greater on the Lindley soil than on the Shelby soil. Growth differences between the two Clarksville soils were not significant. The two Iowa soils produced significantly larger seedlings than the two Missouri soils, but height growth differences among soils were not significant.

The green ash seedlings responded to residual fertilizer in the soil in 1963. Seedling growth was significantly better on fertilized soils in all cases. The increase in total dry weight over seedlings on unfertilized soils ranged from 40 percent on the Lindley soil to 99 percent on the Shelby soil.

Considerable differences were noted in concentration of elements in the leaves of the various hardwood tree species, and in the ability

of the seedlings to absorb the minerals from the fertilizer (Table 48, Appendix). Red oak leaves contained consistently higher concentrations of manganese. Black walnut leaves usually contained higher concentrations of calcium, magnesium, aluminum, and sodium. Green ash leaves generally contained higher concentrations of nitrogen, phosphorus, potassium, and copper, and significantly less manganese and boron than the other two species.

The green ash seedlings were more efficient in absorbing the phosphorus added to these soils in 1962 than the red oak or the black walnut seedlings. There was over a four-fold increase in the concentration of phosphorus in green ash seedlings grown on the fertilized Clarksville old field soil. Two- to three-fold increases in the concentrations of phosphorus were observed in seedlings grown on the other fertilized soils as compared to the green ash seedlings on unfertilized soils.

The foliage analyses for black walnut and green ash confirmed the previous finding with red oak that there was little residual nitrogen fertilizer in these soils. Neither of the species showed any marked increase in nitrogen concentrations on fertilized soils, except on the Lindley soil. In fact, the two species generally had less nitrogen in the leaves on fertilized soil than on unfertilized soil.

DISCUSSION

The results of the study indicate that the Lindley, Shelby, and Clarksville soils differ significantly from the standpoint of growth of hardwood tree seedlings. Seedling growth, in general, was much better on the forest soils than on the non-forest soils. These growth differences may be partly related to differences in soil fertility, which were evident from soil chemical analyses. Other factors, however, must also be involved, because seedling growth on fertilized non-forest soils was not much better than on the unfertilized forest soils, although the supply of readily available nutrients probably was much greater on the former soils. Clark (1964), McComb (1949) and White (1941), also, have found that hardwood tree seedlings grow better on forest soils than on prairie and old field soils, and either have demonstrated or implied that microbiology may be the major difference among such soils. Evidence obtained in the present study also points to absence or inactivity of mycorhizal fungi as a possible cause for poor growth on the non-forest soils.

Results from the basic fertilizer experiment indicate that all of these soils are phosphorus and, to a lesser extent, nitrogen deficient for hardwood seedling growth. Significant growth responses were obtained on all four surface soils from the application of nitrogen and phosphorus fertilizers. The results obtained on the Lindley soil corroborate earlier work by McComb (1949) which indicated Lindley subsoil to be both nitrogen and phosphorus deficient, and nitrogen more limiting than

about the same nitrogen status as the soils used in the present study.

Because of differences in shoot and root growth the shoot/root ratio of the red oak seedlings increased with nitrogen supply on all soils. Similar responses to nitrogen fertilization have been observed frequently by other investigators. It was found, however, that the very high nitrogen applications were detrimental to root growth but shoot growth was not affected as adversely. Mitchell (1939) studied the effect of nitrogen on the relative root and shoot growth of certain conifer seedlings and found that, although shoot/root ratio increased with increasing nitrogen supply, the greatest shoot and root growth occurred at the same external nitrogen concentration. This was not found to be true in the present study, especially on the Clarksville soils. Possibly the pronounced adverse effect of heavy nitrogen applications on root growth in the Clarksville soils was related to the low organic matter content and low exchange capacity of these soils.

A rather definite relation was established between the nitrogen concentration in the leaves and the total dry weight of the seedlings. The optimum nitrogen concentration in the leaves of the red oak seedlings was found to be approximately 2.5 percent dry weight. These results compare with those of Mitchell and Chandler (1939) who found that the optimum nitrogen concentration in leaves of 40-year old red oak trees was between 2.46 and 2.57 percent. These results suggest that the optimum nitrogen concentration in the leaves of red oak is independent, to a large extent, of the age of the trees.

Phosphorus responses were real on all soils. The greatest response

to phosphorus occurred on the Clarksville soils and is believed to be related to the lower organic matter content and exchange capacity of these soils. Fixation factors which affect the availability of phosphorus would not be expected to be as great under these conditions. Phosphorus added to the Clarksville soils, therefore, probably was available immediately after application and especially during the period of most rapid nutrient uptake and growth. Evidence that phosphorus was not entirely fixed in the Lindley and Shelby soils, however, can be seen in the increased phosphorus concentrations in the leaves of the red oak seedlings after adding phosphorus fertilizer to these soils.

The foliage analyses provided rather limited information about the critical phosphorus concentrations in the leaves of the red oak seedlings, mainly because only one rate of phosphorus application was used. However, the fact that significant growth responses were obtained on all soils after adding phosphorus fertilizer indicates this element was deficient in seedlings grown on the unfertilized soils. In the present study the phosphorus content of unfertilized seedlings usually was within the range of 0.10 to 0.15 percent, but with phosphorus fertilization was increased up to 0.25 to almost 0.30 percent. Phosphorus concentrations less than 0.20 percent in leaves of red oak seedlings may be indicative of phosphorus deficiency. The phosphorus concentrations observed in the present study were comparable to those reported by Mitchell and Chandler (1939) and by McComb (1949) for red oak trees and seedlings. The optimum phosphorus percentages, unfortunately, have not been established for this species at the present time.

Potassium apparently was not deficient on these soils, which contained 150 to 200 pounds of exchangeable potassium per acre, because no growth response was obtained with the application of potassium fertilizer. In fact, potassium fertilization commonly depressed growth on all of the soils. McComb (1949) also reported that potassium was not limiting on Lindley and other soils in Iowa, and concluded that on the majority of soils in the State the quantity of exchangeable potassium is adequate for the growth of hardwood tree seedlings.

The response to potassium is somewhat puzzling when viewed in conjunction with the results of the foliar analyses. The concentration of potassium in the leaves of the red oak seedlings usually averaged 0.60 percent or less, and did not increase significantly after adding potassium fertilizer. These values are considerable lower than has been reported for this species in the literature. For example, Mitchell and Chandler (1939) reported potassium concentrations ranging from 0.79 to 2.21 percent in leaves of red oak trees growing on different sites in the northeast. The potassium concentrations reported for this species by Bard (1946) and by Finn and Tryon (1942) also are within this range. It is not clear whether our concentrations were low or whether the higher values reported represented luxury consumption.

The presence of a significant nitrogen x phosphorus interaction on growth indicated that added nitrogen can increase the response to phosphorus, and vice versa. This indication was supported by the foliage analyses which showed that added nitrogen increased both the relative and absolute phosphorus content of the leaves. Nitrogen x

phosphorus interactions have been observed frequently with agricultural plants, but seldom have been reported for forest tree species. Grunes (1959) has reviewed the literature on this subject and has concluded that the increased phosphorus uptake may be due either to an indirect effect of nitrogen on the form and functions of the plant or to a direct chemical effect upon phosphorus solubility. Plant changes mentioned most often include increased root growth and foraging capacity for phosphorus. Nitrogen additions also may affect plant metabolism and increase the ability of unit areas of root surface to absorb phosphorus.

A comparison of growth response and foliage analyses of seedlings on fertilized soils in 1963 with 1962 data indicated that phosphorus was better retained in the soil than nitrogen. The absence of a significant nitrogen response the second year after fertilization is attributed to leaching losses and utilization of nitrogen by the seedlings in the previous year. Phosphorus, on the other hand, is not as subject to leaching because of rapid reaction with the soil and was available to seedlings grown on the soils in 1963. These results suggest that a single application of nitrogen will increase growth of hardwood seedlings directly only a short time on these soils, whereas the benefit of a single application of phosphorus may be longer lasting. The carryover of potassium fertilizer could not be evaluated because no significant growth responses were obtained in either year with this element. All of the soils, however, contained sufficient fine material and organic matter to prevent large leaching losses of applied potassium fertilizers.

The application of lime to the Lindley and the Clarksville soils adversely affected the growth and mineral nutrition of the red oak seedlings on both soils in 1962, but improved growth somewhat on the Lindley soil in 1963. The fact that the adverse effect of liming on the Lindley soil was only temporary is probably related to the high organic matter content and high exchange capacity of this soil.

The acid nature of these soils apparently was not a limiting factor in the growth of red oak seedlings. These results are to be expected because it has been established by solution cultures that hydrogen ion concentration *per se* is not toxic to plant growth, except under extreme conditions when the pH is less than 3.0 (Arnon and Johnson 1942). Calcium does not appear to be deficient on these soils when the calcium content of the foliage is taken into consideration. Stone (1940) has evaluated the calcium requirements for several deciduous tree species. Comparison of the calcium percentages in the leaves indicates that the red oak seedlings were nearly adequately supplied with this element, even though these soils were low base saturated, especially the Clarksville soil. If growth was being limited on these soils because of unfavorable soil reaction, it was more likely the result of aluminum or manganese toxicity or a deficiency of certain mineral nutrients other than calcium.

Significant interactions were observed between lime and some of the elements added in the fertilizers. The response to nitrogen was altered to some extent by liming on both the Lindley and the Clarksville soils. In general, addition of nitrogen reduced the total dry weight of the red

oak seedlings on the unlimed soils, but increased seedling growth on the limed soils. American elm has been found to respond similarly, and significant growth responses to lime were apparent only when soluble nitrogen was added (Wilde 1946). In the present study, the response to nitrogen on limed soils probably was not real. The added nitrogen may only have compensated for the loss of available nitrogen to cellulose decomposing bacteria and fungi which may have been stimulated by the addition of lime.

The most apparent interaction was between lime and phosphorus. The red oak seedlings showed large responses to phosphorus on unlimed soils, but on limed soils the absorption of fertilizer phosphorus was greatly reduced and growth was markedly depressed. Thus, it would seem that at high soil pH values red oak seedlings are unable to absorb fertilizer phosphorus. Under such conditions the soluble phosphorus may combine with free calcium and form relatively insoluble calcium phosphate (Black 1957). Apparently, the red oak seedlings were not able to absorb and utilize the phosphorus from this complex. Similar results have been reported by McComb (1949) who found that red oak seedlings were unable to absorb phosphorus added to Clarion soils which were calcareous. Unfortunately, very little is known about the ability of tree seedlings to extract mineral nutrients from sources of varying solubility.

The reduced uptake of phosphorus on limed soils also may be due to a lack of mycorhizae on roots of seedlings growing on these soils. The occurrence of mycorhizae varied inversely with the application of lime.

The 2-ton rate of liming almost completely suppressed the formation of mycorhizae on the roots of the red oak seedlings the second year after application. Mycorhizal fungi have been found to facilitate greatly the uptake of phosphorus and other nutrients by many forest tree species. Mycorhizae also appear to improve the mineral nutrition and growth of red oak seedlings.

Although potassium additions increased growth slightly on the limed soils there did not appear to be any significant calcium x potassium interaction in the foliage analyses. According to Reitemeier (1951), liming may sometimes increase the uptake of potassium by the plants. Such a response probably would not be important on these soils because they already appear to supply sufficient potassium for the growth of the hardwood seedlings.

The relation between liming and uptake of the micronutrients has not been investigated to any great extent with forest tree species. The analyses of micronutrients in leaves of the red oak seedlings grown on the limed soils indicated that these elements behave in a manner frequently observed in agricultural plants. Liming tended to decrease the concentration of manganese and boron and to increase the concentration of molybdenum in the leaves of the seedlings. The reduction in manganese concentration in the leaves of seedlings on the limed soils was most striking. There was almost a ten-fold decrease in the content of this element in seedlings on soils limed at the 2-ton rate. The reduced absorption of manganese on limed soils is generally believed to be due to a change in the oxidation state (Mulder and Gerretsen 1952). The

absorption of sodium and aluminum, although not essential elements, also tended to decrease on limed soils.

The present study also indicates that the growth of red oak seedlings on forest soils may be limited if the seedlings are subjected to light intensities of less than 30-percent of full daylight. Such conditions exist on sites where overstory trees are present, where light intensities often vary from 0.1 to 20 percent of full daylight (Shirley 1929a, 1929b). Light intensities of 5-percent or less are frequently observed in the understory (Buell and Gordon 1945 and Oosting and Kramer 1946).

The dry weight of the red oak seedlings was linearly related to light intensity up to about 30-percent of full light. Other studies have verified the linearity of this relation up to 20-percent light intensity (Shirley 1929a, 1929b). Dry weight increases were small and usually were not statistically significant above 30-percent light, suggesting that light saturation may occur near this intensity. These conclusions are supported by Kramer and Decker (1944) who found that several hardwood species, including red oak, achieved maximum photosynthesis at one-third or less of full light, and that any further increase in light intensity produced no further increase in photosynthesis.

Morphological features of the red oak seedlings were altered by the reduced light intensities, the most striking was the large increase in shoot/root ratio. Seedlings grown at 30-percent light intensity had about the same total dry weight as seedlings grown at full light but the balance between shoot and root growth was significantly different at

the two light intensities. Shoot growth was increased and root growth was decreased at the 30-percent light intensity as compared to seedlings grown at full light. According to Loomis (1949), root and shoot growth are competitive and root growth is limited by supplies of carbohydrates and other growth materials from the top, and growth of the shoot is limited by supplies of water and minerals obtained through the roots. The most active parts of the seedlings tend to monopolize the use of foods produced by the seedlings. As long as external conditions are favorable for shoot growth, less foods will be translocated to the roots and root growth will be reduced and shoot growth maintained.

A significant result of this experiment was that applications of fertilizers were ineffective in stimulating growth of red oak seedlings grown at 10-percent light intensity. This is further evidence that light is the primary factor limiting growth under these conditions rather than inadequate mineral nutrients. Experiments with green ash also have shown that if the supply of nutrients is sufficient to satisfy the needs of the seedling the minimum light requirements are not lowered by increasing the nutrient supply, and responses to increased supplies of nutrients are obtained only at higher light intensities (Steinbauer 1932).

Mitchell (1939) found that the concentration of nitrogen in Scots and white pine seedlings was higher at half-light than at full-light but the absolute quantity of nitrogen absorbed appeared to be independent of light intensity. The results of the present study support this relationship if one considers only the light intensity range over

which total dry weight of the seedlings remained fairly constant. At the lower light intensities, to which seedlings in the understory are frequently exposed, the ability of the seedlings to absorb nutrients and the total dry weight were greatly reduced. The concentrations of the elements on a percent dry weight basis, however, increased with decreasing light intensity over the entire range, but the absolute amount of elements absorbed was independent of light intensity only to a certain level, below which the amount of nutrients absorbed fell off sharply. The present study indicates that this critical light intensity for red oak may be between 10- and 30-percent of full light. Therefore, the statement that nutrient absorption is independent of light intensity must be greatly qualified.

The investigations were inconclusive regarding the importance of mycorhizae to the growth and nutrition of red oak seedlings on the soils investigated. At least two pieces of evidence, however, indicate that some biological factor may be limiting growth on the old field and the prairie soils. First, sterilization decreased seedling growth on the forest soils but not on the non-forest soils, which indicates that the forest soils contained some biological factor not present or active in the non-forest soils. And secondly, inoculation of the non-forest soils with forest soils increased the growth of the red oak seedlings. Presumably, the biological factor which is different on the forest and non-forest soils is mycorhizal fungi, but the possible contribution of other fungi and bacteria should not be ignored.

The roots of the red oak seedlings on the Lindley and Clarksville

forest soils possessed ectotrophic mycorhizae when examined in 1963. The seedlings on the Clarksville old field soil also were mycorhizal, so lack of the fungus was not a serious problem on this soil. The intensity of infection, however, did not appear to be as great as on seedlings on the forest soils. The seedlings responded to inoculation on these soils. No mycorhizae were observed on seedlings on the Shelby soil, except where intentionally or accidentally inoculated with mycorhizal fungi. Poor growth and development, therefore, may be characteristic of red oak seedlings on this soil unless measures are taken to establish the necessary mycorhizal fungi soon after planting.

There was a definite time lag in growth response to the inoculation treatments on the non-forest soils, suggesting that either the mycorhizal fungus must reach a certain level of activity in the soil to become effective or the conditions were not suitable for infection of the roots. No significant difference in growth of inoculated and uninoculated seedlings was observed in 1962, but during 1963 the seedlings on the inoculated soils grew significantly better than the seedlings on the uninoculated soils. It is frequently noted in the literature that mycorhizae seldom develop on one-year-old seedlings but the present study indicates this is not necessarily true. The seedlings grown on the forest soils and the inoculated soils in 1963 were definitiely mycorhizal, as evidenced by a well defined fungal mantle and presence of a Hartig network of hyphae between cortical cells of the roots. The failure of one-year-old seedlings to become mycorhizal probably is related to the relative abundance of the fungi rather than to the inability

of the seedlings to become mycorhizal.

The physical description of the mycorhizae formed on the roots of the red oak seedlings, although somewhat incomplete, provides new information to the literature on this species. The mycorhizae on red oak have not been described extensively in the literature. McComb (1949) observed much-branched clusters of light grey mycorhizae on red oak seedlings growing on Lindley surface and subsoils. The mycorhizae observed on red oak seedlings on the Lindley soil in the present study also were of this same general appearance, but the clusters were only infrequently found on the root system. The black mycorhizae found on seedlings on the Clarksville soils resemble in almost every detail the jet-black mycorhizae described by Hatch (1934) the fungus of which has been identified as Cenococcum graniforme. Trappe (1962) has cultured this fungus from the roots of red oak, and also cites other workers who have found Clitocybe candicans, Cortinarius rubripes, and Russula emetica to form mycorhizae on red oak. Whether any of these fungus species were present in the soils investigated and were responsible for the formation of mycorhizae was not ascertained, since no attempt was made to culture and isolate the species involved.

Comparisons of the mineral composition of seedlings grown on inoculated and uninoculated soils, and on sterilized and on non-sterilized soils, did not provide much support to the theory that mycorhizae increase the mineral absorption by tree seedlings. Seedlings grown on soils where mycorhizal fungi should have been present contained somewhat greater amounts of several of the elements analyzed, but whether

this was due to increased nutrient uptake or merely associated with greater growth could not be determined. Further complicating the results of the foliage analyses were the direct chemical effects of the soil sterilization on solubility of nutrients, the accidental inoculation of non-infected soils, and the fact that there were different degrees of infection on seedlings within a single pot, while the foliage analyses were based on a composite leaf sample from all seedlings. Obviously, greater control of external conditions is necessary to determine the value of mycorhizae in mineral nutrition of tree seedlings. Such relations probably are best demonstrated on an individual seedling basis rather than on a large number of seedlings, as was attempted in the present investigations.

It has been mentioned frequently in the literature that the occurrence of mycorhizae varies inversely with the nutrient level of the soil in which the seedlings are growing. No significant relation, however, could be established between fertilizer treatment and mycorhizal occurrence when the seedlings were examined in 1963. Possibly this was because the residual fertilizer in the soil was not sufficient to affect the establishment of the fungi.

Definite trends were established, however, between abundance of mycorhizae and the liming and shading treatments. Mycorhizal occurrence was much less on the limed soils than on the unlimed. The 2-ton rate of liming completely suppressed formation of the black mycorhizae on the seedlings on the Clarksville soil but a few white mycorhizae were found on seedlings in the Lindley soil with this treatment. Richards and

Wilson (1963) do not believe that soil pH per se affects the establishment of the mycorhizae, except only as it affects the carbohydrate/total nitrogen ratio in the roots of the seedlings. Goss (1960) has found mycorhizae on pine seedlings growing on soils with rather high pH's.

Shading the seedlings also reduced the occurrence of mycorhizae on the roots of the red oak. At the 10-percent light intensity the white type of mycorhizae on the Lindley soil was completely suppressed. A few of the seedlings on the Clarksville soil, however, possessed the typical black mycorhizae at this light intensity. These results support work by Björkman (1942) and Hacskaylo and Snow (1959), who also have reported a direct relation between light intensity and mycorhizal occurrence. Presumably, seedlings grown at low light intensities do not accumulate sufficient carbohydrates in the roots for the invasion and growth of the mycorhizal fungi.

A comparison of the occurrence of the different types of mycorhizae under the different treatments indicates possible species difference. The black type of mycorhizae appeared to be more sensitive to liming than the white, whereas the white mycorhizae appeared to be more sensitive to shading. Very little is known about the ecology of the different mycorhizal fungi, but this undoubtedly would be a fruitful field for additional research.

The other hardwood species tested in these investigations, which included black walnut, cottonwood, and green ash, also appeared to grow better on the forest soils than on the non-forest soils. None of these species, however, possessed mycorhizae, which suggests that the growth

difference on these soils was due to other microbiological and soil chemical factors. This is not intended to imply that mycorhizae do not form on these species; Trappe (1962) lists several fungi which are capable of forming mycorhizae on these species. Apparently the appropriate fungus species either were not present or were not active in the soils investigated.

The various hardwood species responded somewhat differently to the application of fertilizer. The relative dry weight increase on fertilized soils was much greater with cottonwood and green ash than with black walnut and red oak. Because the soils were primarily phosphorus deficient, the differences among species in response to fertilizer can be explained partly on the basis of differences in ability to absorb fertilizer and soil phosphorus. Sommer (1936) has demonstrated that the ability of plants to absorb phosphorus is primarily a function of the relative size of the root system. The more fibrous rooted cottonwood and green ash, therefore, would be expected to absorb greater quantities of phosphorus and make more growth in response to phosphorus fertilization on these soils. This is supported by the growth response observed and by the chemical analyses of the green ash leaves in 1963, which had higher concentrations of phosphorus than the red oak and black walnut. McComb (1949) and Mitchell and Finn (1935) also have found the fibrous rooted tree species to contain greater concentrations of phosphorus than the tap rooted species.

The concentration of the other elements in the leaves of the red oak seedlings, as well as in the leaves of the other species, cannot

be evaluated at the present time because of the lack of information on the optimum and critical concentrations for these elements. These levels have not been established for any of these species, as far as the author knows. Moreover, very few values are available for other forest tree species for comparison. Such data are available for many agricultural and horticultural plants and have been summarized by Goodall and Gregory (1947). The critical percentages tended to vary with species but, judging from the values cited, none of the micronutrients analyzed in the leaves of the red oak, black walnut, or green ash seedlings appeared to be seriously deficient. The concentrations of many of the elements were often found to be higher than reported for cultivated plants, but this may only reflect luxury consumption.

SUMMARY

Pot experiments were conducted during 1962 and 1963 with Lindley, Shelby, and Clarksville surface soils to determine the significance of a number of fertility and site factors associated with these soils for the growth and nutrition of hardwood tree seedlings. Fertilizer results indicated that all of the soils were nitrogen and phosphorus deficient for the growth of red oak seedlings. Phosphorus was more limiting than nitrogen, and was more deficient on the Clarksville soils than on the Lindley and Shelby soils. Potassium did not appear to be limiting on any of the soils, which contained 150 to 200 pounds of exchangeable potassium per acre.

Nitrogen responses were small but significant in 1962 on all soils. The greatest shoot growth was obtained from the application of 180 pounds of nitrogen per acre. The optimum foliar nitrogen concentration in red oak seedlings was found to be about 2.5 percent dry weight. Heavy applications of nitrogen had a depressing effect on growth, especially root growth. Nitrogen applications also were found to increase the uptake of phosphorus and the response to phosphorus fertilizer by the red oak seedlings. Carryover nitrogen from the first to the second year, however, was small compared to phosphorus. A significant growth response was obtained in 1963 only on the soils that had previously been fertilized with phosphorus.

Liming was detrimental rather than beneficial to the growth of the red oak seedlings on the moderately-acid Lindley and Clarksville soils

in 1962, but improved growth slightly on the Lindley soil in 1963. The detrimental effect of liming was related mainly to insufficient phosphorus nutrition, brought about either by direct fixation effects or indirectly by suppressed mycorhizal formation. Lime-nitrogen and lime-potassium interactions were noted but did not greatly affect growth. The availability and absorption of a number of the micronutrients was greatly affected by the liming treatments.

Heavy shading reduced the growth of red oak seedlings on the forest soils, but moderate shading tended to increase height growth without any decrease in total dry weight. Seedling dry weight increased almost linearly up to 30-percent light intensity, above which the dry weight increase generally was not significant. Root growth was reduced at all light intensities below full light. The shoot/root ratio was greatest with seedlings grown at the lowest light intensity. Fertilizer responses were observed only with seedlings grown at full- and at 30-percent light, no fertilizer responses were obtained with seedlings grown at 10-percent light intensity. Nutrient absorption was not significantly affected by moderate shading but was greatly reduced at the lowest light intensity. The percentage concentration of mineral nutrients in the leaves of the red oak seedlings was greater under the reduced light conditions.

Red oak seedlings grew better on the forest soils than on the non-forest soils. Indirect evidence was obtained that indicated the growth differences on these soils were due to insufficient development of mycorhizae. Sterilization reduced seedling growth on forest soils

but not on non-forest soils, and inoculation of non-forest soils improved the growth of the red oak seedlings. The red oak seedlings possessed ectotrophic mycorhizae when examined in 1963, the type of mycorhizae varying on the different soils. Seedlings on the Lindley soil possessed white mycorhizae, while seedlings on the Clarksville soil were infected by a black mycorhizal fungus. Liming and shading also were found to inhibit the formation of mycorhizae on the red oak seedlings. The mycorhizal seedlings contained somewhat more mineral nutrients than non-mycorhizal seedlings but the results were inconclusive regarding the importance of these structures in the nutrition of red oak seedlings.

Black walnut, cottonwood, and green ash also grew better on the forest soils than on the non-forest soils. Red oak, however, was the only tree species with ectotrophic mycorhizae. The green ash and the cottonwood responded more to fertilizers than black walnut and red oak. This response was attributed mainly to the fibrous root systems of these species which increase the ability of the seedlings to absorb soil and fertilizer phosphorus. These conclusions were supported by foliage analyses. A number of mineral nutrients analyzed in the leaves other than phosphorus also varied greatly among the different tree species.

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APPENDIX

Table 38. Mineral concentration in the leaves of red oak seedlings fro

Soil	Fertilizer	Percent dry weight				
		N	P	K	Ca	Mg
Lindley	-	1.74	.142	.52	0.94	.23
(Forest)	N	2.34	.175	.42	1.14	.23
	P	1.80	.193	.54	1.06	.23
	K	1.98	.151	.48	1.06	.23
	NP	2.16	.218	.46	1.18	.26
	NK	2.24	.159	.44	1.10	.21
	PK	1.80	.245	.46	1.18	.26
	NPK	2.10	.193	.52	1.06	.23
	Mean	2.02	.184	.48	1.09	.24
Shelby	-	1.78	.084	.80	1.02	.29
(Prairie)	N	1.76	.105	.66	1.10	.29
	P	1.64	.136	.48	0.94	.28
	K	1.78	.092	.66	1.10	.25
	NP	2.10	.128	.44	0.94	.26
	NK	1.76	.092	.68	0.87	.21
	PK	1.56	.128	.56	1.02	.25
	NPK	2.26	.142	.48	1.14	.26
	Mean	1.83	.113	.60	1.02	.26
Clarksville	-	2.34	.175	.44	0.98	.20
(Forest)	N	2.54	.227	.44	1.06	.25
	P	2.28	.210	.42	0.94	.23
	K	2.46	.159	.44	0.94	.20
	NP	2.34	.264	.42	0.98	.22
	NK	2.66	.193	.46	0.98	.20
	PK	2.10	.193	.46	0.87	.25
	NPK	2.66	.290	.42	1.14	.23
	Mean	2.42	.214	.44	0.99	.21
Clarksville	-	2.06	.112	.70	1.02	.21
(Old field)	N	1.94	.193	.50	1.31	.22
	P	1.62	.159	.54	1.10	.25
	K	1.90	.092	.66	1.02	.21
	NP	2.12	.210	.42	1.10	.21
	NK	2.04	.151	.60	1.22	.20
	PK	1.56	.142	.54	1.02	.22
	NPK	2.22	.193	.56	1.06	.21
	Mean	1.93	.156	.56	1.16	.22

[a]Manganese contents designated (+) were greater than the range of

ilings from the basic fertilizer experiment, 1962

		Parts per million dry weight							
a	Mg	Fe	Mn[a]	B	Zn	Cu	Mo	Na	Al
94	.23	95	568	41.6	26	6.8	4.8	22	62
14	.23	95	1076	38.0	34	7.6	5.6	29	49
06	.23	78	751	48.2	28	5.0	5.0	36	49
06	.23	82	595	58.0	34	6.8	5.0	29	44
18	.26	75	959	40.4	30	4.3	5.8	48	54
10	.21	85	1167	39.2	34	6.0	5.6	60	49
18	.26	95	920	56.6	34	8.4	5.2	56	58
06	.23	85	659	38.0	26	3.5	4.8	69	54
09	.24	86	837	45.0	31	6.0	5.2	44	52
02	.29	114	848	29.5	19	4.3	4.6	74	72
10	.29	143	1193+	30.7	19	6.0	5.2	104	86
04	.28	98	1102	30.7	19	6.0	4.4	64	66
10	.25	118	738	36.8	24	6.8	5.6	134	72
04	.26	98	985	28.3	22	4.3	4.8	93	66
37	.21	108	985	26.0	22	6.0	4.2	79	76
02	.25	104	972	35.6	22	5.0	5.0	64	72
14	.26	102	1076	28.3	24	5.0	5.8	84	72
02	.26	116	987+	30.7	21	5.4	4.5	87	73
08	.20	95	1193+	41.6	57	6.0	4.4	89	76
06	.25	111	1193+	35.6	47	5.0	4.6	79	72
04	.23	111	1193+	40.4	67	7.6	4.0	60	66
04	.20	98	1193+	35.6	57	6.8	4.0	74	72
08	.22	104	1193+	33.0	54	5.0	4.4	104	66
08	.20	91	1193+	36.8	50	6.0	4.2	56	62
37	.25	88	1193+	35.6	50	4.3	3.6	128	66
.4	.23	108	1193+	35.6	57	6.0	5.2	98	62
09	.21	101	1193+	36.8	55	5.8	4.3	86	68
02	.21	95	1193+	39.2	36	4.3	4.0	89	66
31	.22	108	1193+	34.3	38	3.5	5.8	89	82
.0	.25	104	1193+	42.8	38	4.3	4.4	64	76
02	.21	85	1193+	33.0	30	4.3	4.2	79	76
.0	.21	173	1193+	33.0	24	5.0	4.6	52	58
12	.20	111	1193+	33.0	38	6.8	5.8	79	66
02	.22	197	972	42.8	41	7.6	4.6	69	62
06	.21	108	1193+	35.6	41	5.0	4.6	40	72
.6	.22	123	1165+	36.7	36	5.1	4.8	70	70

range of determination by the spectrograph.

Table 39. Mineral concentration in the leaves of red oak seedlings f

Soil	Fertilizer	Percent dry weight				
		N	P	K	Ca	
Lindley	-	1.80	.120	.60	1.10	.
(Forest)	N	1.96	.159	.63	1.02	.
	P	1.86	.193	.67	1.06	.
	K	1.90	.136	.64	0.98	.
	NP	1.73	.210	.61	1.18	.
	NK	1.80	.142	.60	1.10	.
	PK	2.03	.227	.61	1.06	.
	NPK	2.02	.184	.67	1.02	.
	Mean	1.89	.171	.63	1.06	.
Shelby	-	1.92	.099	.55	0.98	.
(Prairie)	N	1.84	.084	.60	0.98	.
	P	1.60	.159	.60	1.10	.
	K	2.00	.112	.60	0.87	.
	NP	1.78	.175	.61	0.94	.
	NK	1.70	.105	.55	1.02	.
	PK	1.51	.136	.61	0.77	.
	NPK	1.78	.184	.69	0.91	.
	Mean	1.77	.132	.60	0.95	.
Clarksville	-	1.72	.159	.61	0.70	.
(Forest)	N	1.75	.193	.60	0.80	.
	P	1.76	.218	.63	0.77	.
	K	1.87	.159	.60	0.83	.
	NP	1.93	.245	.58	0.77	.
	NK	1.68	.184	.60	0.80	.
	PK	1.68	.210	.60	0.87	.
	NPK	1.50	.227	.61	0.67	.
	Mean	1.74	.199	.60	0.78	.
Clarksville	-	1.56	.142	.58	0.87	.
(Old field)	N	1.72	.136	.64	0.83	.
	P	1.81	.227	.52	0.87	.
	K	1.83	.120	.63	0.91	.
	NP	1.92	.282	.60	0.91	.
	NK	1.90	.151	.57	0.94	.
	PK	1.82	.273	.63	0.83	.
	NPK	1.58	.202	.60	0.87	.
	Mean	1.77	.192	.60	0.88	.

[a]Manganese contents designated (+) were greater than the range o

ς seedlings from the basic fertilizer experiment, 1963

ight		Parts per million dry weight						
Ca	Mg	Fe	Mn[a]	B	Zn	Cu	Na	Al
1.10	.26	114	806	58.0	41	3.5	98	154
1.02	.23	108	1123	56.6	41	3.0	93	148
1.06	.26	118	925	52.4	47	6.0	74	176
0.98	.23	108	925	44.0	44	5.0	110	160
1.18	.30	134	1136	56.6	47	3.5	64	160
1.10	.25	130	1004	55.2	44	4.3	128	176
1.06	.26	85	1037	49.6	36	1.0	60	148
1.02	.25	91	1057	55.2	38	3.5	93	142
1.06	.26	111	1002	53.4	42	3.7	90	158
0.98	.26	134	687	27.2	26	2.0	89	226
0.98	.26	124	687	27.2	30	3.0	110	220
1.10	.29	121	813	41.6	41	6.8	89	220
0.87	.26	118	687	28.3	30	4.3	84	245
0.94	.26	134	885	33.0	44	5.0	110	195
1.02	.25	130	674	31.9	34	3.5	128	350
0.77	.28	114	634	34.3	24	3.0	98	232
0.91	.25	134	714	36.8	44	4.3	93	200
0.95	.26	126	723	32.5	34	4.0	100	236
0.70	.28	108	1202+	47.0	26	2.0	110	195
0.80	.29	121	1202+	47.0	36	3.0	79	170
0.77	.29	137	1202+	51.0	41	3.0	64	226
0.83	.29	134	1202+	38.0	38	3.5	89	213
0.77	.25	102	1202+	48.2	36	3.5	56	154
0.80	.29	124	1202+	51.0	34	2.0	74	160
0.87	.28	150	1202+	48.2	41	3.5	74	220
0.67	.26	111	1202+	51.0	24	1.0	79	184
0.78	.28	123	1202+	47.7	34	2.7	78	190
0.87	.26	124	1202+	55.2	26	1.0	84	170
0.83	.25	124	1202+	38.0	19	3.5	147	245
0.87	.28	150	1202+	49.6	38	3.0	52	190
0.91	.25	127	1202+	52.4	36	3.5	79	184
0.91	.26	118	1202+	49.6	44	3.5	36	142
0.94	.23	98	1202+	36.8	30	4.3	52	120
0.83	.23	118	1202+	56.6	30	2.0	44	148
0.87	.23	111	1202+	45.5	30	3.0	44	160
0.88	.25	121	1202+	48.0	32	3.0	67	170

ı the range of determination by the spectrograph.

Table 40. Mineral concentration in the leaves of red oak seedlings from th

Soil	Nitrogen level Pounds per acre	Percent dry weight				
		N	P	K	Ca	
Lindley	0	1.80	.145	.46	1.18	.
(Forest)	30	1.88	.184	.52	1.10	.
	90	2.10	.193	.52	1.06	.
	180	2.52	.202	.42	1.31	.
	360	2.64	.264	.42	1.63	.
Shelby	0	1.56	.128	.56	1.02	.2
(Prairie)	30	1.86	.128	.52	1.10	.2
	90	2.26	.142	.48	1.14	.2
	180	2.50	.159	.48	1.22	.2
	360	2.52	.151	.58	1.06	.2
Clarksville	0	2.10	.193	.46	.87	.2
(Forest)	30	2.30	.254	.42	.91	.2
	90	2.66	.290	.42	1.14	.2
	180	2.78	.264	.40	1.49	.2
	360	2.78	.193	.44	.98	.2
Clarksville	0	1.56	.142	.54	1.02	.2
(Old field)	30	1.90	.227	.52	1.02	.2
	90	2.22	.193	.56	1.06	.2
	180	2.48	.245	.44	1.14	.2
	360	2.42	.235	.48	1.02	.2

[a]Manganese contents designated (+) were greater than the range of dete

gs from the nitrogen experiment, 1962

		Parts per million dry weight							
Ca	Mg	Fe	Mn[a]	B	Zn	Cu	Mo	Na	Al
.18	.26	95	920	56.6	34	8.4	5.2	56	58
.10	.23	121	595	40.4	30	6.0	4.6	22	86
.06	.23	85	659	38.0	26	3.5	4.8	69	54
.31	.20	108	1193+	29.5	30	7.6	5.4	93	66
.63	.23	111	1193+	29.5	30	5.0	6.7	64	72
.02	.25	104	972	35.6	22	5.0	5.0	64	72
.10	.28	121	712	28.3	38	5.0	4.6	98	102
.14	.26	102	1076	28.3	24	5.0	5.8	84	72
.22	.28	128	1193+	24.8	41	6.0	5.2	116	92
.06	.25	127	1193+	24.8	36	5.0	4.8	141	96
.87	.25	88	1193+	35.6	50	4.3	3.6	128	66
.91	.22	104	1193+	41.6	38	5.0	3.8	93	76
.14	.23	108	1193+	35.6	57	6.0	5.2	98	62
.49	.29	104	1193+	42.8	47	6.8	6.4	116	86
.98	.20	118	1193+	36.8	30	4.3	4.2	121	108
.02	.22	197	972	42.8	41	7.6	4.6	69	62
.02	.22	128	1193+	52.4	34	5.0	4.6	128	92
.06	.21	108	1193+	35.6	41	5.0	4.6	40	72
.14	.21	104	1193+	30.7	36	4.3	5.6	98	82
.02	.20	128	1193+	33.0	34	5.0	4.8	141	102

ge of determination by the spectrograph.

Table 41. Mineral concentration in the leaves of red oak seedlings from the nit

Soil	Nitrogen level Pounds per acre	Percent dry weight				
		N	P	K	Ca	Mg
Lindley	0	2.03	.227	.61	1.06	.26
(Forest)	30	1.84	.193	.66	1.02	.23
	90	2.02	.184	.67	1.02	.25
	180	1.54	.210	.60	1.18	.28
	360	1.96	.273	.54	1.06	.26
Shelby	0	1.51	.136	.61	.77	.28
(Prairie)	30	1.64	.151	.51	1.14	.30
	90	1.78	.184	.69	.91	.25
	180	1.57	.142	.57	1.02	.28
	360	1.37	.175	.51	.91	.28
Clarksville	0	1.68	.210	.60	.87	.28
(Forest)	30	1.66	.202	.61	.73	.25
	90	1.50	.227	.61	.67	.26
	180	1.64	.245	.61	.83	.29
	360	1.94	.202	.54	.77	.18
Clarksville	0	1.82	.273	.63	.83	.23
(Old field)	30	1.74	.264	.69	.80	.23
	90	1.58	.202	.60	.87	.23
	180	1.86	.218	.63	.73	.23
	360	1.52	.168	.54	.87	.18

[a]Manganese contents designated (+) were greater than the range of determinat

lings from the nitrogen experiment, 1953

ght		Parts per million dry weight						
Ca	Mg	Fe	Mn[a]	B	Zn	Cu	Na	Al
1.06	.26	85	1037	49.6	36	1.0	60	148
1.02	.23	114	1096	52.4	44	3.5	29	136
1.02	.25	91	1057	55.2	38	3.5	93	142
1.18	.28	102	1202+	55.2	34	2.0	52	120
1.06	.26	91	1202+	47.0	36	3.0	48	102
.77	.28	114	634	34.3	24	3.0	98	232
1.14	.30	118	667	33.0	34	3.0	48	148
.91	.25	134	714	36.8	44	4.3	93	200
1.02	.28	150	1070	35.6	36	4.3	60	148
.91	.28	91	1202+	27.2	47	1.0	32	120
.87	.28	150	1202+	48.2	41	3.5	74	220
.73	.25	118	1202+	48.2	50	6.0	69	154
.67	.26	111	1202+	51.0	24	1.0	79	184
.83	.29	85	1202+	42.8	34	2.0	44	130
.77	.18	108	1202+	38.0	36	3.0	60	114
.83	.23	118	1202+	56.6	30	2.0	44	148
.80	.23	121	1202+	47.0	38	5.0	98	160
.87	.23	111	1202+	45.5	30	3.0	44	160
.73	.23	91	1202+	40.4	24	1.0	52	148
.87	.18	111	1202+	40.4	26	3.5	84	148

ange of determination by the spectrograph.

Table 42. Mineral concentration in the leaves of red oak seedlings from the liming experi

Soil	Lime level tons/acre	Fertilizer	Percent dry weight				
			N	P	K	Ca	Mg
Lindley (Forest)	0	-	1.74	.142	.52	.94	.23
		N	2.34	.175	.42	1.14	.23
		NP	2.16	.218	.46	1.18	.26
		NPK	2.10	.193	.52	1.06	.23
	1	-	1.94	.142	.52	1.22	.22
		N	2.12	.142	.44	1.49	.22
		NP	2.10	.142	.44	1.06	.21
		NPK	2.00	.168	.56	1.28	.24
	2	-	2.02	.151	.44	1.22	.21
		N	2.22	.159	.46	1.49	.23
		NP	2.30	.168	.46	1.54	.25
		NPK	2.24	.168	.50	1.31	.23
Clarksville (Forest)	0	-	2.34	.175	.44	.98	.20
		N	2.54	.227	.44	1.06	.25
		NP	2.34	.264	.42	.98	.22
		NPK	2.66	.290	.42	1.14	.23
	1	-	2.22	.151	.48	1.31	.22
		N	2.38	.168	.44	1.49	.21
		NP	2.34	.168	.40	1.40	.21
		NPK	2.48	.175	.46	1.35	.23
	2	-	2.22	.136	.46	1.87	.21
		N	2.40	.159	.56	1.72	.20
		NP	2.38	.175	.48	1.72	.21
		NPK	2.44	.168	.48	1.49	.20

[a]Manganese contents designated (+) were greater than the range of determination by t

n the liming experiment, 1962

ight		Parts per million dry weight							
Ca	Mg	Fe	Mn[a]	B	Zn	Cu	Mo	Na	Al
.94	.23	95	568	41.6	26	6.8	4.8	22	62
1.14	.23	95	1076	38.0	34	7.6	5.6	29	49
1.18	.26	75	959	40.4	30	4.3	5.8	48	54
1.06	.23	85	659	38.0	26	3.5	4.8	60	54
1.22	.22	114	286	36.8	47	8.4	5.2	214	92
1.49	.22	114	314	38.0	50	6.8	6.4	110	86
1.06	.21	95	156	35.6	30	5.0	5.0	192	92
1.28	.24	112	170	42.6	48	5.0	6.4	121	80
1.22	.21	102	109	29.5	36	5.0	5.0	203	86
1.49	.23	127	167	28.3	50	7.6	7.3	171	120
1.54	.25	108	145	29.5	38	6.8	6.7	181	102
1.31	.23	102	94	24.8	44	7.6	5.6	310	114
.98	.20	95	1193+	41.6	57	6.0	4.4	89	76
1.06	.25	111	1193+	35.6	47	5.0	4.6	79	72
.98	.22	104	1193+	33.0	54	5.0	4.4	104	66
1.14	.23	91	1193+	35.6	57	6.0	5.2	98	62
1.31	.22	108	247	41.6	38	6.0	5.4	214	114
1.49	.21	127	396	45.5	47	7.6	6.2	147	114
1.40	.21	114	366	39.2	47	7.6	6.7	147	92
1.35	.23	98	354	35.6	38	6.8	5.8	147	92
1.87	.21	85	162	30.7	34	6.0	8.2	171	120
1.72	.20	104	156	29.5	44	8.4	7.1	214	120
1.72	.21	114	215	30.7	34	5.0	6.4	203	102
1.49	.20	91	162	33.0	38	6.8	6.7	235	86

determination by the spectrograph.

Table 43. Mineral concentration in the leaves of red oak seedlings from the liming ex

Soil	Lime level tons/acre	Fertilizer	Percent dry weight				
			N	P	K	Ca	Mg
Lindley (Forest)	0	-	1.80	.120	.60	1.10	.26
		N	1.96	.159	.63	1.02	.23
		NP	1.73	.210	.61	1.18	.30
		NPK	2.02	.184	.67	1.02	.25
	1	-	1.92	.136	.57	1.14	.26
		N	1.73	.112	.60	1.02	.23
		NP	2.06	.218	.61	1.18	.25
		NPK	1.86	.193	.58	1.14	.25
	2	-	1.91	.136	.60	1.14	.23
		N	1.92	.184	.60	1.14	.25
		NP	1.87	.168	.60	1.35	.28
		NPK	2.17	.193	.57	1.22	.25
Clarksville (Forest)	0	-	1.72	.159	.61	.70	.2
		N	1.75	.193	.60	.80	.2
		NP	1.68	.245	.58	.77	.2
		NPK	1.50	.227	.61	.67	.2
	1	-	1.46	.112	.63	.98	.2
		N	2.03	.159	.61	1.06	.2
		NP	1.78	.227	.55	1.06	.2
		NPK	1.86	.218	.66	.98	.2
	2	-	1.71	.128	.60	1.49	.2
		N	1.62	.105	.61	1.26	.2
		NP	1.82	.151	.60	1.26	.2
		NPK	1.84	.159	.66	1.31	.2

[a]Manganese contents designated (+) were greater than the range of determination

s from the liming experiment, 1963

ry weight			Parts per million dry weight						
K	Ca	Mg	Fe	Mn[a]	B	Zn	Cu	Na	Al
.60	1.10	.26	114	806	58.0	41	3.5	98	154
.63	1.02	.23	108	1123	56.6	41	3.0	93	148
.61	1.18	.30	134	1136	56.6	47	3.5	64	160
.67	1.02	.25	91	1057	55.2	38	3.5	93	142
.57	1.14	.26	114	314	39.2	54	5.0	60	130
.60	1.02	.23	85	263	36.8	41	4.3	44	120
.61	1.18	.25	102	384	45.5	44	3.5	52	120
.58	1.14	.25	121	390	39.2	50	5.0	69	130
.60	1.14	.23	108	129	24.8	38	4.3	56	108
.60	1.14	.25	108	172	23.6	41	5.0	52	120
.60	1.35	.28	98	182	27.2	36	3.5	52	108
.57	1.22	.25	130	151	28.3	47	6.0	48	108
.61	.70	.28	108	1202+	47.0	26	2.0	110	195
.60	.80	.29	121	1202+	47.0	36	3.0	79	170
.58	.77	.25	102	1202+	48.2	36	3.5	56	154
.61	.67	.26	111	1202+	51.0	24	1.0	79	184
.63	.98	.26	85	422	48.2	19	1.0	48	142
.61	1.06	.23	95	428	38.0	38	3.5	52	148
.55	1.06	.26	85	687	51.0	44	3.0	48	130
.66	.98	.25	111	536	51.0	50	5.0	56	120
.60	1.49	.22	108	247	34.3	34	2.0	44	125
.61	1.26	.20	91	167	36.8	34	3.5	52	108
.60	1.26	.22	98	193	34.3	36	3.5	52	114
.66	1.31	.25	85	162	33.0	30	3.5	60	108

ge of determination by the spectrograph.

Table 44. Mineral concentration in the leaves of red oak seedlings from the light intensi

Soil	Light intensity percent	Fertilizer	Percent dry weight				
			N	P	K	Ca	
Lindley (Forest)	10	-	2.38	.184	.68	1.31	
		NPK	2.56	.218	.72	1.31	
		N_4PK	2.70	.308	.52	1.26	
	30	-	2.32	.235	.46	1.10	
		NPK	2.10	.175	.48	1.22	
		N_4PK	2.48	.227	.46	1.31	
	100	-	1.88	.142	.52	.94	
		NPK	2.10	.193	.52	1.06	
		N_4PK	2.64	.264	.42	1.63	
Clarksville (Forest)	10	-	2.38	.245	.68	1.06	
		NPK	2.58	.282	.68	.83	
		N_4PK	2.72	.235	.56	.91	
	30	-	2.14	.168	.48	1.10	
		NPK	2.30	.227	.42	.83	
		N_4PK	2.60	.227	.38	.87	
	100	-	2.10	.175	.44	.98	
		NPK	2.66	.290	.42	1.14	
		N_4PK	2.78	.193	.44	.98	

[a]Manganese contents designated (+) were greater than the range of determination by t

e light intensity experiment, 1962

weight			Parts per million dry weight							
	Ca	Mg	Fe	Mn[a]	B	Zn	Cu	Mo	Na	Al
3	1.31	.31	197	985	62.4	38	6.8	5.4	64	136
2	1.31	.28	183	1193+	53.8	24	3.0	6.0	93	195
2	1.26	.22	218	1193+	68.0	24	4.3	5.4	134	200
5	1.10	.26	143	646	44.0	41	6.8	4.6	69	108
3	1.22	.26	153	842	34.3	36	4.3	5.6	98	136
5	1.31	.23	153	1193+	35.6	30	3.5	6.5	104	125
2	.94	.23	95	568	41.6	26	6.8	4.8	22	62
2	1.06	.23	85	659	38.0	26	3.5	4.8	69	54
2	1.63	.23	111	1193+	29.5	30	5.0	6.7	64	72
3	1.06	.34	160	1193+	61.0	26	6.0	5.0	74	130
8	.83	.21	204	1193+	66.6	22	3.0	3.8	84	184
6	.91	.20	214	1193+	62.4	19	6.0	4.2	93	190
8	1.10	.28	156	1193+	41.6	28	4.3	5.2	79	130
2	.83	.22	140	1193+	36.8	19	2.0	3.8	79	120
8	.87	.17	163	1193+	35.6	11	1.0	4.0	89	142
4	.98	.20	95	1193+	41.6	57	6.0	4.4	89	76
2	1.14	.23	108	1193+	35.6	57	6.0	5.2	98	62
4	.98	.20	118	1193+	36.8	30	4.3	4.2	121	108

ermination by the spectrograph.

Table 45. Mineral concentration in the leaves of red oak seedlings from the light inte

Soil	Light intensity percent	Fertilizer	Percent dry weight			
			N	P	K	Ca
Lindley (Forest)	10	-	2.24	.159	.90	1.22
		NPK	2.34	.175	1.03	1.18
		N_4PK	2.42	.210	.99	1.26
	30	-	1.92	.168	.66	1.22
		NPK	1.96	.290	.78	1.18
		N_4PK	2.04	.308	.73	1.26
	100	-	1.80	.120	.60	1.10
		NPK	2.02	.184	.67	1.02
		N_4PK	1.96	.273	.54	1.06
Clarksville (Forest)	10	-	2.27	.175	.64	1.02
		NPK	2.33	.210	.93	1.10
		N_4PK	2.58	.218	.94	.77
	30	-	2.05	.168	.66	.91
		NPK	1.73	.184	.81	.98
		N_4PK	2.12	.245	.66	1.06
	100	-	1.72	.159	.61	.70
		NPK	1.50	.227	.61	.67
		N_4PK	1.94	.202	.54	.77

[a]Manganese contents designated (+) were greater than the range of determination b

from the light intensity experiment, 1963

cent dry weight			Parts per million dry weight						
K	Ca	Mg	Fe	Mn[a]	B	Zn	Cu	Na	Al
.90	1.22	.31	437	1202+	63.8	57	7.6	310	688
1.03	1.18	.33	235	1116	56.6	47	4.3	84	434
.99	1.26	.31	313	1202+	62.4	64	3.0	110	508
.66	1.22	.29	259	885	44.0	57	6.8	160	390
.78	1.18	.30	232	964	51.0	44	5.0	56	252
.73	1.26	.31	262	1202+	49.6	47	5.0	79	350
.60	1.10	.26	114	806	58.0	41	3.5	98	154
.67	1.02	.25	91	1057	55.2	38	3.5	93	142
.54	1.06	.26	91	1202+	47.0	36	3.0	48	102
.64	1.02	.31	375	1202+	58.0	44	6.8	336	705
.93	1.10	.31	325	1202+	58.8	41	4.3	93	562
.94	.77	.23	298	1202+	62.4	38	7.6	89	562
.66	.91	.28	270	1202+	56.6	57	8.4	192	390
.81	.98	.31	218	1202+	47.0	41	6.0	89	307
.66	1.06	.30	224	1202+	45.5	47	2.0	79	307
.61	.70	.28	108	1202+	47.0	26	2.0	110	195
.61	.67	.26	111	1202+	51.0	24	1.0	79	184
.54	.77	.18	108	1202+	38.0	36	3.0	60	114

e of determination by the spectrograph.

Table 46. Mineral concentration in the leaves of red oak seedlings from the mycorhizae

Soil	Fertilizer	Soil treatment	Percent dry weight			
			N	P	K	Ca
Lindley (Forest)	-	Untreated	1.74	.142	.52	.94
		Sterilized	2.16	.159	.58	1.22
		+forest inoculum	2.66	.210	.70	1.31
	NPK	Untreated	2.10	.193	.52	1.06
		Sterilized	2.44	.202	.64	1.26
Shelby (Prairie)	-	Untreated	1.78	.084	.80	1.02
		+forest inoculum	2.04	.099	.67	1.06
		Sterilized	2.16	.151	.68	.98
		+forest inoculum	2.26	.128	.90	.91
		+prairie inoculum	2.12	.099	1.02	.87
	NPK	Untreated	2.26	.142	.48	1.14
		+forest inoculum	2.30	.151	.72	.94
		Sterilized	2.40	.151	.54	1.02
		+forest inoculum	2.70	.142	.75	1.02
Clarksville (Forest)	-	Untreated	2.34	.175	.44	.98
		Sterilized	2.16	.218	.58	.98
		+forest inoculum	2.28	.159	.75	.87
	NPK	Untreated	2.66	.227	.42	1.14
		Sterilized	2.48	.245	.56	1.14
Clarksville (Old field)	-	Untreated	2.06	.112	.70	1.02
		+forest inoculum	1.94	.092	.91	1.02
		Sterilized	2.08	.175	.46	.98
		+forest inoculum	2.47	.159	.58	1.02
		+old field inoculum	2.43	.175	.72	1.06
	NPK	Untreated	2.22	.193	.56	1.06
		+forest inoculum	2.49	.218	.66	.98
		Sterilized	2.28	.202	.62	.80
		+forest inoculum	2.71	.218	.64	.98

[a]Manganese contents designated (+) were greater than the range of determination by

from the mycorhizae experiment, 1962

cent dry weight			Parts per million dry weight							
K	Ca	Mg	Fe	Mn[a]	B	Zn	Cu	Mo	Na	Al
.52	.94	.23	95	568	41.6	26	6.8	4.8	22	62
.58	1.22	.26	124	1193+	36.8	26	3.0	5.6	147	96
.70	1.31	.23	114	1202+	34.3	50	3.5	-	134	102
.52	1.06	.23	85	659	38.0	26	3.5	4.8	69	54
.64	1.26	.23	114	1193+	33.0	34	3.0	5.6	203	86
.80	1.02	.29	114	848	29.5	19	4.3	4.6	74	72
.67	1.06	.25	137	1202+	33.0	30	3.0	-	110	142
.68	.98	.23	124	1193+	31.9	26	5.0	4.6	224	96
.90	.91	.22	137	1202+	29.5	34	3.0	-	224	108
1.02	.87	.23	176	1202+	28.3	30	2.0	-	110	120
.48	1.14	.26	102	1076	28.3	24	5.0	5.8	84	72
.72	.94	.29	130	1077	26.0	41	3.5	-	89	108
.54	1.02	.28	102	1193+	28.3	24	2.5	5.0	147	86
.75	1.02	.25	118	1202+	24.8	47	3.0	-	84	108
.44	.98	.20	95	1193+	41.6	57	6.0	4.4	89	76
.58	.98	.18	98	1193+	39.2	22	4.3	5.2	44	49
.75	.87	.20	98	1202+	31.9	34	1.0	-	93	92
.42	1.14	.23	108	1193+	35.6	57	6.0	5.2	98	62
.56	1.14	.26	108	1193+	44.0	22	2.0	5.6	60	54
.70	1.02	.21	95	1193+	39.2	36	4.3	4.0	89	66
.91	1.02	.22	104	1202+	34.3	30	2.0	-	89	125
.46	.98	.21	114	1193+	44.0	24	4.3	5.0	69	54
.58	1.02	.20	127	1202+	41.6	36	2.0	-	116	102
.72	1.06	.20	108	1202+	39.2	30	2.0	-	93	96
.56	1.06	.21	108	1193+	35.6	41	5.0	4.6	40	72
.66	.98	.21	118	1202+	34.3	38	2.0	-	98	108
.62	.80	.18	102	1193+	36.8	17	2.0	3.6	48	54
.64	.98	.21	121	1202+	36.8	38	1.0	-	89	96

e of determination by the spectrograph.

Table 47. Mineral concentration in the leaves of red oak seedlings from the mycc

Soil	Fertilizer	Soil treatment	Percent dry weight			
			N	P	K	
Lindley (Forest)	-	Untreated	1.80	.120	.60	1.
		Sterilized	1.82	.159	.63	1.
		+forest inoculum	2.08	.202	.54	1.
	NPK	Untreated	2.02	.184	.67	1.
		Sterilized	1.72	.175	.48	1.
Shelby (Prairie)	-	Untreated	1.92	.099	.55	
		+forest inoculum	1.94	.128	.54	
		Sterilized	1.73	.112	.57	1
		+forest inoculum	2.00	.159	.52	
		+prairie inoculum	1.66	.120	.60	1
	NPK	Untreated	1.78	.184	.69	
		+forest inoculum	1.68	.120	.48	1
		Sterilized	1.53	.142	.54	1
		+forest inoculum	1.49	.168	.51	1
Clarksville (Forest)	-	Untreated	1.72	.159	.61	
		Sterilized	1.56	.142	.57	
		+forest inoculum	1.98	.175	.54	
	NPK	Untreated	1.50	.227	.61	
		Sterilized	1.66	.184	.57	1
Clarksville (Old field)	-	Untreated	1.56	.142	.58	
		+forest inoculum	1.89	.105	.60	1
		Sterilized	1.77	.120	.51	
		+forest inoculum	1.40	.159	.55	
		+old field inoculum	1.74	.142	.63	
	NPK	Untreated	1.58	.202	.60	
		+forest inoculum	1.74	.235	.63	
		Sterilized	1.53	.145	.54	1
		+forest inoculum	1.60	.273	.51	

[a]Manganese contents designated (+) were greater than the range of determina

om the mycorhizae experiment, 1963

dry weight			Parts per million dry weight						
K	Ca	Mg	Fe	Mn[a]	B	Zn	Cu	Na	Al
.60	1.10	.26	114	806	58.0	41	3.5	98	154
.63	1.22	.28	134	1202+	51.0	47	5.0	154	154
.54	1.10	.26	137	1202+	63.8	44	3.5	121	160
.67	1.02	.25	91	1057	55.2	38	3.5	93	142
.48	1.32	.33	137	1202+	53.8	38	3.5	235	252
.55	.98	.26	134	687	27.2	26	2.0	89	226
.54	.94	.25	143	568	30.7	57	6.0	141	239
.57	1.02	.29	163	1202+	34.3	30	3.0	154	307
.52	.98	.30	176	1202+	30.7	34	5.0	154	265
.60	1.02	.28	197	1202+	41.6	60	6.8	154	226
.69	.91	.25	134	714	36.8	44	4.3	93	200
.48	1.06	.30	137	720	39.2	47	4.3	121	220
.54	1.06	.30	242	1202+	36.8	41	7.6	141	252
.51	1.54	.35	197	1202+	44.0	47	5.0	224	258
.61	.70	.28	108	1202+	47.0	26	2.0	110	195
.57	.80	.25	150	1202+	44.0	28	3.5	147	265
.54	.87	.23	160	1202+	51.0	57	9.3	104	184
.61	.67	.26	111	1202+	51.0	24	1.0	79	184
.57	1.18	.33	160	1202+	45.5	34	3.0	134	220
.58	.87	.26	124	1202+	55.2	26	1.0	84	170
.60	1.06	.26	153	1202+	45.5	50	6.0	224	265
.51	.91	.28	140	1202+	38.0	34	3.5	171	195
.55	.83	.26	137	1202+	52.4	28	4.3	154	300
.63	.87	.25	114	1202+	42.8	26	4.3	128	200
.60	.87	.23	111	1202+	45.5	30	3.0	44	160
.63	.83	.22	137	1202+	56.6	47	5.0	104	190
.54	1.18	.25	156	1202+	52.4	28	3.0	121	206
.51	.94	.29	146	1202+	56.6	30	3.5	181	226

f determination by the spectrograph.

Table 48. Mineral concentration in the leaves of red oak, black walnut, and gr

Soil	Species	Fertilizer	Percent dry weight			
			N	P	K	
Lindley (Forest)	Red oak	-	1.80	.120	.60	1
		NPK	2.02	.184	.67	1
	Black walnut	-	1.88	.159	.64	1
		NPK	1.94	.193	.75	1
	Green ash	-	1.74	.264	1.05	1
		NPK	2.24	.540	1.05	1
Shelby (Prairie)	Red oak	-	1.92	.099	.55	
		NPK	1.78	.184	.69	
	Black walnut	-	2.00	.175	.64	1
		NPK	1.78	.128	.73	1
	Green ash	-	2.58	.168	1.03	1
		NPK	2.16	.344	.90	
Clarksville (Forest)	Red oak	-	1.72	.159	.61	
		NPK	1.50	.227	.61	
	Black walnut	-	2.21	.120	.73	1
		NPK	2.00	.159	.70	1
	Green ash	-	2.29	.193	1.20	
		NPK	2.21	.401	1.23	
Clarksville (Old field)	Red oak	-	1.56	.142	.58	
		NPK	1.58	.202	.60	
	Black walnut	-	2.06	.120	.97	1
		NPK	2.09	.151	.90	1
	Green ash	-	2.48	.136	1.17	
		NPK	2.00	.571	1.50	

[a]Manganese contents designated (+) were greater than the range of determi

reen ash seedlings from the species experiment, 1963

t		Parts per million dry weight						
Ca	Mg	Fe	Mn[a]	B	Zn	Cu	Na	Al
1.10	.26	114	806	58.0	41	3.5	98	154
1.02	.25	91	1057	55.2	38	3.5	93	142
1.54	.38	183	215	58.0	54	9.3	134	232
1.58	.34	166	215	52.4	38	8.4	224	245
1.06	.28	137	85	17.9	26	9.3	128	154
1.02	.29	150	67	23.6	47	6.8	171	184
.98	.26	134	687	27.2	26	2.0	89	226
.91	.25	134	714	36.8	44	4.3	93	200
1.40	.30	214	242	55.2	54	16.6	224	404
1.40	.33	224	280	44.0	47	10.2	245	419
1.06	.25	284	76	23.6	47	36.0	288	570
.94	.35	222	71	22.5	38	20.3	160	322
.70	.28	108	1202+	47.0	26	2.0	110	195
.67	.26	111	1202+	51.0	24	1.0	79	184
1.14	.29	114	634	51.0	34	3.0	84	170
1.49	.35	156	556	59.6	41	4.3	134	213
.83	.22	134	76	17.9	28	4.3	74	142
.98	.25	153	104	23.6	50	6.8	89	160
.87	.26	124	1202+	55.2	26	1.0	84	170
.87	.23	111	1202+	45.5	30	3.0	44	160
1.35	.29	137	337	55.2	44	5.0	89	170
1.35	.29	156	452	53.8	44	6.8	192	213
.94	.25	137	63	23.6	38	17.6	110	154
.91	.25	124	76	23.6	41	32.0	89	125

ination by the spectrograph.