THE BLACK ROCK FOREST

BULLETIN NO. 11

HENRY H. TRYON, *Director*

THE NITROGEN NUTRITION AND GROWTH OF CERTAIN DECIDUOUS TREES OF NORTHEASTERN UNITED STATES

With a Discussion of the Principles and Practice of Leaf Analysis as Applied to Forest Trees

By
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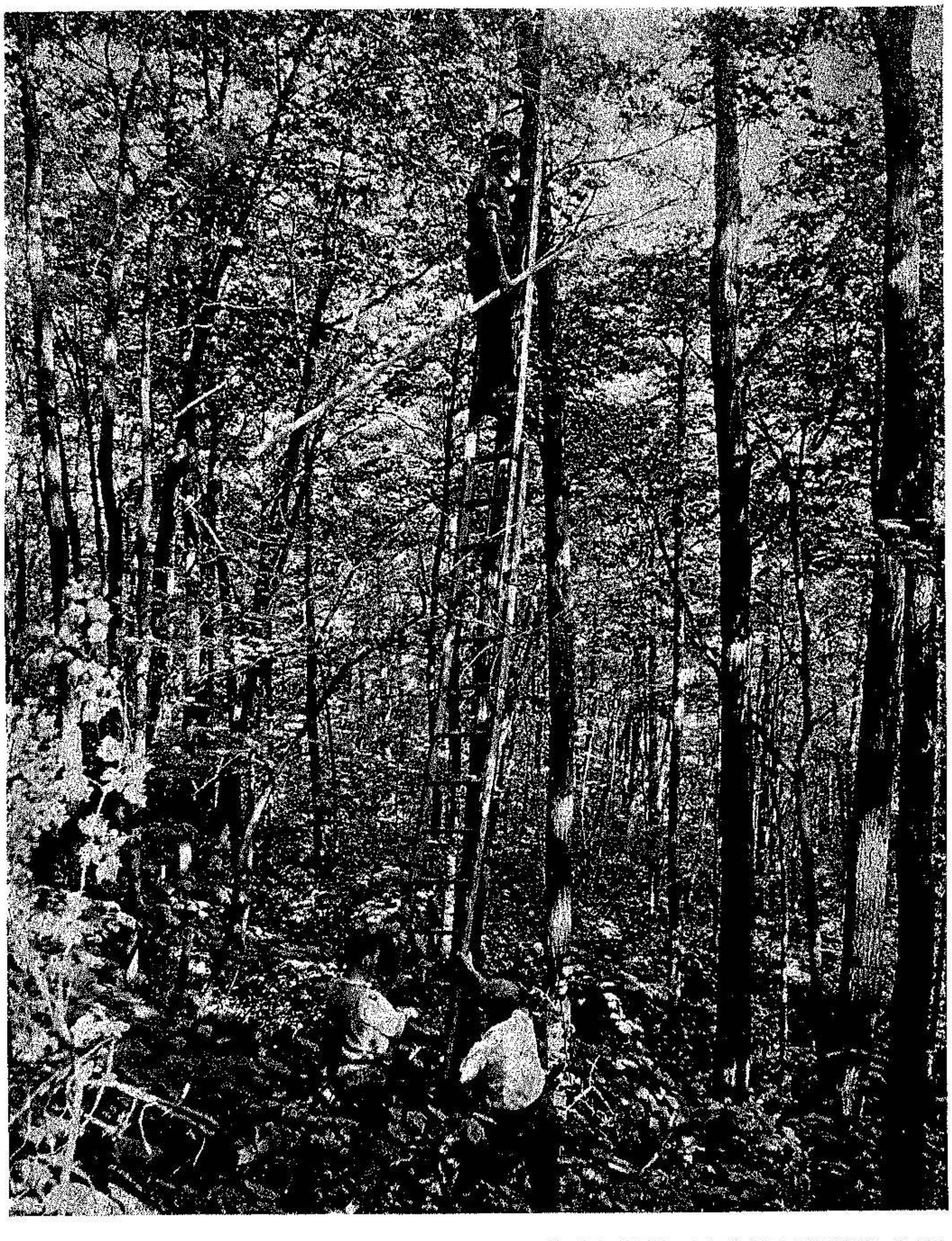

COLLECTING LEAF SAMPLES FROM TREES OF RED OAK-CHESTNUT OAK STAND ON THE BLACK ROCK FOREST

Photo by Hugh M. Raup.

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FOREWORD

About 30 years ago Dr. Fernow defined silviculture as "the tending of woods." A broad definition, concealing beneath its simple exterior a mass of detail then quite unperceived by the majority of American foresters. To many foresters at the outset of their professional careers, applied silviculture seemed to offer interesting but comparatively easy sailing. Until about 1918, I think that many were imbued with the idea of adapting some form of foreign practice (usually German) to our American conditions. But they met with a number of rude awakenings. Variations in soil and climate made plans go awry; the effect of previous, unappreciated, abusive exploitation and fires served further to disarrange their concepts; the problems attendant upon maintaining the local factors were encountered; while perhaps the most puzzling of all was the great array of commercial species growing "higgledy-piggledy," in pure stands, in mixed stands, groupwise and stemwise, and presenting a disturbingly varied assortment of silvical requirements.

Some 40 years of silvicultural growing pains have passed. Mistakes have been made, but in general I think much distinct achievement appears on the record. It has been most interesting to watch the growth in breadth of outlook and of silvicultural concept which began to develop following Dr. Hesselman's visit here in the early '20's. It is my impression that only about then did foresters really begin to think of applied silviculture in terms of accurate site classification, factors of locality and of ecologic influences. It has been a healthy growth, and it must not be permitted to slacken.

The study covered in this Bulletin arose directly out of the complicated mixed hardwood stands in this region. We had made a number of carefully planned improvement cuttings of various types. Nearly all resulted in some natural regeneration. But in some cases where the soil sites appeared to be nearly identical there were sharp and unaccountable variations both in reproduction survival and in the subsequent increment of our principal commercial species. We naturally sought the answer. A searching examination of the gross factors involved shed but little light on these varying responses. So we turned to the laboratory with the hope of working out some sort of ''site indicator yardstick,'' using the technique of leaf-analysis which we had developed in pot-cultures in our nursery, and later in the Forest. We believe that the results, tentative though they may be, are stimulating.

This project was planned and started on the Black Rock Forest in the spring of 1935. In 1936 we enlisted the interest of Professor R. F. Chandler Jr. of Cornell University. Since certain species in which we were interested were infrequent in Black Rock Forest, we obtained the cooperation of both Professor Chandler and various state and federal forest service representatives in the Northeast. This arrangement resulted in a far more complete study, for neither our data, nor that derived from the various cooperating agencies will stand alone. Together they make a substantial and interesting array.

The study, while opening a somewhat new and stimulating field, is far from complete. If the results set forth be found to withstand the acid test of large-scale, practical field trials, their effect upon silvicultural practice may be marked. To take one example; it has been growing more and more evident that in our local old-field successions the usual transitory associations appear to be quite necessary for the proper growth and development of the subsequent permanent type. Analyses made here indicate that these preliminary weed stages are essential to insure adequate advance preparation of the soils for the support of the more valuable final species associations which are, according to our findings, usually less "efficient" feeders than are their weed predecessors. In my recent trip through Germany I found such recognition of the soil-improving value of the weed successions to be common knowledge. I was shown, in fact, a number of interesting areas where comparatively expensive effort had been made to encourage these successions, even to the extent of making advance plantings of weed trees, to be followed after a few years by underplanting with the commercial species selected for the final crop.

While the preliminary findings presented in this bulletin have added a little to our silvicultural knowledge, they make the date of thorough comprehension of silviculture even more distant. If we are to complete the project started here, we are faced with the necessity of knowing the "feeding habits" and the comparative "feeding efficiency" of nearly all of the 42 arborescent species common to this Forest. But should extensive applied use of leaf analysis substantiate the findings presented herein, we feel the work should be undertaken, for we are convinced that successful forest management should be based on distinctly broader and more accurate knowledge than we now possess.

It is my personal opinion that the management systems applied to some of our American forests are not given sufficient advance study. There seems to be too much hurried marking for cuttings of various sorts without adequate advance study of the local ecologic factors. Owing to our numerous species, we are faced with a far more complicated picture than are the foresters in Germany, Denmark, or the North Cape countries where, at the most, only 5 to 8 species are commonly found. There also, economic conditions warrant the application of many more man-hours of cultural work than our market conditions will now permit. So it would seem that we should make every effort to develop the habit of thinking along much broader lines. The older men in the profession, and especially the teachers in our forest schools should lead the way. Let us consider more and more the history of a stand of timber. What are the ecologic, edaphic and biologic reasons for its presence and condition? Knowing these, we can then plan our silviculture in sound fashion.

HENRY H. TRYON,
Director.

INTRODUCTION

Because of the intricate interdependence of various environmental factors, it is extremely difficult properly to evaluate the soil factors which influence the growth and distribution of forest tree species. In most cases no one factor limits growth, and a favorable change in any one of several soil constituents increases the growth rate.

The influence of soil nitrogen supply upon the nitrogen content of the leaves and the growth of certain deciduous forest trees of the northeastern United States was considered in the study here reported. Quarter-acre plots were established in stands of mixed hardwoods on various forest sites, and nitrogenous fertilizers were applied in different amounts. For a given series of plots on relatively uniform soil, any differences in the growth rate or the chemical composition of the leaves may be attributed largely to changes in soil nitrogen supply resulting from fertilization.

Significant data on the nitrogen requirements of the species studied were obtained by determining the nitrogen content of the leaves and by measuring the increase in diameter of trees receiving varying amounts of nitrogen fertilizer. Definite and reproducible relationships were established between soil nitrogen supply, the concentration of this element in the foliage, and tree growth. These relationships can be expressed with the Mitscherlich equation. Evidence is presented to show that tree growth is highly correlated with the internal (leaf) nitrogen concentration, which is a function of the external (soil) supply. The experimentally determined relationship between nitrogen supply and the concentration of this element in the foliage provides an apparently reliable basis for estimating the relative nitrogen-supplying capacity of sites of unknown fertility. The experimental data here reported are offered as a tentative standard of comparison for use in evaluating soil nitrogen supply by the method of leaf analysis.

By presenting this report on nitrogen, the writers in no way imply that this element is the only important soil productivity factor. Any one of the essential elements can, of course, limit growth. The physical properties of the soil, including water relations, are very important and should receive as much attention as any chemical factors. The nitrogen problem was first studied because evidence was at hand to indicate the existence of a nitrogen deficiency in many forest soils of New York, Pennsylvania and the southern New England States. It is hoped that the data here reported will lead to a complete investigation of all essential nutrient elements.

METHODS

SERIES of from three to six sample plots were established in stands of mixed hardwoods on each of six different sites. Four series of plots (the *N, ON, AN* and *BN* Series) were located on or near the Black Rock Forest, and two (the *CN* and *DN* Series) on the Arnot Forest. All trees on each plot over 2 inches d. b. h. were numbered with white paint or aluminum tags and measured for diameter previous to treatment. The basal area, in square feet per acre, was summed for each plot. Ring counts and height measurements were made to determine the average age and height of trees in the dominant crown class.

One plot of each series served as a control, and the others were supplied varying amounts of nitrogenous fertilizer. All fertilized plots were one-quarter acre in area. The control plots varied in size. The majority exceeded one-quarter acre, since every effort was made to include on the check plot an adequate number (10 if possible) of trees of each species represented on the fertilized plots of the series.

All fertilizer treatments were made between April 20 and May 14. Except for the *ON* Series plots, which received varying amounts of dried blood, the source of nitrogen used throughout the experiment consisted of an equal mixture (by weight) of commercial nitrate of soda and sulphate of ammonia. This material was broadcast by hand. Being readily soluble, it was carried into the soil with the first heavy rain. An even distribution of the fertilizer was obtained by gridironing the plots with chalkline, and by increasing the bulk of light applications with equal parts of sawdust.

Near the end of the same growing season in which the fertilizer was applied, leaf samples, for chemical analysis, were taken from dominant and codominant trees on each plot. Since the chemical composition of leaves is influenced to some extent by many factors other than soil nutrient supply, the collection of samples was standardized according to the technique described in detail in a previous report (Mitchell, 1936). From 10 to 50 leaves were picked from one or more branches located near the top of the crown and on the south side of each tree. All collections were made between 9 A.M. and 3 P.M. Because leaves with insect galls and those formed late in the growing season as a result of defoliation by insects are known to be abnormal chemically (Mitchell, unpublished data), they were discarded. Those formed late in the season can be distinguished from the older "spring" leaves on the basis of color, the older leaves being a darker green. Samples were taken only during that three to four week period just previous to yellowing, when leaf size and chemical composition are relatively constant. Leaves at this physiological stage are referred to in the present report as "physiologically mature." The fresh samples were placed in kraft paper bags, in which they were subsequently air dried.

For trees up to 40 feet in height, a five-man crew equipped with two ladders and two extension pruners can sample as many as 200 trees in from four to six hours. With taller trees, however, it is usually simpler, faster and cheaper to shoot off the desired branches with a 12-gauge shotgun loaded with buckshot.

After removing the petioles, each sample of air-dried leaves was ground in a Wiley mill, placed in a labeled glassine envelope, and then dried at +70° C. in an electric oven. Chemical analyses of the ground samples were made according to methods previously described (Mitchell, 1934, '36).

The radial growth of dominant and codominant trees on each plot was determined by means of increment borings. In the majority of cases three separate borings (from different sides of the bole) were made of each tree, and the mean of three measurements taken as the radial increment of the tree for any given year.

Data regarding the location of the various series of plots, plot series designations, and the dates of fertilization, leaf sample collection and radial increment measurement are summarized in Table A.

TABLE A

SERIES DESIGNATION, LOCATION OF PLOTS, AND DATES OF FERTILIZATION, LEAF SAMPLE COLLECTION AND RADIAL INCREMENT MEASUREMENT

Plot Series Designation	*Place*	*Fertilization Date*	*Foliage Sampling Date*	*Radial Increment Measurements Taken*	
				For Growing Season of	*For Years Following Fertilization*
(1)	*(2)*	*(3)*	*(4)*	*(5)*	*(6)*
N	Black Rock Forest	May 14, 1935	Sept. 1-5, 1935	1936	1
ON	" " "	May 6, 1936	Aug. 31, 1936	1937	1
AN	" " "	May 5, 1937	Sept. 1-2, 1937	1937	0
BN	" " "	May 6, 1937	Aug. 30, 1937	1937	0
CN	Arnot Forest	April 20-21, 1936	Sept. 16-18, 1936	1937	1
DN	" "	April 24-31, 1937	Sept. 12-15, 1937	1938	1

DESCRIPTION OF PLOTS

Black Rock Forest Plots

N Series Plots—The *N* Series plots were established in the spring of 1935. They are located within the boundaries of the Black Rock Forest, on a gentle eastern slope of Black Rock, and at an elevation of about 1100 feet above sea level (see map, Raup, 1938). The Gray-Brown Podzolic soil of this site is a stony clay loam. It derived from a shallow glacial till composed mostly of crystalline rocks, including granite, gneiss, schist, metamorphosed limestone and associated intrusives.[1] That the rate of incorporation of organic matter into the mineral soil is rather rapid is evidenced by the absence of more than one year's accumulation of leaf litter. There is essentially no F-layer (Romell and Heiberg, 1931). The humus layer may be classed as a coarse mull (Heiberg, 1937), and is about 4 inches deep.

Red oak and chestnut oak are the primary elements of the stand in which these plots are located, with white oak, sugar maple, red maple, white ash, pignut hickory and black gum as secondary species.[2] The stand is largely of sprout origin, and may be classed as even-aged. Trees in the dominant crown class average 47 years in age and 47 feet in height. Basal area figures and other basic data for these plots are summarized in Table 2.

ON Series Plots.—The *ON* Series plots, also within the boundaries of the Forest, were established in the spring of 1936. They are located at an elevation of about

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[1] For a discussion of the glacial geology and the physical properties of the cove soils of the Black Rock Forest, the reader is referred to Denny (1938) and Scholz (1931).

[2] Scientific equivalents of all common names used in the above discussion and elsewhere in this report are given in Table 1.

850 feet on a gentle northerly slope of Frog Hill. So far as structure, texture and color are concerned, the surface soil of this site is essentially the same as that on which the *N* Series plots are located. However, the mull horizon is deeper (6 inches thick), possibly because of the nature of the parent material, which is somewhat different from that of the *N* Series site. This soil, like that on

TABLE 1

List of Tree Species Mentioned

Scientific Name	Common Name
Acer rubrum L.	Red Maple
Acer saccharum Marsh.	Sugar Maple
Betula lenta L.	Black Birch
Betula lutea Michx.	Yellow Birch
Betula papyrifera Marsh.	Paper Birch
Betula populifolia Marsh.	Gray Birch
Fagus grandifolia Ehrh.	Beech
Fraxinus americana L.	White Ash
Hicoria glabra (Mill.) Sweet	Pignut Hickory
Hicoria ovata (Mill.) Britton	Shagbark Hickory
Liriodendron tulipifera L.	Yellow Poplar
Nyssa sylvatica Marsh.	Black Gum
Ostrya virginiana (Mill.) Koch	Ironwood (Hornbeam)
Populus grandidentata Michx.	Large-Toothed Aspen
Populus tremuloides Michx.	Trembling Aspen
Quercus alba L.	White Oak
Quercus borealis Michx.	Red Oak
Quercus coccinea Muench.	Scarlet Oak
Quercus montana Willd.	Chestnut Oak
Quercus palustris Muench.	Pin Oak
Quercus rubra L.	Spanish Oak
Quercus stellata Wang.	Post Oak
Quercus velutina Lam.	Black Oak
Tilia americana L.	White Ash

many of the other lower northern slopes, derived from glacial deposits which are thicker and contain a higher proportion of softer rocks—sandstone and shale—than those found elsewhere on the Forest (Denny, 1938). Moisture conditions are more favorable in the deeper glacial till soils.

The forest stand, which is largely of sprout origin, is even-aged. Red oak, red maple and sugar maple are the primary species, with an admixture of white ash, white oak, chestnut oak, pignut hickory, black gum, basswood and yellow poplar. Trees in the dominant crown class average 59 feet in height at 59 years of age. Basal area figures and other basic data for these plots are entered in Table 3.

AN Series Plots.—These plots were established in the spring of 1937. They are located about two miles west of the Black Rock Forest on a northwesterly exposure of a western spur of the Hudson Highlands. The elevation is approximately 600 feet above sea level. The Gray-Brown Podzolic soil of this site is a stony clay loam. It derived from a glacial till which contains a greater proportion of sandstone and shale than is common on the Forest, where crystalline rocks predominate. The humus layer, which is about 8 inches deep, may be classed as a coarse mull. As with the soils of the other sites, the F-layer is almost entirely absent.

The forest stand is essentially even-aged, contains many trees of seedling origin and consists largely of red oak, white ash and yellow poplar, with sugar maple, white oak and basswood as secondary species. The presence of stone walls and dead and dying red cedars suggests that this stand is a phase (probably temporary) of the forest succession which has been noted by Raup (1938, p. 67) on certain abandoned agricultural lands of the region.

Trees of the dominant crown class average 71 feet in height and 57 years of age. The greater rate of height growth for trees on this site indicates that the site is considerably better than those on which the *N* and *ON* Series plots are located. Basal area figures and other basic data for the *AN* Series plots are entered in Table 4.

BN Series Plots.—The *BN* Series plots were also established in the spring of 1937. They are located about one and a half miles north of the Black Rock Forest on a gentle westerly slope of Round Top. The elevation is approximately 400 feet. So far as depth and physical properties are concerned, the soil of this site is almost identical with that of the *AN* Series plots.

The forest stand is even-aged. It originated from seedlings which invaded an abandoned field which had once been under cultivation. An adjacent field is at present seeding in to the same species, which include sugar maple, white ash and pignut hickory. Trees of the dominant crown class average 65 feet in height at 40 years of age. This site, like that on which the *AN* Series plots are located, is considerably better than the sites where the *N* and *ON* Series plots were established. Basal area figures and other basic data on the *BN* Series plots are summarized in Table 5.

ARNOT FOREST PLOTS

CN Series.—These plots were established in the spring of 1936. They are located on the Arnot Forest in southeastern Schuyler County, New York, at an elevation of about 1600 feet above sea level. The Gray-Brown Podzolic soil of this site is a Lordstown stony silt loam, which is a relatively shallow glacial till soil originating from acid shales and sandstones. The pH of both the surface soil and the subsoil average about 5.0. The humus layer type is a root mor (Romell and Heiberg, 1931) with an F-layer not over 0.5 inch in thickness and an H-layer about 1 to 2 inches in thickness.

The forest stand is essentially even-aged and consists

TABLE 2

THE NITROGEN CONTENT OF THE LEAVES AND THE ANNUAL RADIAL INCREMENT OF FOREST TREES GROWING ON PLOTS SUPPLIED VARYING AMOUNTS OF NITROGEN

N Series Plots, Black Rock Forest[1]

Plot Number	N-0			N-1			N-2			N-3		
Basal Area (sq. ft. per A.)[2]	56.0			57.3			68.3			65.5		
N Mix Applied (lbs. per A.)[3]	None			1600			3200			4800		
Nitrogen Applied (lbs. per A.)	None			288			576			864		
Relative N Supply (lbs. per A.)[4]	$x + 15$			$x + 303$			$x + 591$			$x + 879$		
Species	*No.*[5]	*N% of Leaves*[6]	*Radial Increment (mm.)*[7]	*No.*[5]	*N% of Leaves*[6]	*Radial Increment (mm.)*[7]	*No.*[5]	*N% of Leaves*[6]	*Radial Increment (mm.)*[7]	*No.*[5]	*N% of Leaves*[6]	*Radial Increment (mm.)*[7]
(1)	*(2)*	*(3)*	*(4)*	*(5)*	*(6)*	*(7)*	*(8)*	*(9)*	*(10)*	*(11)*	*(12)*	*(13)*
Red Oak	*23*	**1.73±.04**[8]	1.15±.10[8]	*15*	**2.49±.06**[8]	2.31±.16[8]	*19*	**2.61±.04**[8]	2.11±.14[8]	*13*	**2.77±.08**[8]	2.30±.21[8]
White Oak	*14*	**1.96±.07**	1.42±.19	*2*	**2.65** ..	2.30 ..	*7*	**2.89±.11**	2.30±.19	*1*	**2.92** ..	2.36 ..
Chestnut Oak	*14*	**2.04±.04**	1.40±.18	*2*	**2.75** ..	2.40 ..	*12*	**2.83±.06**	2.14±.18	*11*	**2.85±.05**	2.40±.18
Sugar Maple	*6*	**1.55±.05**	1.24±.10	*5*	**2.75±.08**	2.72±.34	*4*	**2.98±.11**	2.60±.31	..	... ..	... ..
Red Maple	*8*	**1.60±.04**	1.12±.18	*1*	**2.62** ..	2.06 ..	*1*	**2.81** ..	2.12 ..	*12*	**2.81** ..	2.06±.19
White Ash	*9*	**1.53±.05**	0.71±.17	*3*	**2.58±.09**	2.65±.40	*2*	**2.87** ..	3.00 ..	*2*	**2.98** ..	3.16±.96
Pignut Hickory	*8*	**1.60±.06**	1.10±.09	*1*	**2.25** ..	... ..	..	... ..	... ..	*1*	**2.43** ..	2.33 ..
Black Gum	*6*	**1.61±.05**	1.40±.41	..	... ..	... ..	*2*	**2.88** ..	2.55 ..	*5*	**3.03±.26**	2.45±.42

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[1] A description of the stand in which these plots are located is given in the text of this report. The plots were fertilized May 14, 1935, and leaf samples were collected September 1-5 of the same year.

[2] Basal area is the cross-sectional area of a stand, in square feet, measured at 4.5 feet from the ground.

[3] N mix is an equal mixture (by weight) of commercial nitrate of soda and sulphate of ammonia. This mixture analyzes 18% water-soluble nitrogen, as is indicated by the data presented in horizontal column 4.

[4] The values entered in horizontal column 5 are estimates of available nitrogen supply in relation to that of the soil on the poorest site studied (see Fig. 1 and discussion). Data from plots on all sites are coordinated on this basis.

[5] The number of trees of a given species from which increment cores were taken for measurement and leaf samples for analysis.

[6] $N_{\%}$ is the symbol used to denote the nitrogen content of leaves expressed as percent dry weight. The $N_{\%}$ values entered in the above table are averages based upon the results of analyses of leaf samples from *individual* trees.

[7] The radial increment data are for 1936, the growing season following the year the fertilizer was applied.

[8] Standard error of the mean.

TABLE 3

THE NITROGEN CONTENT OF THE LEAVES AND THE ANNUAL RADIAL INCREMENT OF FOREST TREES GROWING ON PLOTS SUPPLIED VARYING AMOUNTS OF NITROGEN

O N Series Plots, Black Rock Forest[1]

Plot Number	ON-0			ON-1			ON-2			ON-3		
Basal Area (sq. ft. per A.)[2]	76.5			73.7			76.9			78.9		
Dried Blood Applied (lbs. per A.)	none			1600			3200			4800		
Available N Applied (lbs. per A.)[3]	none			60			120			180		
Relative N Supply (lbs. per A.)[4]	$x + 0$			$x + 60$			$x + 120$			$x + 180$		
Species	*No.*[5]	*$N_{\%}$ of Leaves*[6]	*Radial Increment (mm.)*[7]	*No.*[5]	*$N_{\%}$ of Leaves*[6]	*Radial Increment (mm.)*[7]	*No.*[5]	*$N_{\%}$ of Leaves*[6]	*Radial Increment (mm.)*[7]	*No.*[5]	*$N_{\%}$ of Leaves*[6]	*Radial Increment (mm.)*[7]
(1)	*(2)*	*(3)*	*(4)*	*(5)*	*(6)*	*(7)*	*(8)*	*(9)*	*(10)*	*(11)*	*(12)*	*(13)*
Red Oak	*13*	**1.66±.04**[8]	1.33±.12[8]	*11*	**1.93±.07**[8]	2.21±.32[8]	*15*	**2.07±.03**[8]	2.60±.23[8]	*17*	**2.75±.05**[8]	2.65±.15[8]
White Oak	*9*	**2.00±.03**	1.35±.20	*6*	**2.13±.07**	1.95±.16	*1*	**2.69** . .	2.41 . .	*3*	**2.67±.09**	2.55±.19
Chestnut Oak	*6*	**1.99±.07**	1.52±.24	*1*	**2.24** . .	2.20 . .	*2*	**2.34** . .	2.52 . .	. .	. . . . .	. . . . .
Sugar Maple	*11*	**1.38±.04**	1.07±.12	*8*	**1.91±.17**	1.50±.30	*8*	**2.20±.08**	2.10±.25	*11*	**2.35±.07**	2.60±.32
Red Maple	*7*	**1.38±.04**	1.21±.15	*19*	**1.70±.15**	1.47±.27	*19*	**2.00±.12**	1.80±.19	*8*	**2.14±.07**	2.06±.46
White Ash	*8*	**1.74±.05**	1.30±.26	*10*	**1.90±.05**	1.60±.17	*13*	**2.19±.09**	2.47±.07	*18*	**2.44±.03**	3.17±.03
Pignut Hickory	*11*	**1.53±.05**	1.20±.19	*2*	**1.82** . .	1.61 . .	*5*	**1.78±.04**	1.85±.20	*4*	**2.11±.09**	2.10±.43
Black Gum	*6*	**1.55±.06**	1.12±.17	*7*	**1.92±.07**	1.25±.47	*9*	**2.01±.09**	1.44+.28	*4*	**2.39±.08**	1.87±.37
Basswood	*5*	**2.03±.11**	. . . . .	*4*	**2.51±.14**	. . . . .	*3*	**2.80±.06**	. . . . .	*4*	**2.87±.14**	. . . . .
Yellow Poplar	*10*	**1.70±.03**	1.52±.25	*3*	**2.01±.12**	2.12±.27	*7*	**2.46±.09**	3.30±.42	*3*	**2.69±.23**	3.58±.46

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[1] A description of the stand in which these plots are located is given in the text of this report. The plots were fertilized May 6, 1936, and leaf samples were collected August 31 of the same year.

[2] Basal area is the cross-sectional area of a stand, in square feet, measured at 4.5 feet from the ground.

[3] The dried blood used analyzed 12% *total* nitrogen, or 192 lbs. total N per 1600 lbs. of dried blood. However, under conditions of the present experiment, only 31% of the N contained in this organic compound proved to be readily available—that is, 60 lbs. readily available N per 1600 lbs. of dried blood (see Fig. 1).

[4] Data from plots on the various sites studied are coordinated on the basis of "relative N supply," which is the estimated available N supply of any given soil in relation to that of the soil on the poorest site. Since the *ON* Series plots are located on the poorest soil, the values entered in horizontal columns 4 and 5 of the above table are identical.

[5] The number of trees of a given species from which increment cores were taken for measurement and leaf samples for analysis.

[6] $N_{\%}$ is the symbol used to denote the nitrogen content of leaves expressed as percent dry weight. The $N_{\%}$ values entered in the above table are averages based upon the results of analyses of leaf samples from *individual* trees.

[7] The radial increment data are for 1937, the growing season following the year the fertilizer was applied.

[8] Standard error of the mean.

TABLE 4

THE NITROGEN CONTENT OF THE LEAVES AND THE ANNUAL RADIAL INCREMENT OF FOREST TREES GROWING ON PLOTS SUPPLIED VARYING AMOUNTS OF NITROGEN

A N Series Plots, Black Rock Forest [1]

Plot Number	AN-0			AN-1			AN-2		
Basal Area (sq. ft. per A.)[2]	99.4			103.8			95.1		
N Mix Applied (lbs. per A.)[3]	none			1600			3200		
Nitrogen Applied (lbs. per A.)	none			288			576		
Relative N Supply (lbs. per A.)[4]	*x* + **167**			*x* + **455**			*x* + **743**		
Species	*No.*[5]	*N% of Leaves*[6]	*Radial Increment (mm.)*[7]	*No.*[5]	*N% of Leaves*[6]	*Radial Increment (mm.)*[7]	*No.*[5]	*N% of Leaves*[6]	*Radial Increment (mm.)*[7]
(1)	*(2)*	*(3)*	*(4)*	*(5)*	*(6)*	*(7)*	*(8)*	*(9)*	*(10)*
Red Oak	*13*	**2.22**±.06[8]	1.69±.19[8]	*11*	**2.61**±.06[8]	2.02±.24[8]	*17*	**2.71**±.09[8]	2.07±.25[8]
Sugar Maple	*4*	**2.09**±.09	0.82±.10	*4*	**2.78**±.07	1.06±.08	*6*	**2.81**±.07	1.18±.17
White Ash	*6*	**2.13**±.05	0.94±.11	*10*	**2.53**±.06	1.18±.16	*7*	**2.91**±.24	1.34±.21
Basswood	*3*	**2.46**±.10	... ..	*1*	**2.88** ..	... ..	*1*	**3.21** ..	... ..
Yellow Poplar	*8*	**2.28**±.07	1.10±.09	*6*	**2.92**±.11	1.50±.21	*7*	**3.06**±.10	1.67±.28

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[1] A description of the stand in which these plots are located is given in the text of this report. The plots were fertilized May 5, 1937, and leaf samples were collected September 1-2 of the same year.

[2] Basal area is the cross-sectional area of a stand, in square feet, measured at 4.5 feet from the ground.

[3] N mix is an equal mixture (by weight) of commercial nitrate of soda and sulphate of ammonia. This mixture analyzes 18% water-soluble nitrogen, as is indicated by the data presented in horizontal column 4.

[4] The values presented in horizontal column 5 are estimates of available nitrogen supply in relation to that of the soil on the poorest site studied (see Fig. 1 and discussion). Data from plots on all sites are coordinated on this basis.

[5] The number of trees of a given species from which increment cores were taken for measurement and leaf samples for analysis.

[6] $N_{\%}$ is the symbol used to denote the nitrogen content of leaves expressed as percent dry weight. The $N_{\%}$ values entered in the above table are averages based upon the results of analyses of leaf samples from *individual* trees.

[7] The radial increment data are for 1937, the same growing season the fertilizer was applied.

[8] Standard error of the mean.

TABLE 5

THE NITROGEN CONTENT OF THE LEAVES AND THE ANNUAL RADIAL INCREMENT OF FOREST TREES GROWING ON PLOTS SUPPLIED VARYING AMOUNTS OF NITROGEN

B N Series, Black Rock Forest[1]

Plot Number	BN-0			BN-1			BN-2			BN-3		
Basal Area (sq. ft. per A.)[2]	56.4			61.3			49.7			58.1		
N Mix Applied (lbs. per A.)[3]	none			1600			3200			4800		
Nitrogen Applied (lbs. per A.)	none			288			576			864		
Relative N Supply (lbs. per A.)[4]	$x + 145$			$x + 433$			$x + 721$			$x + 1009$		
Species	*No.*[5]	*N% of Leaves*[6]	*Radial Increment (mm.)*[7]	*No.*[5]	*N% of Leaves*[6]	*Radial Increment (mm.)*[7]	*No.*[5]	*N% of Leaves*[6]	*Radial Increment (mm.)*[7]	*No.*[5]	*N% of Leaves*[6]	*Radial Increment (mm.)*[7]
(1)	*(2)*	*(3)*	*(4)*	*(5)*	*(6)*	*(7)*	*(8)*	*(9)*	*(10)*	*(11)*	*(12)*	*(13)*
Sugar Maple	*10*	**2.23±.08**[8]	1.24±.17[8]	*6*	**2.65±.03**[8]	1.45±.11[8]	*25*	**2.86±.07**[8]	1.56±.15[8]	*17*	**3.00±.09**[8]	1.53±.09[8]
White Ash	*19*	**2.30±.04**	2.27±.16	*5*	**2.70±.08**	2.83±.40	*8*	**2.82±.08**	3.00±.31	*5*	**2.99±.09**	3.21±.35
Pignut Hickory	*7*	**2.14±.09**	0.84±.11	*17*	**2.44±.05**	2.10±.10	*2*	**2.38** . .	2.25 . .	. .	. . . . .	. . . . .
Basswood	. .	. . . . .	. . . . .	. .	. . . . .	. . . . .	*1*	**3.24** . .	. . . . .	. .	. . . . .	. . . . .

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[1] A description of the stand in which these plots are located is given in the text of this report. The plots were fertilized May 6, 1937, and leaf samples were collected August 30 of the same year.

[2] Basal area is the cross-sectional area of a stand, in square feet, measured at 4.5 feet from the ground.

[3] N mix is an equal mixture (by weight) of commercial nitrate of soda and sulphate of ammonia. This mixture analyzes 18% water-soluble nitrogen, as is indicated by the data presented in horizontal column 4.

[4] The values presented in horizontal column 5 are estimates of available nitrogen supply in relation to that of the soil on the poorest site studied (see Fig. 1 and discussion). Data from plots on all sites are coordinated on this basis.

[5] The number of trees of a given species from which increment cores were taken for measurement and leaf samples for analysis.

[6] $N_{\%}$ is the symbol used to denote the nitrogen content of leaves expressed as percent dry weight. The $N_{\%}$ values entered in the above table are averages based upon the results of analyses of leaf samples from *individual* trees.

[7] The radial increment data are for 1937, the same growing season the fertilizer was applied.

[8] Standard error of mean.

TABLE 6

THE NITROGEN CONTENT OF THE LEAVES AND THE ANNUAL RADIAL INCREMENT OF FOREST TREES GROWING ON PLOTS SUPPLIED VARYING AMOUNTS OF NITROGEN

C N Series Plots, Arnot Forest[1]

Plot Number	CN-0				CN-1				CN-2				CN-3			
Basal Area (sq. ft. per A.)[2]	86.0				82.9				72.7				97.2			
N Mix Applied (lbs. per A.)[3]	none				1600				3200				4800			
Nitrogen Applied (lbs. per A.)	none				288				576				864			
Relative N Supply (lbs. per A.)[4]	$x + 70$				$x + 358$				$x + 646$				$x + 934$			
Species	*No.*[5]	*N% of Leaves*[6]	*No.*[7]	*Radial Increment (mm.)*[8]	*No.*[5]	*N% of Leaves*[6]	*No.*[7]	*Radial Increment (mm.)*[8]	*No.*[5]	*N% of Leaves*[6]	*No.*[7]	*Radial Increment (mm.)*[8]	*No.*[5]	*N% of Leaves*[6]	*No.*[7]	*Radial Increment (mm.)*[8]
(1)	*(2)*	*(3)*	*(4)*	*(5)*	*(6)*	*(7)*	*(8)*	*(9)*	*(10)*	*(11)*	*(12)*	*(13)*	*(14)*	*(15)*	*(16)*	*(17)*
Beech	*19*	2.03±.05[9]	*10*	1.33±.09[9]	*2*	2.62±.07[9]	*8*	1.84±.25[9]	*2*	2.69±.11[9]	*9*	2.88±.32[9]	*3*	2.98±.10[9]	*10*	2.65±.23[9]
Basswood	*12*	2.11±.07	*10*	0.88±.09	*3*	2.69±.12	*7*	2.43±.19	*1*	3.20 ..	*10*	3.72±.47	..	... ..	..	... ..
Trembling Aspen[10]	*9*	2.06±.05	*9*	2.04±.20	*1*	2.86 ..	*11*	3.21±.21	*2*	2.91±.01	*10*	3.33±.26	*4*	2.91±.11	*11*	3.35±.40
White Ash	*8*	1.85±.07	..	... ..	*4*	2.64±.06	..	... ..	..	... ..	..	... ..	..	... ..	..	... ..
Sugar Maple	*21*	1.55±.05	..	... ..	*3*	2.78±.01	..	... ..	*2*	2.83±.07	..	... ..	..	... ..	..	... ..

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[1] A description of the stand in which these plots are located is given in the text of this report. The plots were fertilized April 20-21, 1936, and leaf samples were collected September 16-18 of the same year.

[2] Basal area is the cross-sectional area of a stand, in square feet, measured at 4.5 feet from the ground.

[3] N mix is an equal mixture (by weight) of commercial nitrate of soda and sulphate of ammonia. This mixture analyzes 18% water-soluble nitrogen, as is indicated by the data presented in horizontal column 4.

[4] The values entered in horizontal column 5 are estimates of available nitrogen supply in relation to that of the soil on the poorest site studied (see Fig. 1 and discussion). Data from plots on all sites are coordinated on this basis.

[5] The number of trees of a given species from which leaf samples were taken for analysis.

[6] $N_{\%}$ is the symbol used to denote the nitrogen content of leaves expressed as percent dry weight. The $N_{\%}$ values entered in the above table are averages based upon the results of analyses of leaf samples from *individual* trees.

[7] The number of trees of a given species from which increment cores were taken for measurement.

[8] The radial increment data are for 1937, the growing season following the year the fertilizer was applied.

[9] Standard error of the mean.

[10] There were a few large-toothed aspen on plots *CN-0* and *CN-3*. Data on this species were averaged in with the analytical results for trembling aspen, which did not differ significantly.

TABLE 7

THE NITROGEN CONTENT OF THE LEAVES AND THE ANNUAL RADIAL INCREMENT OF FOREST TREES GROWING ON PLOTS SUPPLIED VARYING AMOUNTS OF NITROGEN

D N Series Plots, Arnot Forest[1]

Plot Number	DN-0				DN-1				DN-2			
Basal Area (sq. ft. per A.)[2]	64.2				61.6				74.9			
N Mix Applied (lbs. per A.)[3]	none				400				800			
Nitrogen Applied (lbs. per A.)	none				72				144			
Relative N Supply (lbs. per A.)[4]	$x + \mathbf{0}$				$x + \mathbf{72}$				$x + \mathbf{144}$			
Species	*No.*[5]	*N% of Leaves*[6]	*No.*[7]	*Radial Increment (mm.)*[8]	*No.*[5]	*N% of Leaves*[6]	*No.*[7]	*Radial Increment (mm.)*[8]	*No.*[5]	*N% of Leaves*[6]	*No.*[7]	*Radial Increment (mm.)*[8]
(1)	*(2)*	*(3)*	*(4)*	*(5)*	*(6)*	*(7)*	*(8)*	*(9)*	*(10)*	*(11)*	*(12)*	*(13)*
Beech	*9*	**1.78**±.01[9]	*18*	1.30±.11[9]	*8*	**2.00**±.06[9]	..	... ..	*6*	**2.23**±.06[9]	..	... ..
Basswood	*9*	**1.90**±.04	*17*	1.52±.10	*5*	**2.11**±.09	*8*	1.80±.20[9]	*5*	**2.36**±.08	*12*	2.64±.16[9]
Trembling Aspen	*10*	**1.81**±.05	*27*	2.26±.13	*2*	**2.13**±.01	..	... ..	*10*	**2.27**±.05	*22*	2.56±.14
Red Maple	*10*	**1.40**±.04	*16*	1.63±.08	*10*	**1.51**±.06	*13*	1.83±.12	*6*	**1.84**±.07	*6*	1.90±.18

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[1] A description of the stand in which these plots are located is given in the text of this report. The plots were fertilized the last week in April, 1937, and leaf samples were collected September 12-15 of the same year.

[2] Basal area is the cross-sectional area of a stand, in square feet, measured at 4.5 feet from the ground.

[3] N mix is an equal mixture (by weight) of commercial nitrate of soda and sulphate of ammonia. This mixture analyzes 18% water-soluble nitrogen, as is indicated by the data presented in horizontal column 4.

[4] The values entered in horizontal column 5 are estimates of available nitrogen supply in relation to that of the soil on the poorest site studied (see Fig. 1 and discussion). Data from plots on all sites are coordinated on this basis.

[5] The number of trees of a given species from which leaf samples were taken for analysis.

[6] $N_{\%}$ is the symbol used to denote the nitrogen content of leaves expressed as percent dry weight. The $N_{\%}$ values entered in the above table are averages based upon the results of analyses of leaf samples from *individual* trees.

[7] The number of trees of a given species from which increment cores were taken for measurement.

[8] The radial increment data are for 1938, the growing season following the year the fertilizer was applied.

[9] Standard error of the mean.

TABLE 7—*(Continued)*

Plot Number	DN-3				DN-4				DN-5			
Basal Area (sq. ft. per A.)[2]	72.3				65.2				69.5			
N Mix Applied (lbs. per A.)[3]	1200				1600				3200			
Nitrogen Applied (lbs. per A.)	216				288				576			
Relative N Supply (lbs. per A.)[4]	$x +$ **216**				$x +$ **288**				$x +$ **576**			
Species	*No.*[5]	*N % of Leaves*[6]	*No.*[7]	*Radial Increment (mm.)*[8]	*No.*[5]	*N % of Leaves*[6]	*No.*[7]	*Radial Increment (mm.)*[8]	*No.*[5]	*N % of Leaves*[6]	*No.*[7]	*Radial Increment (mm.)*[8]
(14)	*(15)*	*(16)*	*(17)*	*(18)*	*(19)*	*(20)*	*(21)*	*(22)*	*(23)*	*(24)*	*(25)*	*(26)*
Beech	*7*	**2.44**±.06[9]	..	... ..	*10*	**2.75**±.07[9]	..	... ..	*4*	**2.79**±.08[9]	..	... ..
Basswood	*7*	**2.56**±.12	*7*	2.57±.22[9]	*2*	**2.88**±.20	*4*	2.75±.22[9]	*7*	**2.86**±.07	*15*	2.79±.16[9]
Trembling Aspen	..	... ..	..	... ..	*5*	**2.42**±.05	*19*	2.56±.16	..	... ..	..	... ..
Red Maple	..	... ..	..	... ..	..	... ..	..	... ..	..	... ..	..	... ..

largely of sugar maple and beech, with small admixtures of red maple, basswood, white ash, black birch and aspen. Trees in the dominant crown class average 55 feet in height at 45 years of age. Basal area figures and other basic data for these plots are summarized in Table 6.

DN Series.—Plots of this series were established in the spring of 1937. They are located on the same forest as the *CN* Series plots, but at an elevation of about 1000 feet. With the exception of plot *DN-5,* the soil type is the same. This one plot of the series was located on Volusia stony silt loam, which is derived from similar parent material as the Lordstown, but is characterized by a tight clay layer at a depth of about 12 inches. This clay layer impedes drainage and root penetration. In general, Volusia soils are less productive than Lordstown.

The stand in which these plots are located may be classed as uneven-aged. It is composed chiefly of beech, basswood, red and sugar maple which came in following a cutting some 45 years ago, and a younger age class of aspen which seeded in after a fire at a later date. The aspen are approximately 35 years of age and average 35 feet in height. The other species average 50 feet in height at age 45. Basal area figures and other basic data for these plots are entered in Table 7.

COORDINATION OF DATA FROM PLOTS ON DIFFERENT SITES

Certain tree species differ so greatly in their mineral nutrient, soil moisture and other requirements that they are rarely found growing together on the same site. For example, such species as white ash, yellow poplar and basswood are generally limited to the more fertile soils, whereas chestnut oak, although more widely distributed, seldom occurs in abundance except on the poorer sites. Consequently, in order to include in the present study an adequate representation of the more important tree species found in the Northeast, it was necessary to establish series of variously fertilized plots on each of several different site qualities. This lack of uniformity tends to complicate coordination of data from plots on the various sites.

However, an apparently satisfactory procedure, based on the method of leaf analysis, was developed to evaluate the relative nitrogen-supplying capacity of the different soils. A calibration technique which uses the principle of diminishing returns was discovered. Estimates of available nitrogen supply are based on the narrower intervals of increasing leaf nitrogen content with additions of nitrogen fertilizer. Thus is provided a common basis for the comparison of analytical data, and, to a lesser extent, the growth data from all plots studied. Details of the procedure followed are illustrated by the data presented in Fig. 1.

In Fig. 1 (A) values representing the nitrogen content of the leaves of red oaks growing on the *N* Series plots are shown plotted over the *actual* amounts (upper scale) of nitrogen applied to each of these plots (data from

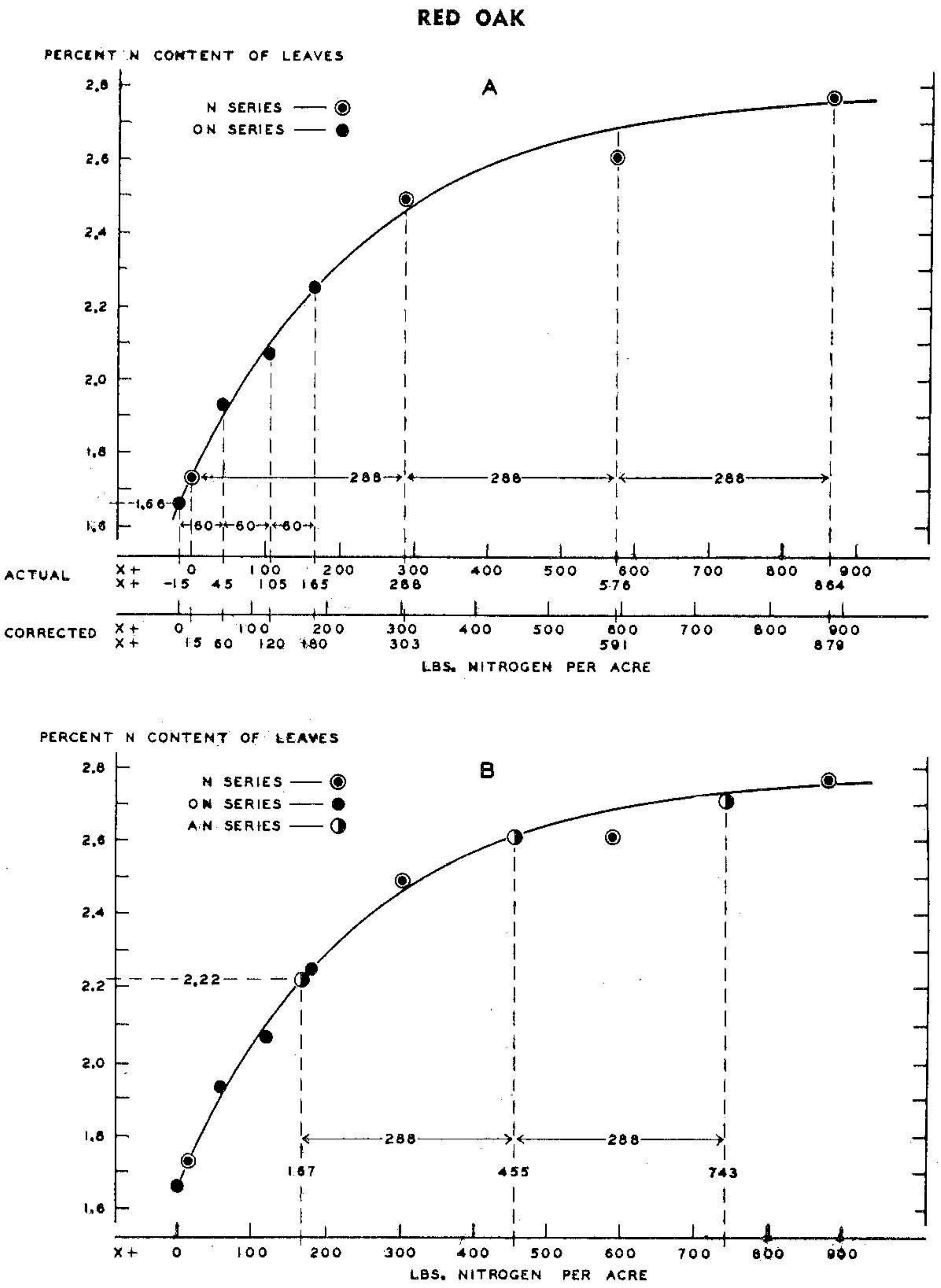

FIG. 1.—Diagrams illustrating the method used to coordinate data from plots on different sites.

Table 2). Trees on the control plot (*N-0*), which was not fertilized, received no nitrogen other than that supplied by the soil, *i.e.*, the unknown quantity x. The nitrogen available to trees growing on plots *N-1, N-2* and *N-3*, respectively, can be expressed quantitatively as: $x + 288$, $x + 576$ and $x + 864$ pounds per acre. The curve of average relationship shown in Fig. 1, as based upon the *N* Series data only, was calculated according to the Mitscherlich equation,

$$N_{\%} = A\ (1 - 10^{-c\,[N+b]}),$$

in which $N_{\%}$ = the nitrogen content of the leaves expressed as percent dry weight, N = the amount of nitrogen added, as pounds per acre, and A, b and c are constants.[1] A detailed discussion of the Mitscherlich formula and its adaptability to this purpose was given in previous reports (Mitchell, 1934, '39) and need not be repeated here.

The experimentally determined relationship between N supply and $N_{\%}$, as based on the *N* Series data, can be utilized to bring into line data from the *ON* Series plots, which were located on a slightly different site. The leaves of red oaks growing on plot *ON-0,* the control plot of the *ON* Series, had a nitrogen content of 1.66% (Table 3). As shown in Fig. 1 (A), a line extended from 1.66 on the ordinate axis intersects the calculated curve at a point corresponding to —15 on the abscissa scale against which the *N* Series data were plotted. This indicates a difference of 15 pounds per acre in the nitrogen-supplying capacity of the two soils, the *ON* Series plots being located on the poorer. With the nitrogen availability of the *ON* Series soil thus esimated on a relative basis at $x - 15$, the $N_{\%}$ values for plots *ON-1, ON-2* and *ON-3,* which received increasing amounts of nitrogen differing by 60 pounds per acre (Table 3), were then plotted over

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[1] The constants used in calculating the curve shown in Fig. 1 have the following numerical values: A, 2.786; b, 219.77; and c, 0.00179.

the appropriate nitrogen supplies: $x + 45$ ($-15 + 60 = 45$), $x + 105$ and $x + 165$, respectively. The experimental data thus plotted are in almost perfect agreement with the calculated curve.

So as to avoid working with negative quantities the available nitrogen supply of the poorest control plot, *ON-0,* was assigned a value of $x + 0$ instead of $x - 15$, and proportionate corrections were made in the nitrogen supplies of all other plots of the two series. The resulting values, which express nitrogen supply in relation to that of the poorest soil, are shown on the "corrected" scale of Fig. 1 (A). These are the "relative N supplies" entered in bold-faced type in horizontal column 5 of Tables 2 and 3.

Fig. 1 (B) illustrates how data from the *AN* Series plots, located on a considerably better site, were brought into line. The $N_{\%}$ of red oaks on the control plot (*AN-0*) was 2.22%, as compared to 1.66% for plot *ON-0* and 1.73% for plot *N-0.* By interpolation (or solving the curve formula for $N_{\%} = 2.22$), the relative nitrogen supply of plot *AN-0* is found to be equivalent in effect to $x + 167$ pounds of nitrogen per acre (see Fig. 1, B).[1] Thus plot *AN-1,* which received 288 pounds of nitrogen per acre, has a relative N supply of $x + 455$, and plot *AN-2,* which was fertilized at the rate of 576 pounds of N per acre, has a relative N supply of $x + 743$. The precision with which the experimental data fall upon the calculated curve is perhaps the best measure of the accuracy of the method used to evaluate the nitrogen-supplying capacity of the various sites.

Red oak is found on a rather wide variety of sites

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[1] Although the statistical measures of accomplishment for the curve of average relationship, as plotted in Fig. 1, are relatively favorable (Table 8), the prediction of nitrogen supply from the dependent variable ($N_{\%}$), as in Fig. 1, is not necessarily justified. However, with the data reclassified —that is, $N_{\%}$ as independent and nitrogen supply as dependent variable— and the curve equation solved for nitrogen supply, the correlation index is .99 and the standard error of estimate ± 8.6. Neither statistic is less favorable than those calculated for the data plotted as shown in Fig. 1.

TABLE 8

Summary of Statistical Analysis of Relationships between Relative Nitrogen Supply (Independent Variable) and the Nitrogen Content of the Leaves (Dependent Variable) of Various Tree Species[1]

Species	*No. of Plots*	*No. of Trees*	*Correlation Index*	*Standard Error of Estimate*
(1)	*(2)*	*(3)*	*(4)*	*(5)*
Red Oak	11	167	0.99	0.03
White and Chestnut Oaks	8	91	0.99	0.06
Red Maple	11	101	0.97	0.14
Pignut Hickory	10	58	0.97	0.08
Trembling Aspen	8	43	0.98	0.09
Sugar Maple	17	151	0.97	0.14
Beech	10	70	0.97	0.09
Basswood	17	73	0.84	0.22
Yellow Poplar	7	44	0.97	0.12
Black Gum	7	39	0.99	0.05
White Ash	17	137	0.97	0.10

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[1] Curves of average relationship, which may be calculated with the Mitscherlich equation, are shown in Figs. 1, 2, 3, 4, 5, 6, 9, 10, 11, 14, 15 and 16 (basic data from Tables 2, 3, 4, 5, 6 and 7).

throughout the Northeast and is a primary element of the stands in which most of the fertilized plots were located. For this reason red oak was selected as what might be termed the principal ''indicator species'' for the present study. However, red oaks are infrequent to absent on the *BN* Series plots and the two sites on the Arnot Forest where the *CN* and *DN* Series plots were established. This necessitated the use of other trees as ''indicators.'' Sugar maple, for example, which is frequent on the *BN* Series plots (Table 5) and is fairly well represented on the other Black Rock Forest plots, was used to bring the *BN* Series data into line. The two series of plots (*CN* and *DN*) on the Arnot Forest were coordinated on the basis of beech, the most frequent element of the stands, all plots considered. And red maple, the most numerous species common to both the Arnot Forest and the Black Rock Forest plots, served as a basis for comparison. The procedure followed in each case was exactly the same as that discussed in connection with the red oak data summarized in Fig. 1. As will be apparent from the data presented in the following sections of this discussion, it makes little difference which tree is used as indicator species so long as it occurs in sufficient numbers on the plots compared.

EXPERIMENTAL DATA

THE NITROGEN CONTENT OF THE LEAVES AND THE GROWTH OF FOREST TREES SUPPLIED VARYING AMOUNTS OF NITROGEN

Red Oak.—Data on the annual diameter increment and the nitrogen content of the leaves of red oaks growing on plots supplied varying amounts of nitrogen are presented in Fig. 2. It is well known that tree growth is influenced by many environmental and other factors besides nitrogen supply—*i.e.,* age and condition of trees, volume and density of stocking of stands, soil moisture, depth and physical properties of soil, the available supply of other essential mineral elements, elevation, exposure and local climate. Furthermore, in the present study the various series of plots were not only located on different sites but were established and fertilized in different years. Thus, in order to analyze the effect of the single growth factor, nitrogen supply, it is necessary to plot separately the radial increment data for each series of variously fertilized but otherwise uniform plots (Fig. 2, A).

Nitrogen fertilizer was applied to the *N* Series plots in the spring of 1935 and to the *ON* Series plots in the spring of 1936 (Tables A, 2 and 3). In each case the radial increment data presented in Fig 2 (A) are for the growing season following the year of fertilization—that is, 1936 for the *N* Series, and 1937 for the *ON* Series. The relatively greater response, to equal increments of nitrogen, of trees on the *ON* Series plots is believed attributable partly to the greater depth and more favorable moisture conditions of that soil, as compared to the *N* Series soil, and partly to the fact that rainfall was normal during 1937 whereas there was a severe drought during the 1936 growing season. Plots of the *AN* Series,

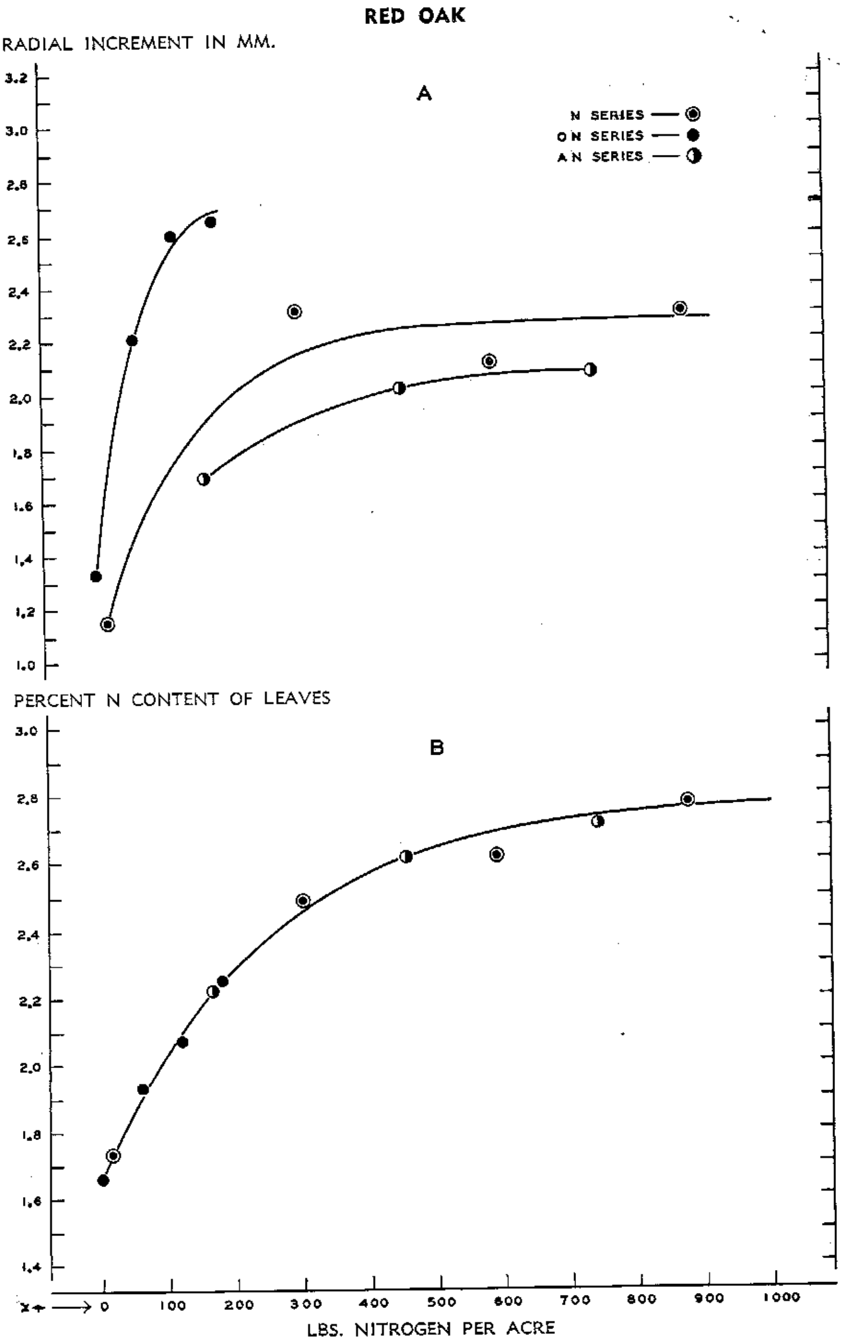

FIG. 2.—The relationship between nitrogen supply and the annual radial increment and the nitrogen content of the leaves of red oak trees growing in even-aged stands of mixed hardwoods.

which were located on the most favorable site studied, were fertilized in the spring of 1937. However, the growth data for these plots, unlike those of the *N* and *ON* Series, are for the *same* growing season in which the fertilizer was applied. This helps to explain the relatively meagre growth response of trees on the *AN* Series plots. Available data indicate that maximum radial increment does not occur until the year following fertilization.

There is another factor which tends to limit the response of trees on the *AN* Series plots. As shown in Table 4, the average basal area of the stand in which these plots are located is significantly greater than that of either the *N* or the *ON* Series plots (Tables 2 and 3). It is assumed that basal area is a measure of the root competition for soil moisture and mineral nutrients in stands which are fairly comparable as regards age and composition. The influence of root competition upon the response of trees to increments of nitrogen is discussed further in connection with data on other species. Aboveground competition for space and light is not of primary importance in the present study since growth measurements and leaf sampling were confined to trees in the dominant and codominant crown classes.

Although it is impossible to coordinate growth data from plots on the different sites studied, it will be noted (Fig. 2, A) that maximum growth for each series of variously fertilized plots is approached at about the same relative nitrogen supply. Also that nitrogen supplements sufficient to increase the $N_{\%}$ of the leaves from 1.66 to around 2.46 to 2.57% result in an increase of approximately 100 percent in the annual radial growth of red oaks. This proves that nitrogen is relatively deficient on the poorer sites studied.

Unlike the growth measurements, which in some cases are for the growing season the fertilizer was applied and in others for the following year, the analytical results are in every case based upon leaf samples collected in the fall of the same year that the fertilizer was applied.[1] Available data indicate that the nitrogen content of leaves from trees which are supplied readily soluble nitrogenous fertilizers in the early spring is usually maximum in the fall of the same growing season. Thereafter soil nitrogen supply, and therefore $N_{\%}$ of leaves, tends to decrease.

To facilitate further discussion the nitrogen concentration of the leaves, expressed as a percentage of dry weight, may be referred to as the "internal nitrogen concentration". The data presented in Fig. 2 (B) indicate that the internal nitrogen concentration of red oak trees is proportional to the nitrogen-supplying capacity of the soil, and that this relationship is relatively unaffected by those variations in soil moisture, age of trees, depth and physical properties of soil, local climate, elevation and exposure which were encountered during the present study. For example, leaves were collected from trees on the *N* Series plots in the fall of 1935, following a season of normal rainfall, and from the *ON* Series plots in the fall of 1936, a year of drought. Despite this difference the analytical results, as shown in Fig. 2 (B), are in almost perfect agreement with the curve of average relationship between relative N supply and $N_{\%}$. Additional data on this subject are summarized in Table 9. These data show that leaf samples taken at the end of the 1935 and 1936 growing seasons from white and chestnut oaks on the same *unfertilized* plot do not differ significantly in nitrogen content. Similarly, the various differences in site and age of stand—discussed in connection with the stand descriptions—apparently have little or no effect upon internal nitrogen concentration,

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[1] It would have been desirable to compare the growth data for all plots on the basis of radial increment during the growing season following fertilization, when the benefits therefrom are maximum. However, the 1938 radial increment measurements for trees on the *AN* and *BN* Series plots, which were established in the spring of 1937, were not available when this report was prepared for publication.

TABLE 9

COMPARISON OF THE NITROGEN CONTENT OF LEAF SAMPLES TAKEN FROM TREES ON THE SAME PLOT FOLLOWING A SEASON OF NORMAL RAINFALL (1935) AND ONE OF SEVERE DROUGHT (1936)

Date Sampled	*White Oak*		*Chestnut Oak*	
	No.[1]	*N Content of Leaves (N%)*	*No.*[1]	*N Content of Leaves (N%)*
Sept. 26, 1935	8	2.04±.06 [2]	9	1.99±.07 [2]
Sept. 1, 1936	14	1.96±.07	14	2.04±.04
Difference	0.08		0.05	
Fisher's t	0.87		0.62	
Significance of difference	Not significant [3]		Not significant [3]	

[1] The number of trees from which leaf samples were taken for analysis.

[2] Standard error of the mean.

[3] See Snedecor, 1937, Table 3.8.

which is proportional to the nitrogen-supplying capacity of the soil.

Root competition, of which basal area is perhaps the best measure obtained, is apparently the only factor other than nitrogen supply which has any appreciable influence upon the nitrogen content of the leaves as well as the growth response of various tree species on the plots studied. As shown in Fig. 2, for example, not only the growth but the N content of the leaves of red oak trees on plot *N-2* is somewhat out of line—that is, lower than might be expected on the basis of data from other plots of the series. The same is true of chestnut oak and certain other species growing on plot *N-2*. This is interesting in view of the fact that the basal area of the stand in which this plot is located is significantly greater than for any of the other *N* Series plots. These observations suggest that root competition is a factor which may have to be taken into account in comparing the nitrogen content of the leaves of trees in stands which differ greatly in this respect. However, the various plots of the present experiment are sufficiently uniform so that, aside from certain minor variations, the $N_{\%}$ data from all plots can be coordinated on the basis of relative nitrogen supply with a surprisingly high degree of precision. The inconsistencies believed attributable to differences in root competition are noted throughout the discussion of data regarding the other species studied.

White and Chestnut Oaks.—There appears to be no significant difference in either the radial increment or the internal nitrogen concentration of white and chestnut oaks growing on the same site (Tables 2 and 3). Hence the data plotted in Fig. 3 are averages of analytical results and growth measurements for the two species. As with red oak, there is a high degree of correlation between nitrogen supply and the nitrogen content of the foliage of white and chestnut oaks. The curve of average relationship (Fig. 3, A) was similarly calculated, with the

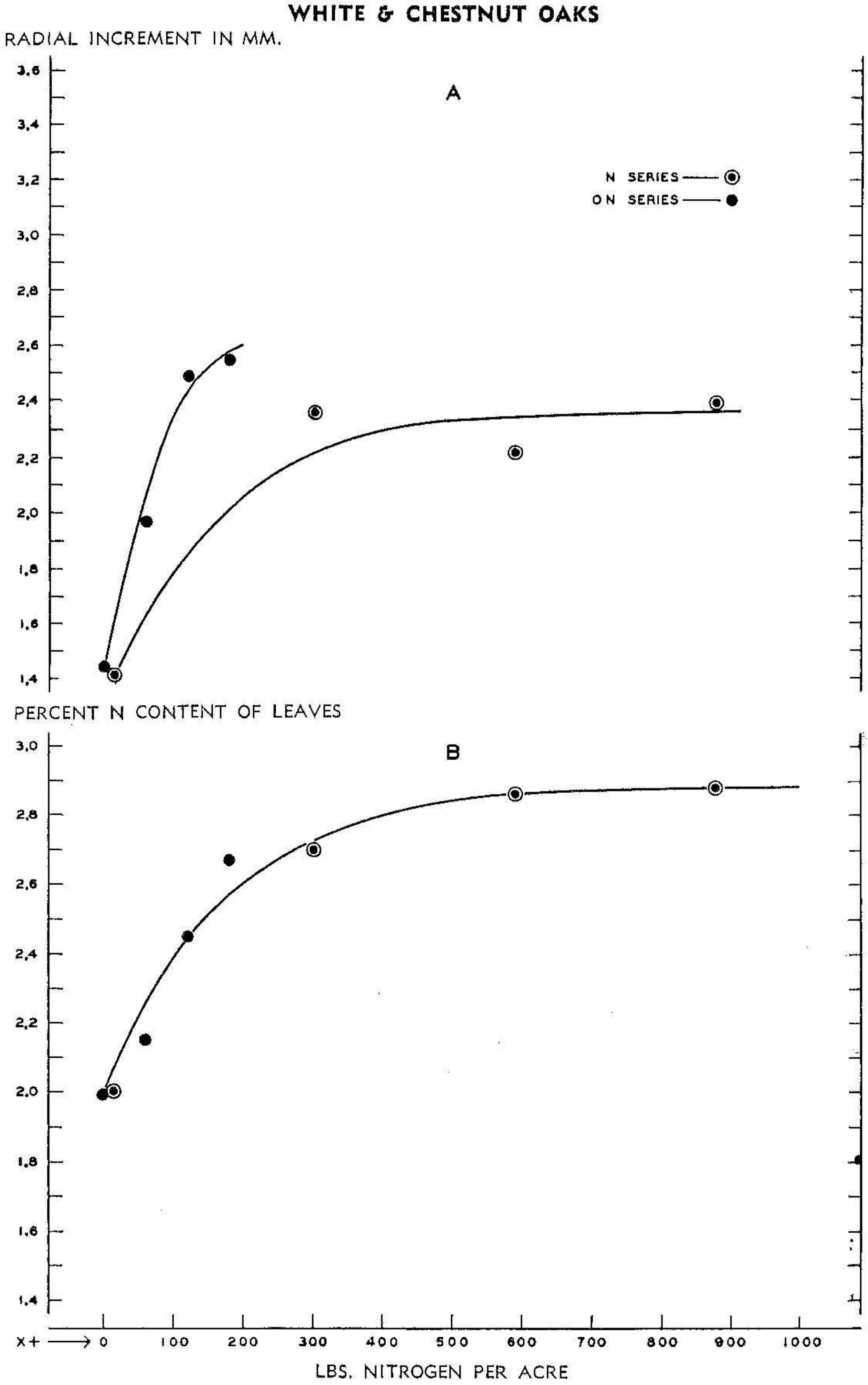

FIG. 3.—The relationships between nitrogen supply and the annual radial increment and the nitrogen content of the leaves of white and chestnut oak trees growing in even-aged stands of mixed hardwoods.

Mitscherlich equation, and the results of statistical analyses are summarized in Table 8. Apparently the only major point of difference is that the leaves of white and chestnut oaks growing on the control plot of the poorest site (Plot *ON-0*) have a significantly higher nitrogen concentration than the leaves of red oaks on the same site, *i.e.*, 2.00% for the former as compared to 1.66% for red oak. This difference in $N_{\%}$ is true not only for the poorest soil but is relatively constant over the entire range of nitrogen supplies studied.

The growth response of white and chestnut oaks to increasing nitrogen supplies is essentially the same as in the case of red oak. A relatively greater increase was observed on the *ON* Series site for the 1937 season than on the *N* Series site for the drought year of 1936. As with red oak, the radial increment measurements of trees on the *N* and *ON* Series plots are for the year following fertilization. It is also apparent that white and chestnut oaks on plots of both series approach maximum growth at a nitrogen supply sufficient to produce, in leaves, a nitrogen concentration of around 2.72 to 2.80%. This optimum is found at a relative nitrogen supply of between $x + 300$ and 400 pounds per acre, the same as for red oak.

Red Maple.—The growth and $N_{\%}$ data for red maple are shown in Fig. 4. It appears that the internal nitrogen concentration of red maple trees on the poorest control plot is significantly less than that of red, white or chestnut oaks (Fig. 4, Table 3). At nitrogen supplies greater than $x + 200$ pounds per acre the concentration of nitrogen in the leaves of red maple is greater than for red oak but less than that of white and chestnut oaks. Increments of nitrogen sufficient to increase the concentration of this element in the leaves of red maple from 1.38 up to around 2.55 to 2.68%, the apparent optimum, result in an increase of approximately 75 per cent in annual radial growth. This response is somewhat less than

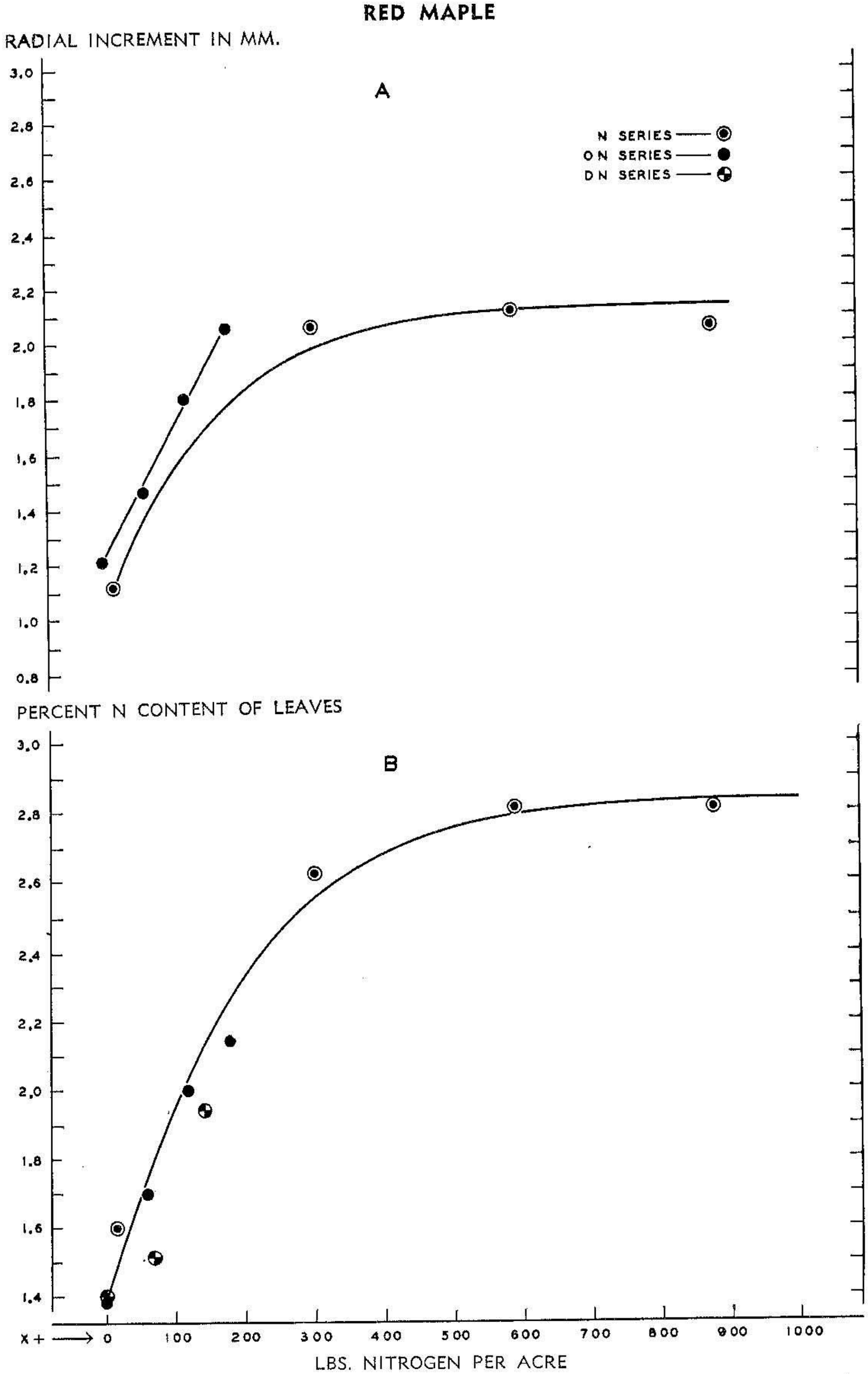

FIG. 4.—The relationships between nitrogen supply and the annual radial increment and the nitrogen content of the leaves of red maple trees growing in even-aged stands of mixed hardwoods.

that of the oaks to equal increments of nitrogen supply (Fig. 2 and 3).

Trembling Aspen.—Since trembling aspen occurred only on plots of the *CN* and *DN* Series, and were infrequent on certain of these plots, the data regarding this species are relatively meagre. The radial increment and the nitrogen content of the leaves of trembling and large-toothed aspen appear to be almost identical, as in the case of white and chestnut oaks. Hence the data entered in Table 6 are averages of the analytical results and growth measurements for the two species. As with all other trees studied, the nitrogen content of the leaves of aspen is proportional to the nitrogen supply (Fig. 5). The curve of average relationship, based largely on data for trembling aspen, may be similarly expressed with the Mitscherlich equation. It will be observed that the leaves of aspen growing on the poorer sites have a significantly greater nitrogen concentration than the majority of other species included in the present study (Fig. 13).

As shown in Fig. 5 (A), increments of nitrogen sufficient to increase the concentration of this element in the leaves of aspen from 2.00% up to around 2.64 to 2.77% have a definitely stimulating effect upon radial increment. On the basis of the rather scanty data available, it appears that aspen approach maximum radial growth at a relative nitrogen supply of from $x + 300$ to 400 pounds per acre, which is the same as for the oaks and red maple.

Sugar Maple.—The growth and analytical data for sugar maple are presented in Fig. 6. As with the other species studied, there is a high degree of correlation between nitrogen supply and the nitrogen concentration of the leaves of sugar maple. This is evident from the data plotted in Fig. 6 (B) and from the results of statistical analyses summarized in Table 8. It will be noted, however, that the $N_{\%}$ data for certain plots are somewhat out of line. In general, those points which fall considerably below the curve of average relationship shown in Fig.

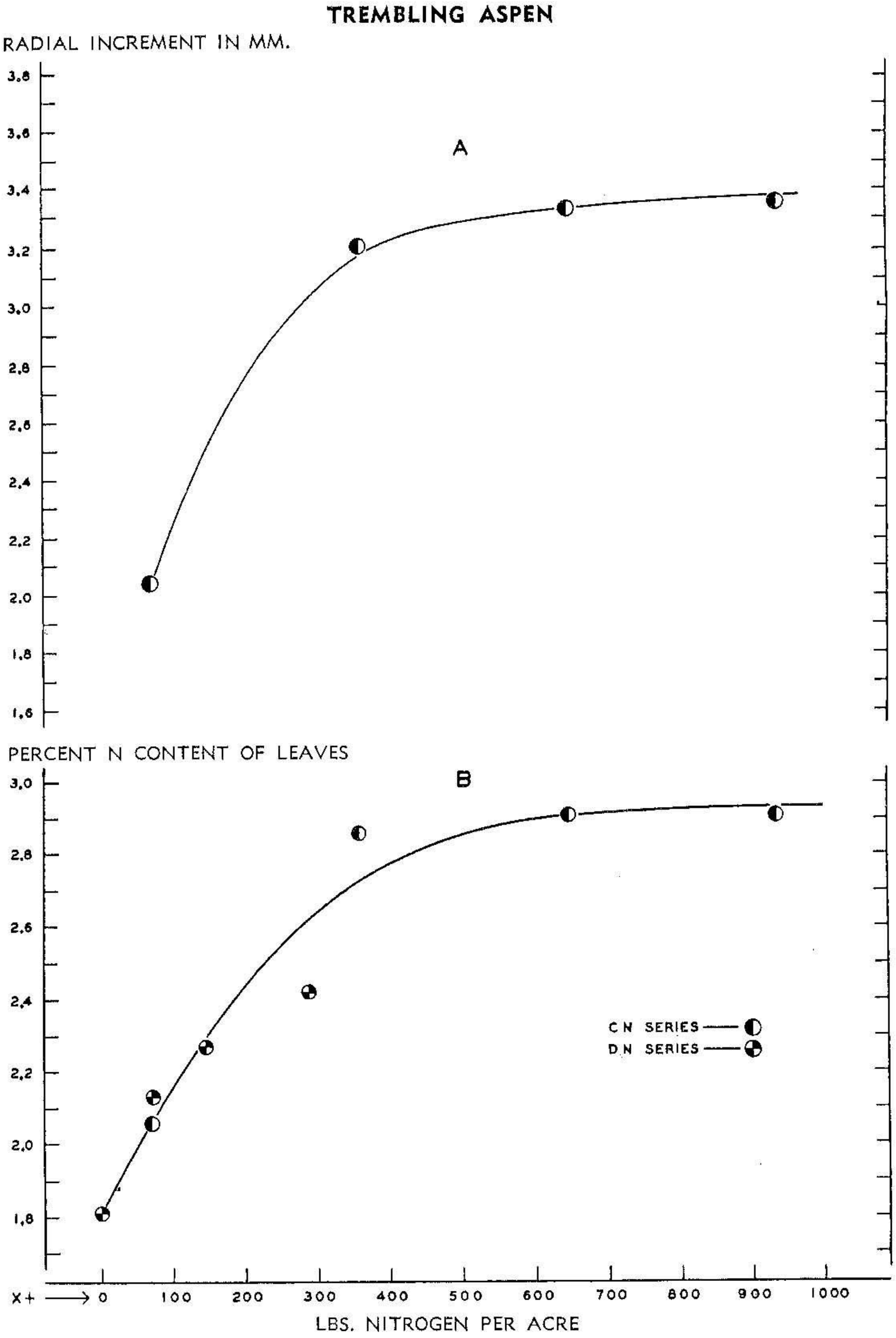

FIG. 5.—The relationships between nitrogen supply and the annual radial increment and the nitrogen content of the leaves of trembling aspen trees growing in even-aged stands of mixed hardwoods.

6 (B) represent plots located in stands with significantly higher than average basal areas. The opposite trend is not so apparent since, in fitting the curve, greater weight was given to data from plots in stands which were more nearly average as regards basal area, all plots considered. This tendency toward an inverse relationship between basal area and $N_{\%}$ of leaves is the most convincing evidence thus far presented of the influence of root competition upon internal nitrogen concentration.

The leaves of sugar and red maples growing on the poorest plot (*ON-0*) have the same nitrogen content, *i.e.*, 1.38%. This is considerably less than for white and chestnut oaks, which appear to have the greatest internal nitrogen concentration, or for any of the other species studied. At the higher nitrogen supplies, however, the leaves of sugar maple have a greater nitrogen concentration than those of either the oaks or red maple (Fig. 13).

The data presented in Fig. 6 (A) show that sugar maple trees on each series of variously fertilized plots approach maximum radial growth at approximately the same relative nitrogen supply—that is, from $x + 400$ to 500 pounds per acre, considerably higher than for the oaks, red maple and trembling aspen. These supplies are sufficient to produce in the leaves of sugar maple a nitrogen concentration of from 2.77 to 2.85%. As with all other species, the *AN* and *BN* Series growth data on sugar maple are for the same year that the fertilizer was applied, whereas the *N* and *ON* Series data plotted in Fig. 6 (A) represent the average annual radial increment for the growing season following fertilization. This explains in part the difference in response to equal increments of nitrogen. The relatively lower rate of growth on control plots *AN-0* and *BN-0,* as compared to the *N* and *ON* Series plots of equal nitrogen supply, is attributed to differences in age, condition and basal area of stands and to factors of site other than nitrogen supply.

Thus far in the discussion tree growth has been

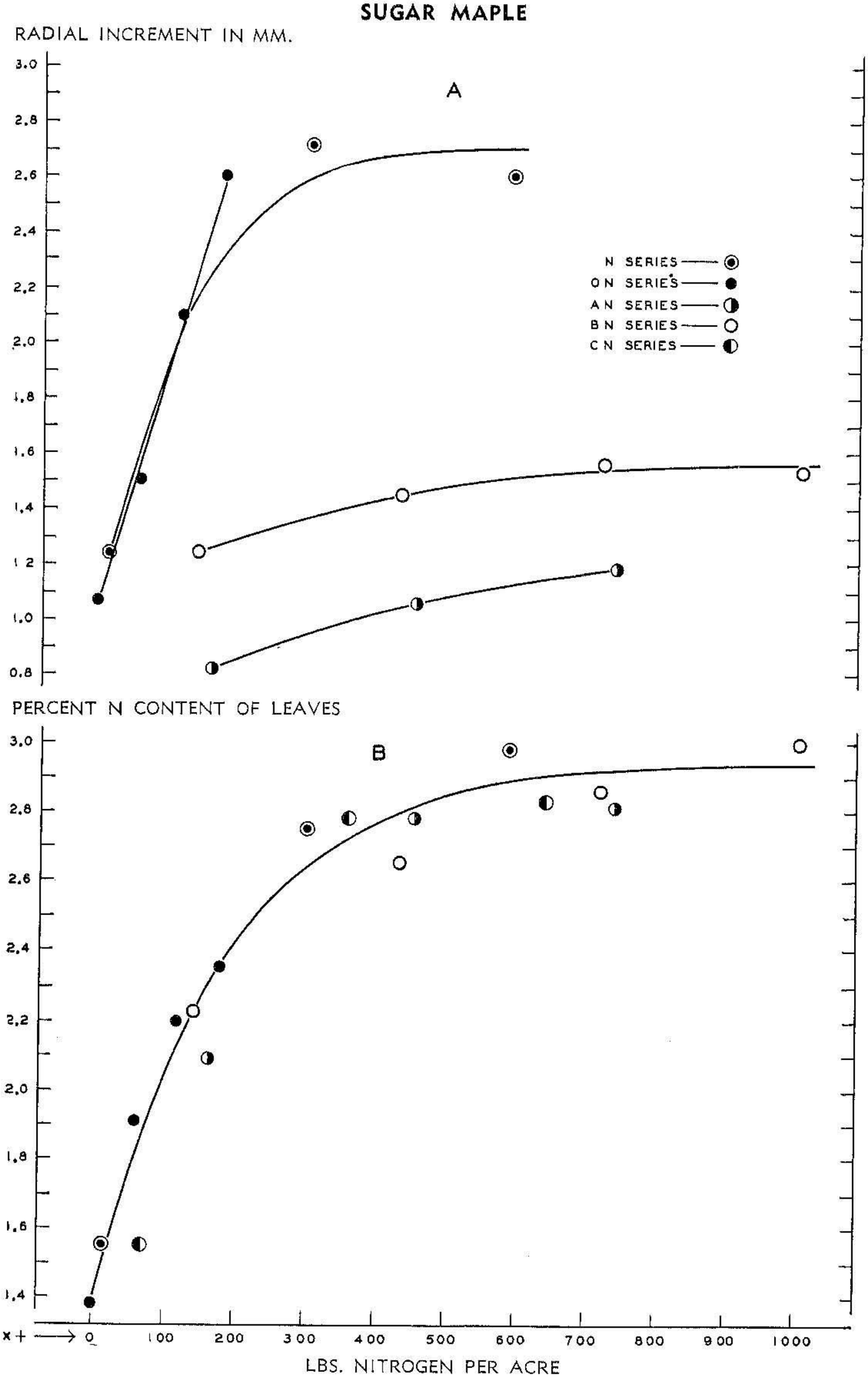

FIG. 6.—The relationships between nitrogen supply and the annual radial increment and the nitrogen content of the leaves of sugar maple trees growing in even-aged stands of mixed hardwoods.

considered only in terms of annual radial increment. Because of the many difficulties involved, the cost of measuring accurately the yearly height growth of all trees included in the present study was deemed prohibitive. However, data were obtained on the twig elongation of two species, sugar maple and beech, on the *CN* Series plots (Table 10). Since it was found that the yearly extension of the entire crown was essentially the same as that of the terminal leader, the twig measurements may in this case be considered as a fairly accurate estimate of height growth as well as crown extension. The relationships between nitrogen supply and the 1936 and 1937 twig growth of sugar maples on the *CN* Series plots, which were fertilized in the spring of 1936, are shown on Fig. 7. As with radial increment, the full benefits of nitrogen supplements are not reflected in twig elongation until the growing season following fertilization. Unlike the average relationship between nitrogen supply and radial growth, the average trend of twig elongation is best expressed by an S-shaped curve.

Beech.—The twig elongation measurements for beech are summarized in Fig. 8. It is apparent that the relationships between nitrogen supply and the 1936 and 1937 twig growth of beech are very similar to those for sugar maple. In each case the 1936 twig growth is linearly related to nitrogen supply, whereas an S-shaped curve corresponds most nearly to the average trend for the following year. The chief difference between the two species is that the response of beech to equal increments of nitrogen is significantly greater, especially the year following fertilization.

A comparison of data presented in Figs. 7 and 8 reveals that the twig growth of beech on the unfertilized plot (*CN-0*) was greater during 1936 than 1937, whereas the reverse was true in the case of sugar maple on the same plot. Since factors of site were relatively uniform throughout the control plot, the only apparent explana-

TABLE 10

THE 1936 AND 1937 TWIG GROWTH OF BEECH AND SUGAR MAPLE TREES GROWING ON PLOTS SUPPLIED VARYING AMOUNTS OF NITROGEN [1]

CN Series Plots, Arnot Forest [2]

Plot No.	Relative Nitrogen Supply [3]	Twig Elongation in Cm.[4]					
		Beech			Sugar Maple		
		No.	1936	1937	No.	1936	1937
CN-0	$x+70$	223	4.77±.30 [5]	3.71±.25 [5]	187	2.86±.21 [5]	3.18±.24 [5]
CN-1	$x+358$	74	5.63±.46	6.93±.69	59	3.12±.36	4.65±.71
CN-2	$x+646$	34	6.03±.50	11.20±.92	59	2.95±.26	6.68±.44
CN-3	$x+934$	70	6.51±.79	11.51±.87	59	3.87±.38	7.30±.87

[1] Curves of average relationship are shown in Figs. 7 and 8.

[2] The *CN* Series plots were fertilized April 20-21, 1936 (see Table 6).

[3] See footnote 4, Table 6.

[4] The averages for each species are based upon data from approximately 18 trees on the control plot (*CN-0*) and 6 trees on each of the other plots. Measurements were made of the growth of the terminal leader, and of twigs from an average of 10 different locations throughout the crown of each tree.

[5] Standard error of the mean.

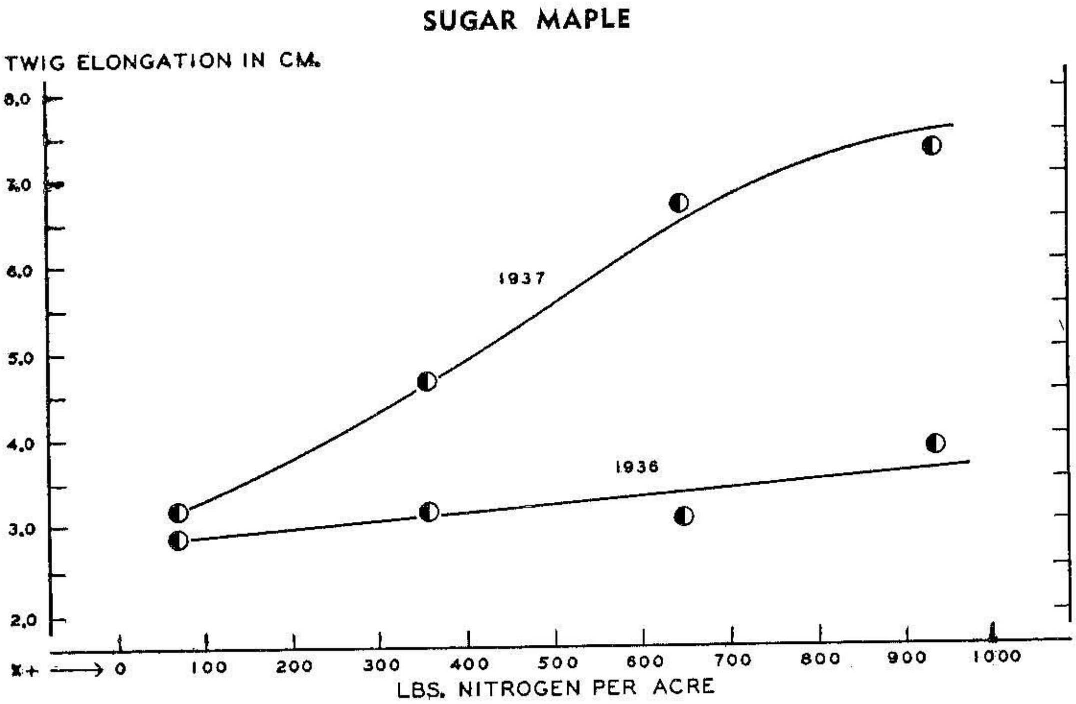

FIG. 7.—The 1936 and 1937 twig elongation of sugar maple trees growing on plots fertilized with varying amounts of nitrogen in the spring of 1936.

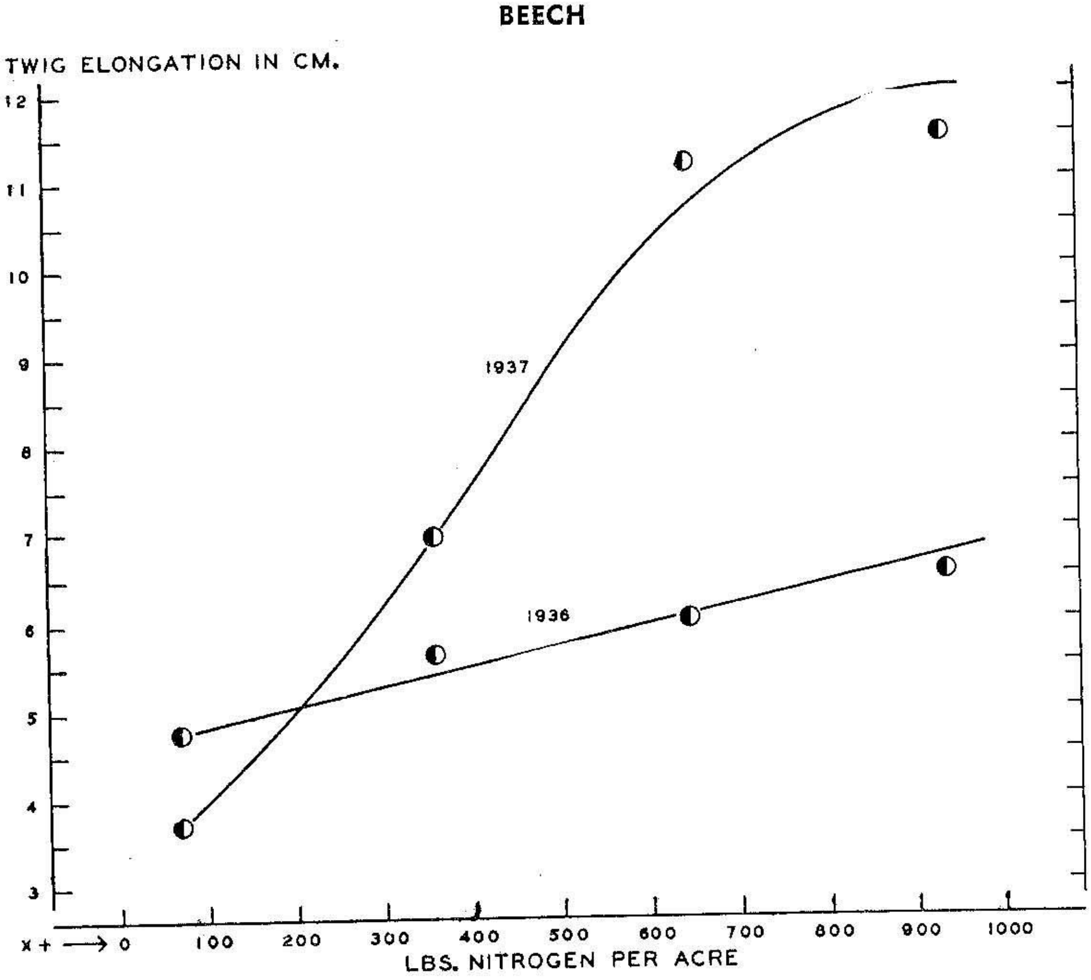

FIG. 8.—The 1936 and 1937 twig elongation of beech trees growing on plots fertilized with varying amounts of nitrogen in the spring of 1936.

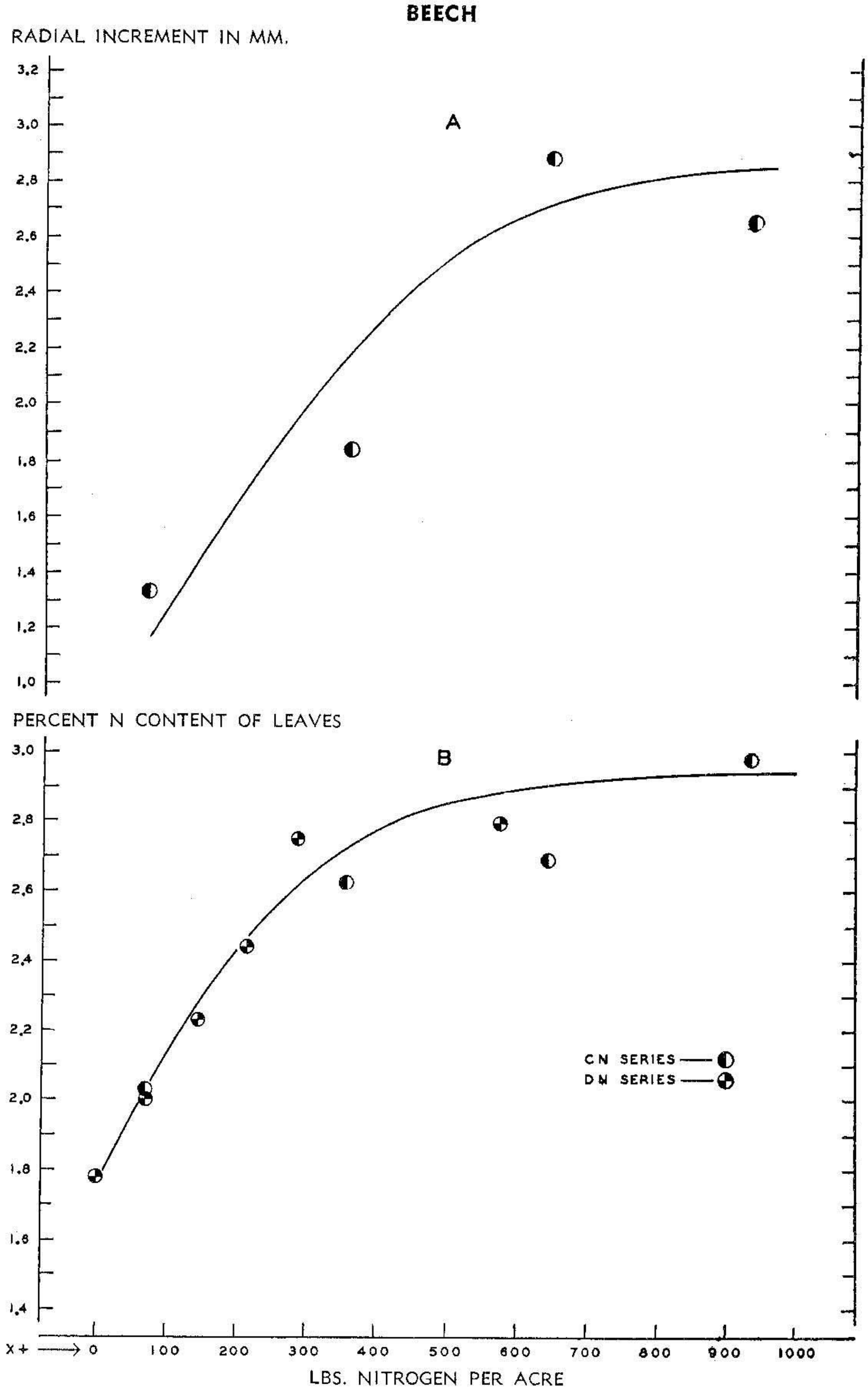

FIG. 9.—The relationships between nitrogen supply and the annual radial increment and the nitrogen content of the leaves of beech trees growing in even-aged stands of mixed hardwoods.

tion is that in 1936 climatic conditions—the quantity and quality of solar radiation, temperature, rainfall, humidity, etc.—were more favorable for the twig growth of beech, but less favorable to sugar maple, than those which obtained during the 1937 season.

Beech trees were relatively numerous only on the *CN* and *DN* Series plots. Thus the data regarding this species are few in comparison with many of the other species studied. However, the analytical results plotted in Fig. 9 indicate a high degree of correlation between nitrogen supply and the concentration of this element in the leaves of beech (see statistical data entered in Table 8). Aside from the fact that the leaves of beech growing on the poorer sites have a significantly higher nitrogen content, the $N_{\%}$ curve for beech is almost identical with that of sugar maple (Fig. 13).

The radial increment data for beech are relatively meagre, and as shown in Fig. 9, not very satisfactory. However, it appears that beech approach maximum radial growth at a relative nitrogen supply of from $x + 400$ to 500 pounds per acre, the same as for sugar maple. These supplies are sufficient to produce in the leaves nitrogen concentrations of 2.77 to 2.85%.

Pignut Hickory.—The data presented in Fig. 5 (B) indicate that the curve of average relationship between nitrogen supply and the concentration of this element in the leaves of pignut hickory trees has essentially the same shape as the other $N_{\%}$ curves thus far considered. The major point of difference is that increments of nitrogen above $x + 100$ pounds per acre result in significantly lower concentrations of nitrogen in the leaves of pignut hickory than in those of any of the other species studied (Fig. 13). Although there were a few hickories on each of the *ON* Series plots and on plots *N-0, 1* and *3,* they occurred as a primary element of the stand only on plots *BN-0, 1* and *2.* Hence the growth data for this species are relatively meagre. However, as shown in Fig. 10 (B),

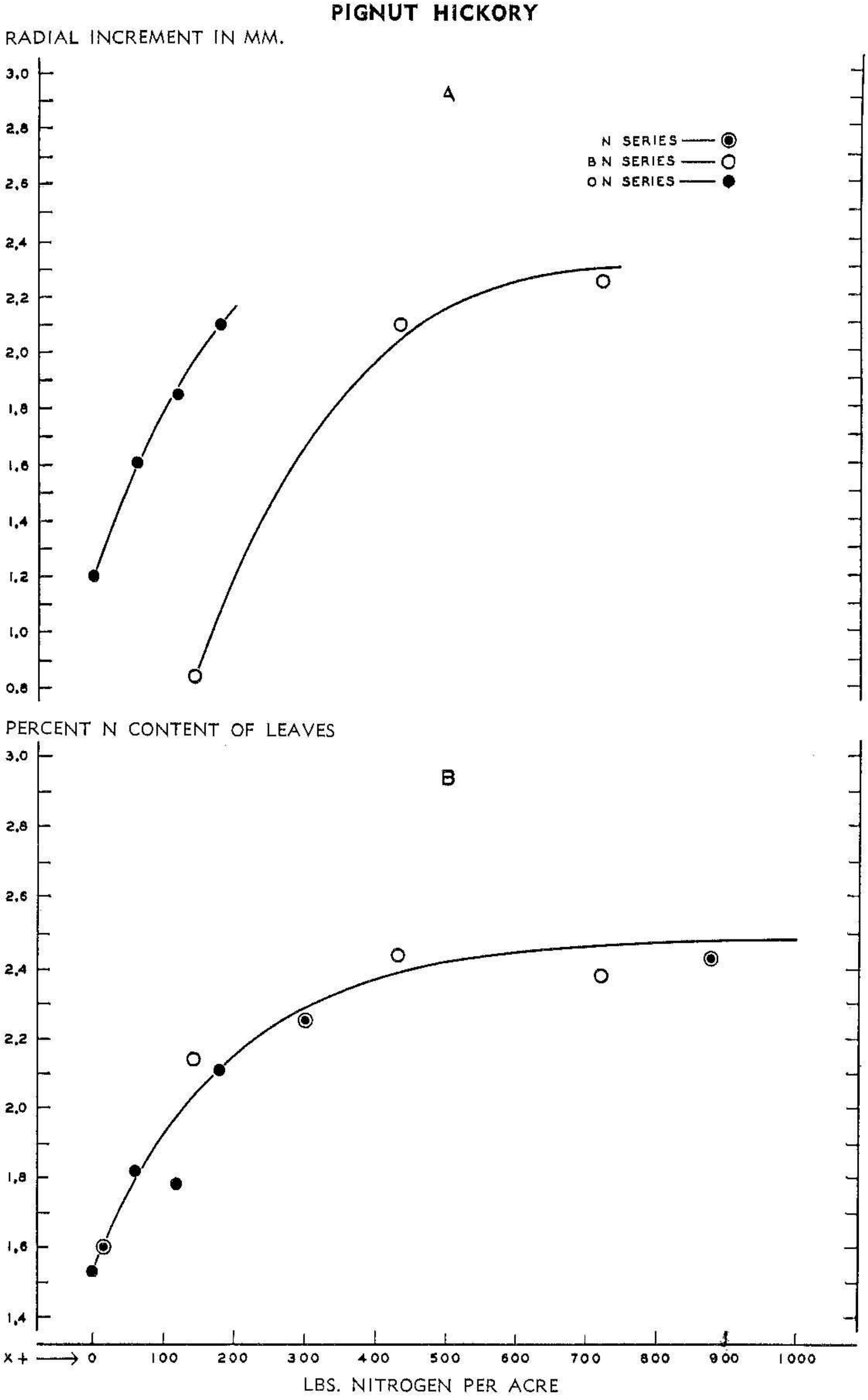

FIG. 10.—The relationships between nitrogen supply and the annual radial increment and the nitrogen content of the leaves of pignut hickory trees growing in even-aged stands of mixed hardwoods.

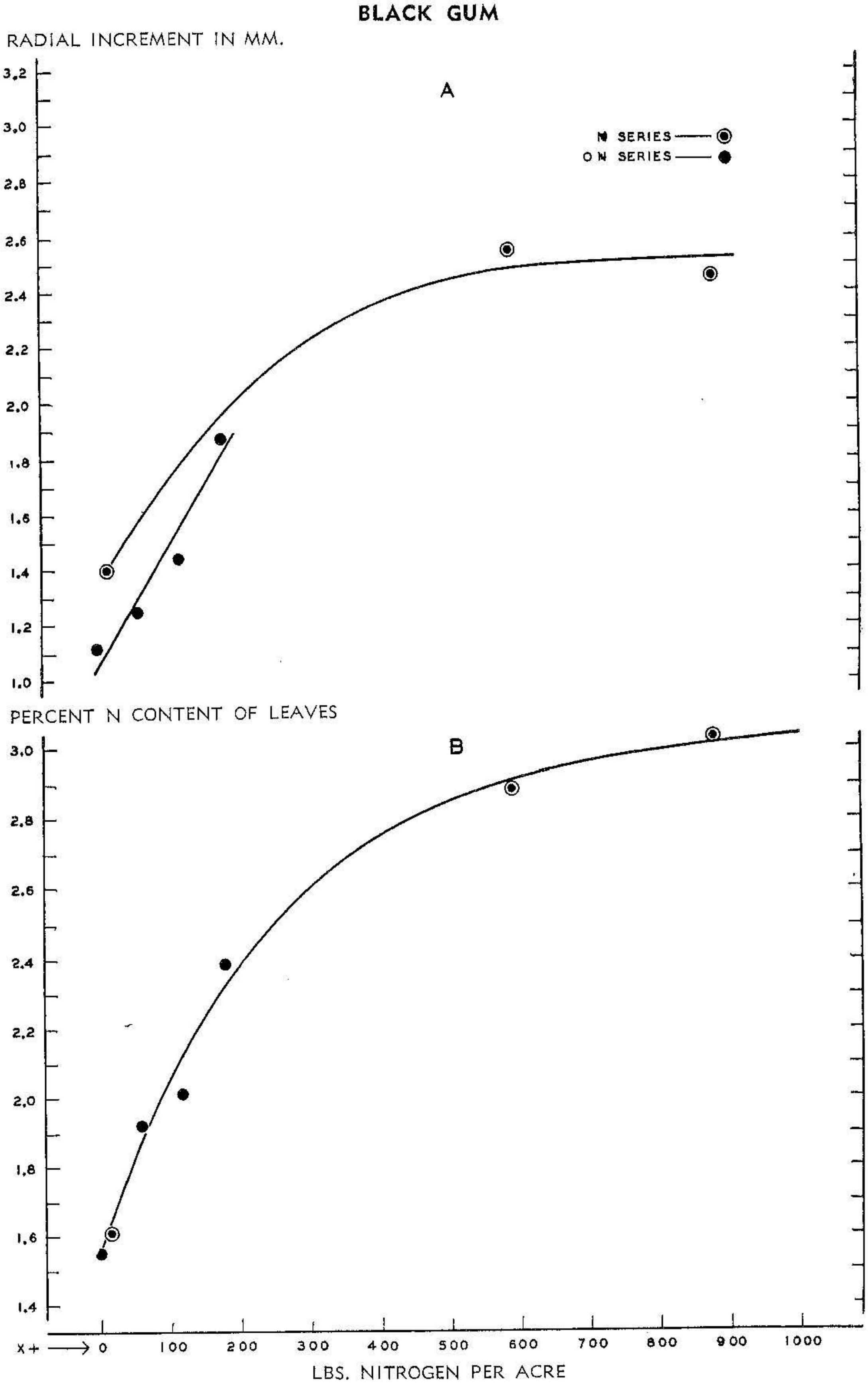

FIG. 11.—The relationships between nitrogen supply and the annual radial increment and the nitrogen content of the leaves of black gum trees growing in even-aged stands of mixed hardwoods.

maximum growth apparently occurs at a nitrogen supply of from $x +$ 400 to 500 pounds per acre, which is sufficient to produce in the leaves a nitrogen concentration of 2.37 to 2.42%.

Black Gum.—The growth measurements and analytical results for black gum, which occurred only on plots of the *N* and *ON* Series, are shown in Fig. 11. Although based upon relatively few data at the higher nitrogen supplies, the $N_{\%}$ curve for this species appears to be very similar to those for sugar maple, beech and white ash (Fig. 13). As with sugar maple and white ash, the internal nitrogen concentration of black gum is comparatively low on nitrogen-deficient sites but high on those soils which were heavily fertilized. The data presented in Fig. 11 (A) indicate that, like sugar maple, beech and pignut hickory, black gum approach maximum radial growth at a relative nitrogen supply of from $x +$ 400 to 500 pounds per acre. The internal nitrogen concentrations corresponding to these supplies are 2.75 to 2.85%.

Yellow Poplar.—As with the other species studied, the nitrogen content of the leaves of yellow poplar is highly correlated with nitrogen supply. The curve of average relationship, which may be expressed with the Mitscherlich equation, is shown in Fig. 14 (B), and the results of statistical analyses are summarized in Table 8. Compared with other species growing on the poorest soils, yellow poplar appears to be intermediate as regards internal nitrogen concentration. However, at the higher nitrogen supplies, the leaves of yellow poplar are second only to those of basswood in nitrogen concentration (Fig. 13).

According to the data presented in Fig. 14 (A), increasing the nitrogen supply by 180 pounds per acre resulted in an increase of approximately 250 percent in the annual radial increment of yellow poplar trees on the *ON* Series plots. Since the average trend is a linear increase, with the growth curve showing no tendency to flatten even at

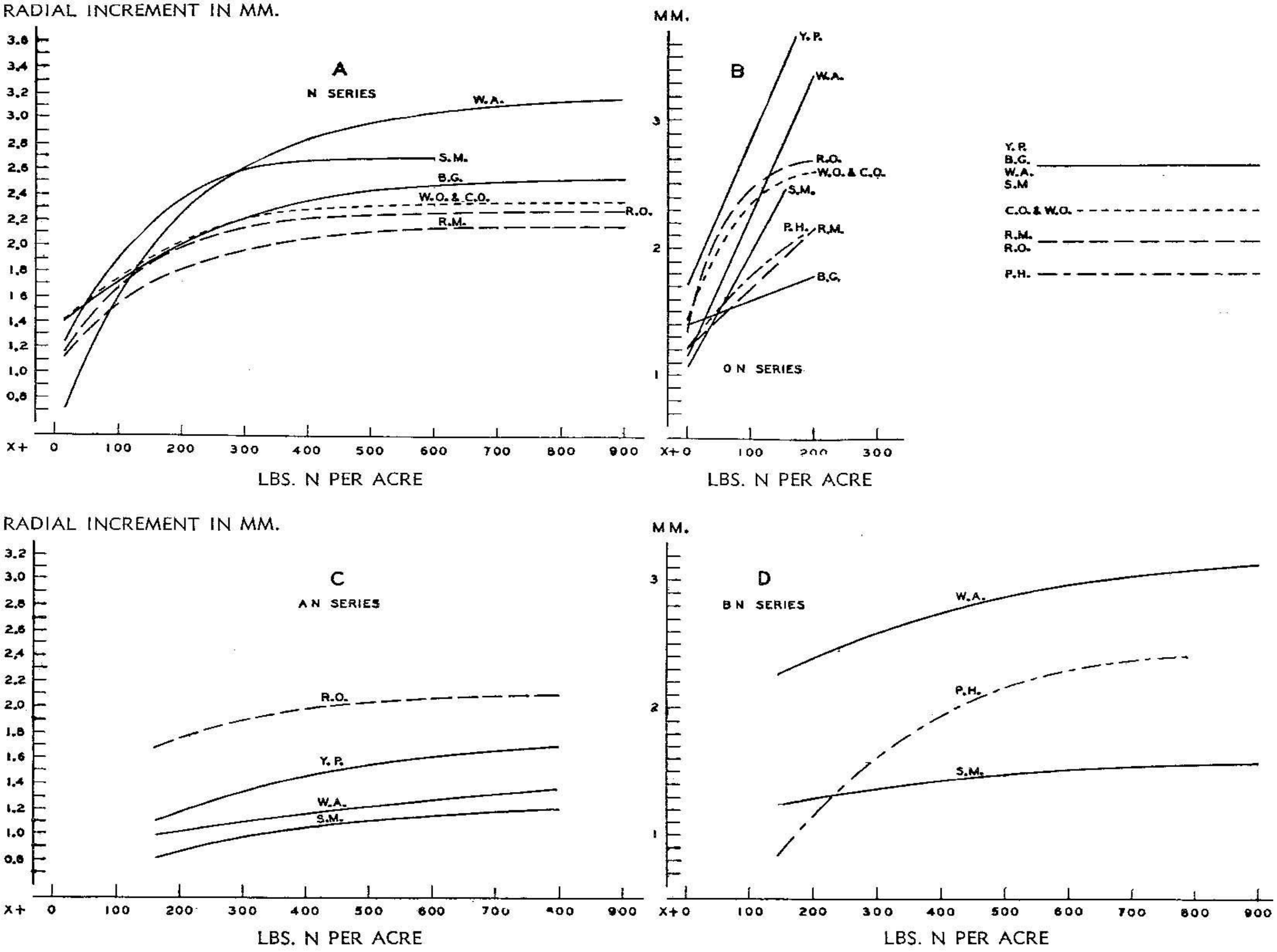

FIG. 12.—The relationships between nitrogen supply and the annual radial increment of various tree species on: A, the *N* Series plots; B, the *ON* Series plots; C, the *AN* Series plots; and D, the *BN* Series plots.

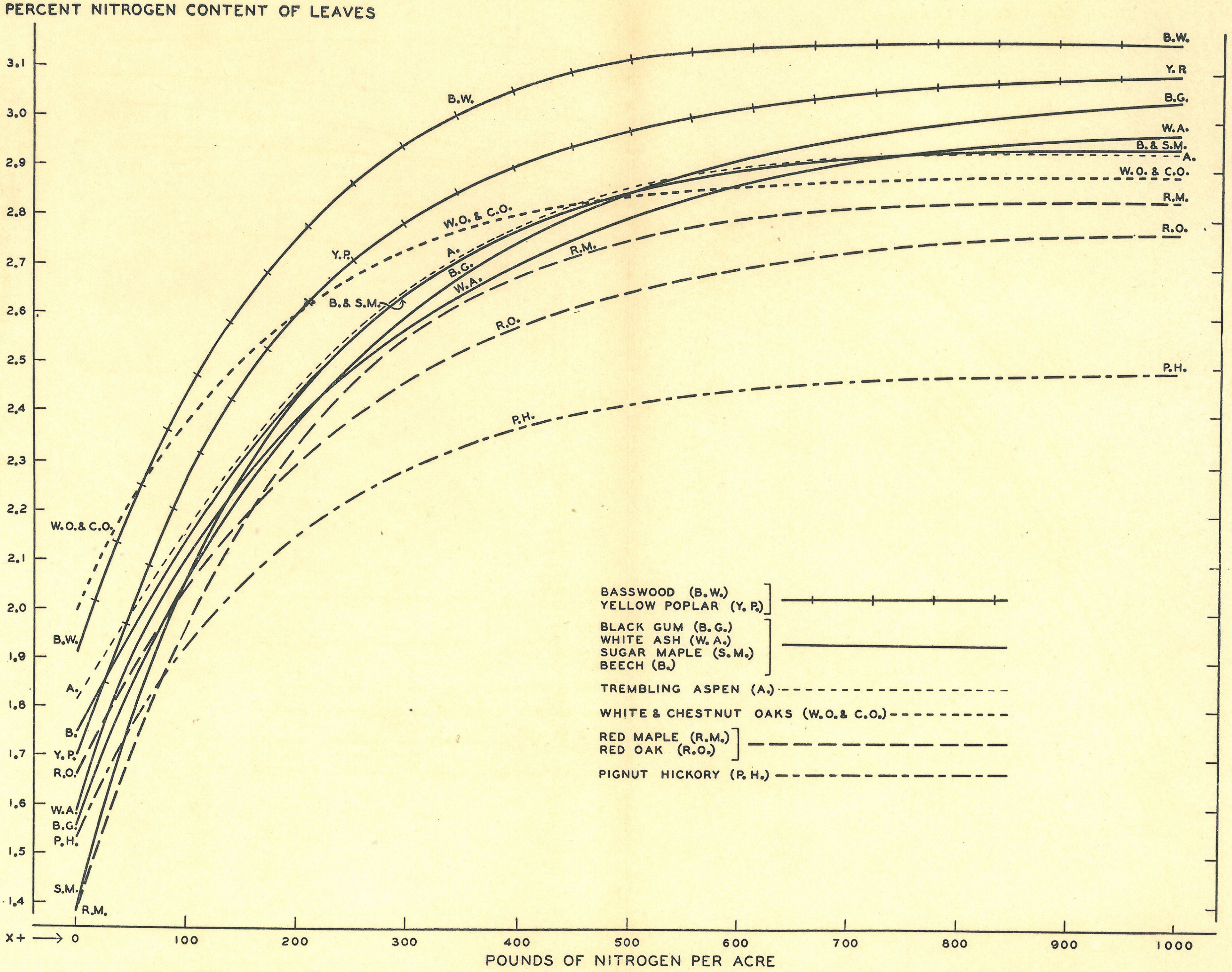

FIG. 13.—Comparison of the nitrogen content of the foliage of different tree species growing on plots supplied varying amounts of nitrogen.

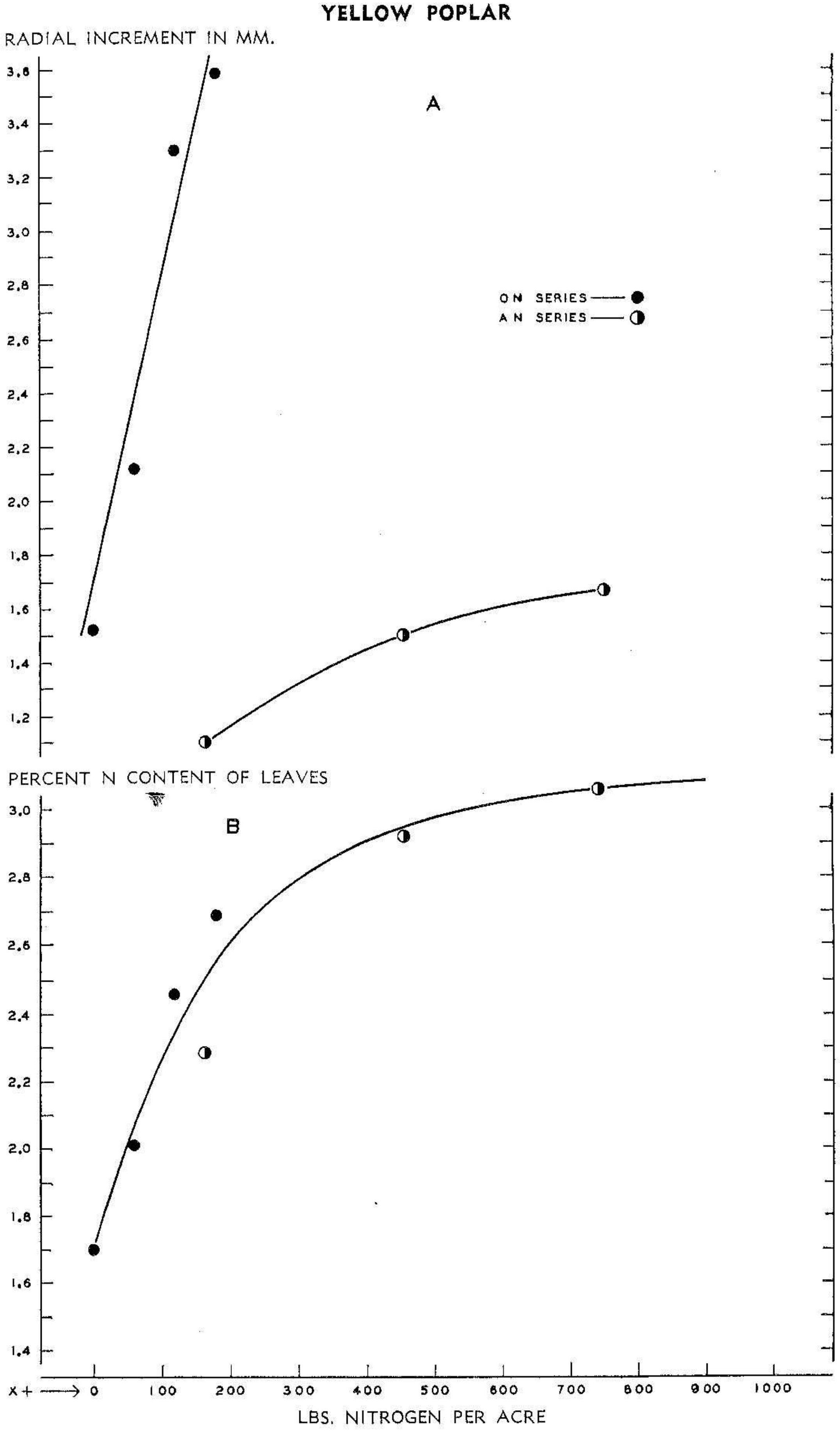

FIG. 14.—The relationships between nitrogen supply and the annual radial increment and the nitrogen content of the leaves of yellow poplar trees growing in even-aged stands of mixed hardwoods.

the highest nitrogen supply, it is probable that the trees on this site would benefit significantly by even greater nitrogen supplements. The relative nitrogen supply of $x + 180$ pounds per acre is by no means optimum for the species, as is further evidenced by data on trees of the *AN* Series plots, which include a wider range of nitrogen supplies. These growth measurements, although for the same year that the fertilizer was applied, indicate that maximum radial increment is approached at a relative nitrogen supply significantly higher than for any of the other species thus far considered. That is, a nitrogen supply of from $x + 500$ to 600 pounds per acre. The internal nitrogen concentrations associated with these supplies are 2.97 to 3.02%.

Basswood.—Although there were a few basswoods on each of the *ON* Series plots and one to three trees on various *AN* and *BN* Series plots, this species was relatively frequent only on plots of the *CN* and *DN* Series. The curve of average relationship between nitrogen supply and the nitrogen content of the leaves of basswood is shown in Fig. 15 (B). The scantiness of the data, especially the small number of observations which determine the location of many of the plotted points, is reflected in the deviations from the curve and is further evidenced by the results of statistical tests, as summarized in Table 8. However, it is apparent that the average trend is essentially the same as for the other species studied. The most numerous data are for the lower ranges of nitrogen supply. These indicate that the leaves of basswood on the poorer sites have a nitrogen concentration second only to those of white and chestnut oaks. At the higher levels of nitrogen availability the internal nitrogen concentration of basswood appears to be significantly greater than that of the oaks or any other species included in the present study. As to the deviations from the curve of average relationship, it is significant that, in general, those points which fall considerably below the curve rep-

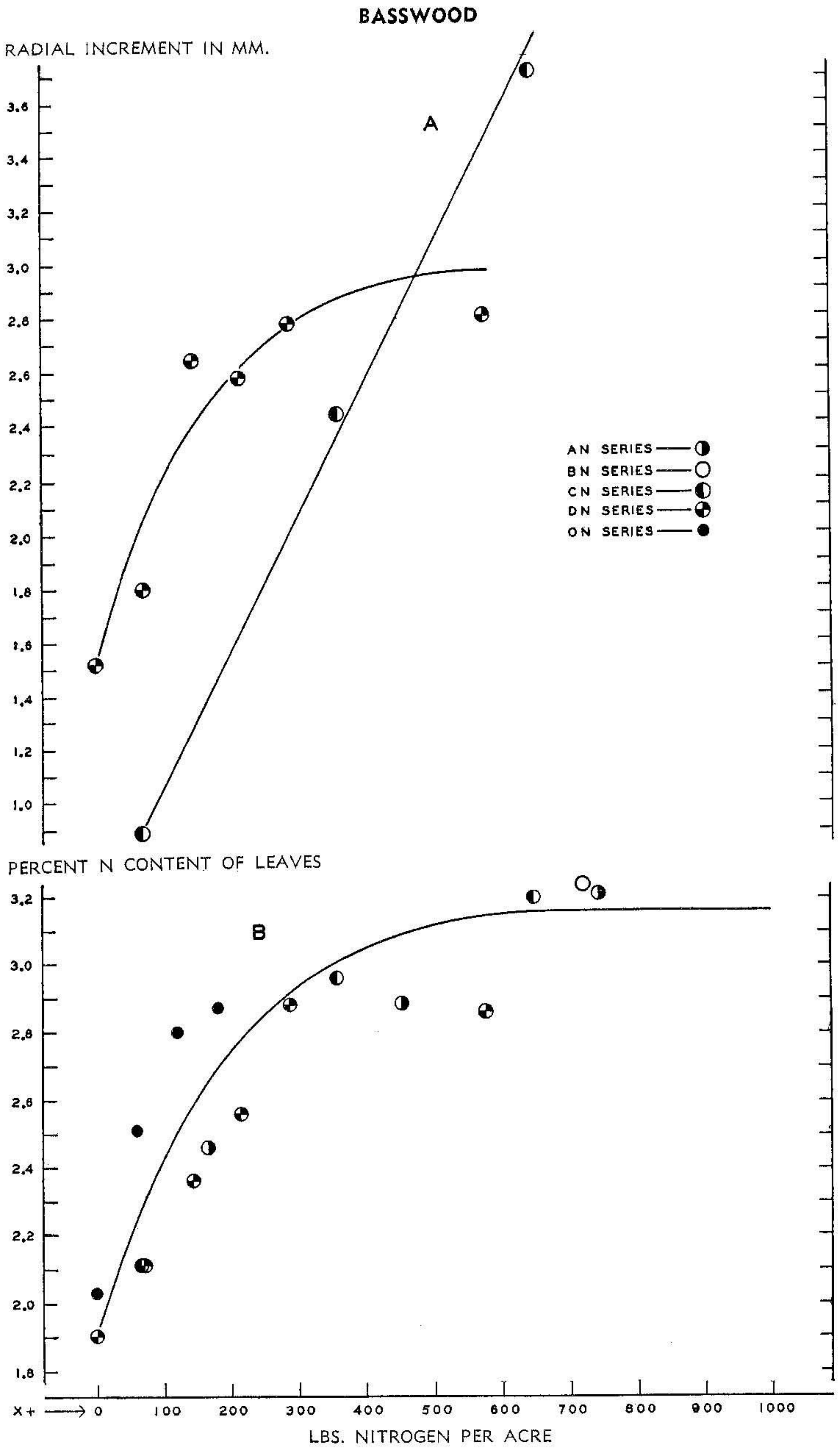

FIG. 15.—The relationships between nitrogen supply and the annual radial increment and the nitrogen content of the leaves of basswood trees growing in

resent plots located in stands with significantly higher than average basal areas.

According to the *DN* Series data presented in Fig. 15 (A) it appears that, in view of the relatively poor growth response of trees on plot *DN-5*, maximum radial growth for the species is approached at a relative nitrogen supply of from $x + 300$ to 400 pounds per acre. However, many of the basswood trees on this particular plot (*DN-5*) are in poor condition compared to other elements of the stand; only a few of those measured were in the dominant or codominant crown classes. It is doubtful, therefore, if the data for this plot, which determine the shape of the growth curve at the higher nitrogen supplies, should be given much weight. As regards the growth response of this species to nitrogen supplies greater than $x + 300$, the data for trees on the *CN* Series plots are believed to be much more reliable. The two growth curves shown in Fig. 15 (A) have approximately the same slope over the range of from $x + 0$ to $x + 300$ pounds of nitrogen per acre. At greater nitrogen supplies the curve based on the more reliable *CN* Series data shows no tendency to flatten. Thus, as with yellow popular, basswood trees probably approach maximum radial increment at a relative nitrogen supply of not less than $x + 500$ to 600 pounds per acre. The internal nitrogen concentrations corresponding to these supplies are 3.12 to 3.15%.

White Ash.—This species is a primary element of the stands in which the *AN* and *BN* Series plots were located, and occurs to some extent on practically all of the other sites. The curve of average relationship between nitrogen supply and the nitrogen content of the leaves of white ash is shown in Fig. 16 (B). That there is a high degree of association between the two variables, N supply and $N_{\%}$, is evidenced by the statistical data presented in Table 8. As with the other species discussed, the average trend may be expressed with the Mitscher-

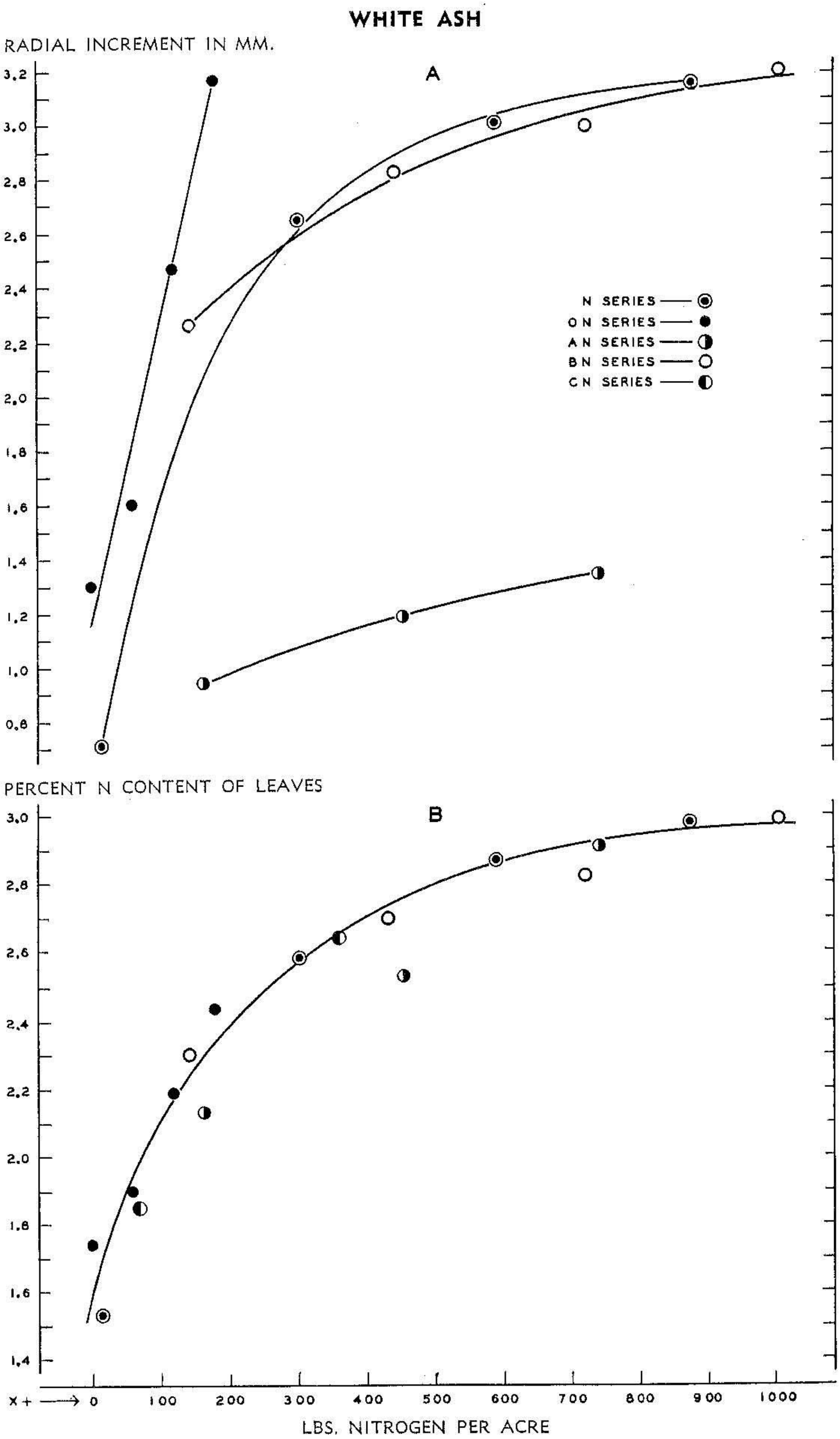

FIG. 16.—The relationships between nitrogen supply and the annual radial increment and the nitrogen content of the leaves of white ash trees growing in even-aged stands of mixed hardwoods.

lich equation. It is interesting that, in general, those points which fall significantly below the curve (Fig. 16, B) represent $N_{\%}$ data from trees in stands of greater than average basal area. This is additional proof of the influence of root competition upon the nitrogen intake of trees. According to the comparative data summarized in Fig. 13, the internal nitrogen concentration of white ash growing on poor sites is relatively low, all species considered. However, like black gum, beech, sugar maple, yellow poplar and basswood, the nitrogen content of the leaves of ash on plots rich in this element is significantly higher than for the white oaks, which apparently excel all other species on the poorest soils.

The data presented in Fig. 16 (A) indicate that the growth response of white ash to increasing nitrogen supplies is somewhat similar to that of basswood and yellow poplar, and far greater than the response of any other species studied. Trees on plot *N-0* and those on the most heavily fertilized plot of the *N* Series differed in annual radial increment by over 300 percent, a highly significant increase. The relationship between nitrogen supply and the growth of ash on variously fertilized plots of the other sites show similar trends. Trees on each of the different sites approach maximum radial increment at about the same relative nitrogen supply, *i.e.,* between $x + 500$ and 600 pounds per acre. These supplies are sufficient to produce in the leaves of ash a nitrogen concentration of from 2.80 to 2.86%. As discussed in connection with various other species, the relatively poor growth of trees on the *AN* Series site is attributed to the greater age and basal area of this stand, and to factors of site other than nitrogen supply.

The Influence of Nitrogen Upon the Leaf Color and Size

One of the outstanding results of this study was the influence of the fertilizer upon leaf size and color.

Nitrogen was applied to plots of each series in the early spring. By the first of July the darker green color of the leaves on the fertilized plots was noticeable. By September this difference was very great. Even three years after the fertilizer was applied the leaves of trees on the treated plots showed a dark green color which contrasted markedly with the light yellowish-green of those on the check plots.

The leaf size was also increased greatly by nitrogen fertilizer applications. Comparative measurements were made of the leaves of sugar maple from plot *CN-3,* which received 864 pounds of nitrogen per acre, and the control plot of the *CN* Series. The former were from 30 to 150 percent greater in size than those from trees on the untreated plot. Similar differences were observed in the size of the leaves of dogwood and other species growing on the *N* Series plots (Mitchell and Hosley, 1936).

It seems probable that the deeper green color (doubtless indicating an increased chlorophyll content) and the larger leaf size contributed markedly to the abundant seed crop produced the second year after fertilization, as reported by Chandler (1938) for the plots at the Arnot Forest.

DISCUSSION

THE OPTIMUM NITROGEN SUPPLY

SINCE foresters are primarily interested in merchantable volume, the optimum nitrogen supply for a given tree species may be defined as one which will result in the greatest volume increment. For trees of the age classes included in the present study, radial growth is believed to be an acceptable index to volume increment. The optima for the various species were determined on this basis.[1]

In the present experiment six series of variously fertilized but otherwise uniform plots were established over a period of three years on each of several different site qualities, and in stands which differed somewhat as regards age, composition, condition and basal area. Because of these differences the average radial increment of a given species on a plot of any one series may be quite different from that of the same species on a plot of another series, even though the two sites are identical as regards relative nitrogen supply. On certain sites, such as that on which the *AN* Series plots are located, tree growth is definitely limited by factors other than nitrogen. Thus the *magnitude* of the growth response to

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[1] In the present experiment no data were obtained on the relative quality of the wood produced by trees supplied varying amounts of nitrogen. However, the studies of Paul (1930) are of interest in this connection. The specific gravity and the strength of wood are known to be highly correlated (*cf.* Newlin and Wilson, 1919). Paul found a good relationship between diameter growth rate and the specific gravity of the wood produced by various deciduous and coniferous trees. For all deciduous species studied—white ash, pignut hickory, shagbark hickory, rock elm, sugar maple and yellow poplar—relief from unfavorable growing conditions was always accompanied by an increase in the specific gravity of the wood. In discussing the application of these data, Paul states: ''Improvement of the soil is suggested as a means of improving wood quality.''

equal increments of nitrogen is different for each series of plots. However, a very significant point brought out by the data thus far discussed is that trees of a given species on each series of variously fertilized plots approach maximum radial growth, for the site, at approximately the same relative nitrogen supply (Figs. 2, 3, 4, 5, 6, 9, 10, 11, 12, 14, 15 and 16).

To facilitate further discussion, the entire range of nitrogen supplies included in these experiments may be divided into regions upon the basis of growth response. In the case of red oak, for example, nitrogen supplies up to around $x + 50$ pounds per acre, which are definitely limiting, may be termed the "region of minima." Other factors being favorable, the growth response of red oak trees to increments of nitrogen through this range of supplies exceeds a direct proportion (Fig. 2). Those supplies from $x + 50$ and increasing up to $x + 300$ to 400 pounds of nitrogen per acre, through the upper ranges of which the growth curve tends to flatten, may be called the "working region." As will be brought out later in the discussion, quantitative estimates of nitrogen-supplying capacity place approximately 65 percent of the forest sites of the Northeast within the limits of this region. The upper limits of the working region, at which supplies the trees approach maximum radial growth, will be considered the optimum for the species. That range of supplies from $x + 300$ to 900, through which increments of nitrogen result in little or no change in radial growth, may be termed the "region of tension." The various range divisions are summarized in Table 11.

The curves of average relationship between nitrogen supply and the radial increment of nearly mature deciduous trees are essentially the same as those which express the dry weight increase of one-year-old coniferous seedlings grown in nutrient-sand cultures of varying nitrogen concentration (*cf.* Fig. 11, Gast, 1937; Fig. 8-A, Mitchell, 1939). In each case that part of the nitrogen supply

TABLE 11

THE RANGE OF NITROGEN SUPPLIES DIVIDED INTO REGIONS ACCORDING TO THE GROWTH RESPONSE OF THE VARIOUS SPECIES STUDIED [1]

Nitrogen-Tolerance Group (1)	*Species* (2)	*Region of Minima* (3)	*Working Region* (4)	*Estimated Optimum Supply* (5)	*Region of Tension* (6)
I	Red Oak White and Chestnut Oaks Trembling Aspen Red Maple	Up to $x + 50$	$x + 50$ to 300-400	$x + 300$ to 400	$x + 300$ to 900
II	Pignut Hickory Sugar Maple Beech Black Gum	Up to $x + 50$	$x + 50$ to 400-500	$x + 400$ to 500	$x + 400$ to 900
III	White Ash Yellow Poplar Basswood	Up to $x + 75$	$x + 75$ to 500-600	$x + 500$ to 600	$x + 500$ to 900

[1] Curves of average relationship between relative nitrogen supply (as pounds per acre) and the annual radial increment of the various species are shown in Figs. 2, 3, 4, 5, 6, 9, 10, 11, 12, 14, 15 and 16.

range which includes levels of nitrogen availability—expressed as pounds per acre or milligrams per liter of solution—equivalent in effect to those found in nature may be divided into corresponding regions upon the basis of growth response. At exceedingly high nitrogen supplies—that is, external concentrations greater than 300 to 350 ppm—the yield of culture-grown coniferous seedlings varies inversely as the nitrogen concentration. Those supplies which depress seedling growth have been termed the "toxic region" (Gast, 1937; Mitchell, 1934, '39). However, in the present experiment there was no evidence of decreased radial growth of trees even on those plots where the available nitrogen supply exceeded that of the most fertile natural soils. As shown in the various illustrations, the growth curves tend to flatten at the higher nitrogen supplies, but there is no toxic region. Apparently the largest applications of nitrogen which were made during the present study were not sufficient to produce the deleterious effects which, on the basis of experience with shade and fruit trees, are known to result from excessive fertilization. Although of academic interest, the effects of nitrogen supplies significantly higher than those found in nature are of minor importance to the silviculturist and forest ecologist.

According to the growth data presented in Figs. 2, 3, 4, 5 and 12 white and chestnut oaks, red maple and trembling aspen respond to equal increments of nitrogen in much the same way as do red oaks. Thus, for these species, similar divisions may be made in the range of relative nitrogen supplies, as indicated in Table 11.

The response of such species as pignut hickory, sugar maple, beech and black gum to equal increments of nitrogen is somewhat different from that of the oaks, red maple and aspen. Whereas species of the latter group approach maximum radial increment at a relative nitrogen supply of from $x + 300$ to 400 pounds per acre, the yield curves for sugar maple, beech, pignut hickory and black gum (Figs. 6, 9, 10, 11 and 12) flatten at a higher nitrogen supply—*i.e.*, $x + 400$ to 500 pounds per acre.

The stimulating effect of increasing nitrogen supply is much more pronounced for yellow poplar, basswood and white ash than for any of the other species studied. Whereas variously fertilized trees of the oak-red maple-aspen group differ in growth rate by from 75 to 100 percent, and the order of variation for those of sugar maple-beech-hickory-black gum group is between 100 to 150 percent, the growth rates of yellow poplar, basswood and white ash on the poorest and most heavily fertilized plots differ by from 250 to 300 percent (Figs. 12, 14, 15 and 16). Thus, for the latter species, the upper limit of the region of minima is somewhat higher—$x + 75$ as compared to $x + 50$ for trees of the other two groups—and the optimum supply appears to be between $x + 500$ and 600 pounds per acre (Table 11).

CONCEPT OF TOLERANCE

On the basis of field observations and the results of controlled experiments foresters have classified the more important tree species according to shade tolerance. Such trees as beech, sugar maple and basswood, which are capable of sustaining growth in relatively low light intensities, are considered as tolerant species, whereas such light-demanding trees as aspen, grey birch and the willows are known as intolerant. It is apparent from the data thus far discussed that tree species may also be classified, as in Table 11, on the basis of their growth at varying levels of nitrogen supply. Since the term tolerance is equally applicable to environmental factors other than solar radiation,[1] there is no need to coin a new term to use in the classification of trees according to their nitrogen requirements or their requirements for

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[1] The word tolerant is defined (Merriam-Webster, 1935): ''3. *Biol.* Capable of sustaining unfavorable environment.''

phosphorus, potassium, calcium or any other essential nutrient element. Thus the species in group I (Table 11), which are apparently capable of sustaining a relatively satisfactory rate of growth in nitrogen-deficient soils, and which approach maximum radial increment at significantly lower levels of nitrogen supply than do species of the other two groups, may be considered as "nitrogen-deficiency tolerant."[1] Trees in group II, which includes beech, sugar maple, pignut hickory and black gum, appear to be intermediate in the scale of nitrogen tolerance. Such species as yellow poplar, white ash and basswood, which are infrequent or absent on poor sites, make relatively meagre growth in nitrogen-deficient soils, and attain maximum growth only at very high levels of nitrogen availability, may be considered as "nitrogen requiring" or "nitrogen demanding."[2]

Nitrogen-Deficiency Tolerance

No one of the different sites on which series of variously fertilized plots were established supported a stand in which every species studied was represented. Since certain of the species differ widely not only in nitrogen tolerance but in moisture requirements and shade tolerance as well, it is doubtful if a stand of the desired composition can be found in nature. In any event, so far as the present investigation is concerned it is impossible to compare, in absolute terms, the influence of varying nitrogen supply upon the radial increment of all the different trees. However, from the data at hand and various supplementary measurements and observations in the field it is possible to piece together a composite diagram which illustrates, on a relative rather than an

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[1] Abbreviated in the present discussion to "nitrogen tolerant."

[2] Because of the teleological connotation of demanding, requiring is perhaps the better term. However, since light demanding occurs frequently in forestry literature as an antonym for shade tolerant, nitrogen demanding is used synonymously with nitrogen requiring in the present discussion.

absolute basis, the characteristic differences between species of the various nitrogen-tolerance groups summarized in Table 11. Such a schematic diagram is shown in Fig. 17.

As illustrated by this diagram, the nitrogen-tolerant trees are not only capable of better growth in nitrogen-deficient soils than are the nitrogen-demanding species, but they approach maximum radial increment at significantly lower relative nitrogen supplies. These trends are apparent from the data presented in Tables 2, 3, 4, 5, 6 and 7, and are further substantiated by field studies which will be described later in the discussion. Another important difference is that the average growth rate of nitrogen-tolerant trees in soils of low nitrogen availability is very much greater, in comparison with the maximum of which they are capable at any level of nitrogen supply, than for the more demanding species.

At the lower levels of nitrogen supply there appears to be less difference between the growth of the intermediate species—*i.e.,* sugar maple, beech, black gum and pignut hickory—and that of the nitrogen-requiring trees of group III than between trees of these two groups and the nitrogen-tolerant species. In this range of nitrogen supplies the only clear-cut difference between trees of groups II and III is that the average growth rate of the former is significantly greater, in relation to the maximum of which they are capable, than for such species as white ash, yellow poplar and basswood. As regards response to higher levels of nitrogen availability, it is evident that trees of the intermediate group approach maximum growth at a lower relative nitrogen supply than the nitrogen-requiring species.

It is believed that the experimental evidence thus far examined clearly demonstrates that tree species differ widely in what has been termed nitrogen tolerance. The separation of species into three groups according to similarity of response to varying nitrogen supplies facili-

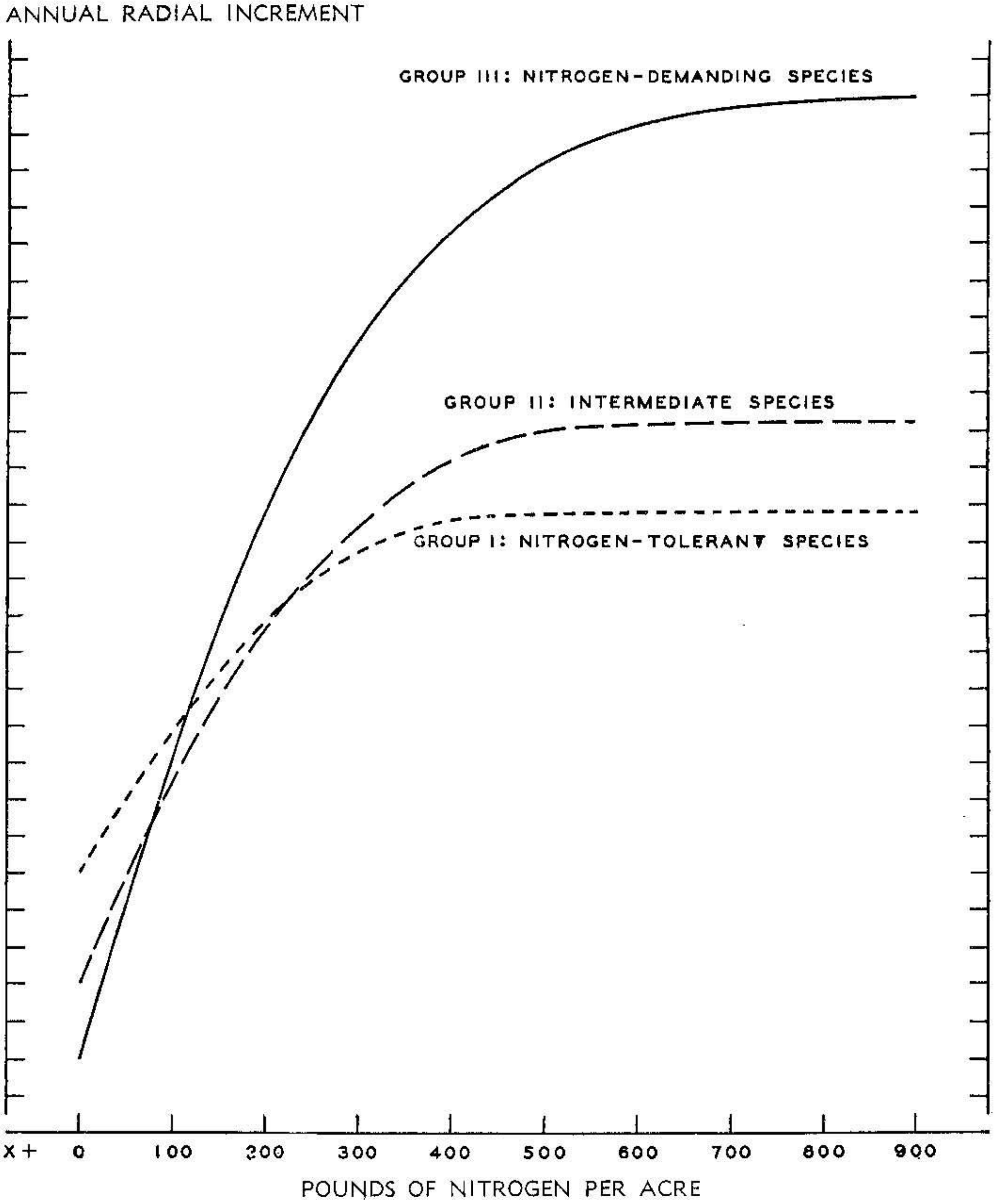

FIG. 17.—The relative growth response to increasing nitrogen supplies of nitrogen-tolerant, intermediate and nitrogen-demanding tree species.

tates discussion and interpretation of the data. It should be emphasized, however, that the dividing lines between the groups are arbitrary rather than hard and fast. Also that for such species as black gum, beech and basswood the growth data, especially those for trees growing at the higher levels of nitrogen availability, are too meagre to be regarded as highly reliable. Thus it may be necessary to reclassify, on the basis of the results of future studies, certain species which the present data place near the borderline between two groups. On the other hand there can be little doubt that such trees as red oak and white ash, for which the growth data are numerous and consistent, belong at opposite extremes of the nitrogen-tolerance scale.

THE RELATIONSHIP BETWEEN THE NITROGEN CONTENT OF THE LEAVES AND TREE GROWTH

The results of previous studies (Gast, 1937; Mitchell, 1934, '39) indicate that for various species of pine seedlings there is a high degree of correlation between the nitrogen content of the plants, or their needles, and seedling yield. Such a correlation is to be expected within certain critical ranges of nitrogen availability since internal nitrogen concentration, which is a function of the external supply, is the more precise measure of the nitrogen which enters into or otherwise influences the physiological processes that control growth. Inspection of the data presented in Figs. 2, 3, 4, 5, 6, 9, 10, 11, 14, 15 and 16 reveals similar relationships between the nitrogen content of the leaves and the radial increment of the various deciduous trees included in the present study. These trends are more apparent when the growth data are reclassified and plotted over $N_{\%}$ of leaves rather than relative nitrogen supply, as is shown in Fig. 18 for four species growing on the *ON* Series plots. When similarly plotted, the data for the various species on the

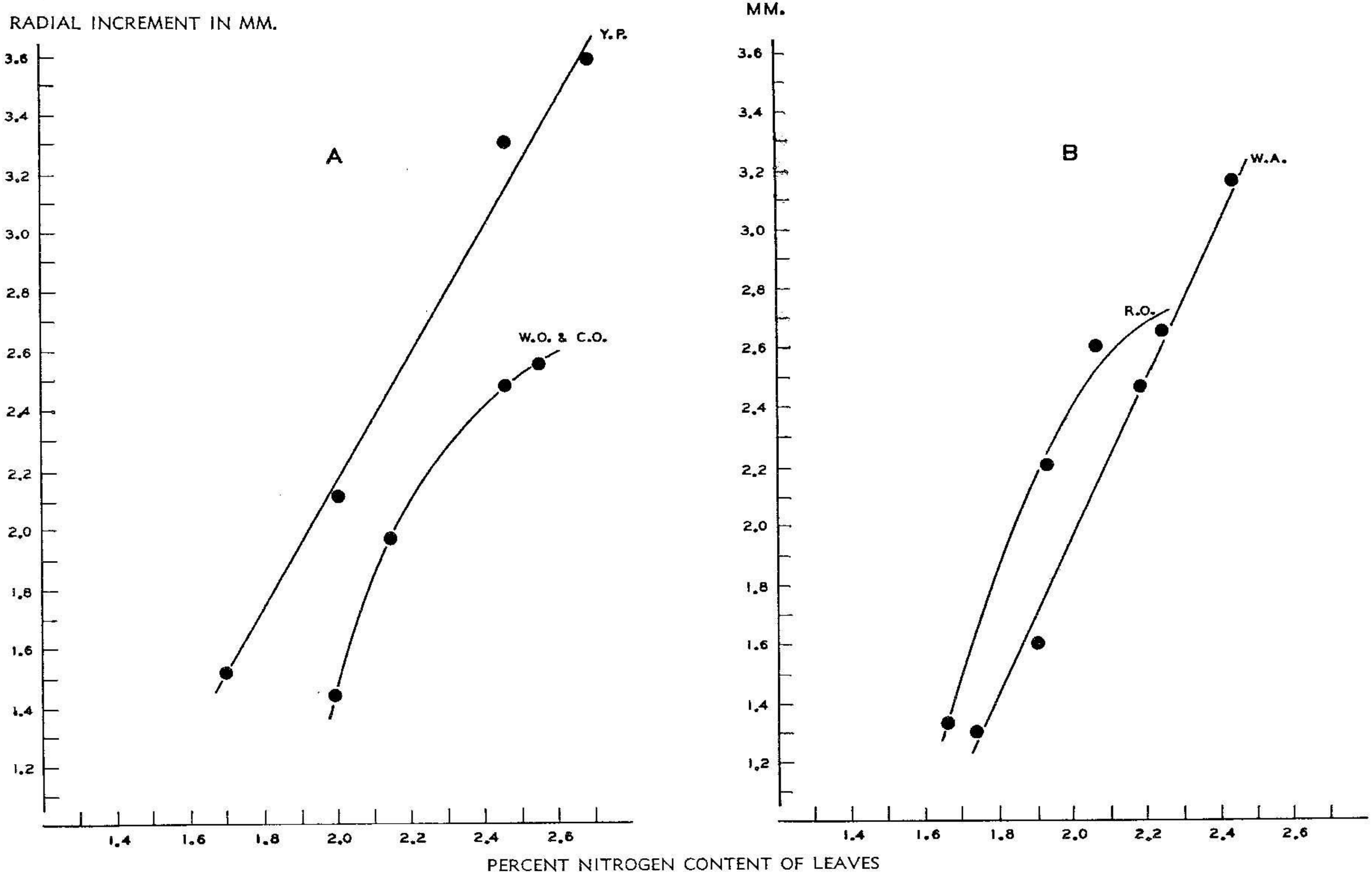

FIG. 18.—The relationships between the nitrogen content of the leaves and the annual radial increment of various tree species growing on the *ON* Series plots.

The point plotted over 2.25 on the abscissa in Fig. 18(B) determines the shape of the red oak yield curve through the upper limits of the internal nitrogen concentration range (basic data from Table 3).

other sites studied reveal the same relationships between $N_{\%}$ of leaves and radial increment.

As with coniferous seedlings (Mitchell, 1939), the internal (leaf) nitrogen concentrations of the various deciduous trees may be separated, upon the basis of growth response, into regions which correspond almost exactly to those into which the relative nitrogen supplies were divided. Thus, in the case of red oak (Figs. 2 and 18), the $N_{\%}$ range up to 1.87, where nitrogen is definitely a limiting factor and increments thereof result in a growth response which exceeds a direct proportion, may be termed the region of minima. Internal nitrogen concentrations from 1.87 and increasing up to 2.46—2.57, which, as will be shown, are equivalent to those of trees growing in average to good natural soils, can be called the working region. The $N_{\%}$ values from 2.46 to 2.57, which are associated with trees approaching maximum radial increment (Fig. 2), may be considered the optimum region. That range of from 2.46 and increasing up to 2.76—the latter value being highest internal concentration attained with any amount of fertilizer applied—through which increments in internal nitrogen concentration appear to have little or no effect upon radial growth, may be termed the region of tension. The internal nitrogen concentration ranges of the other species studied may be similarly divided, as summarized in Table 12, on the basis of growth response at varying levels of *internal* nitrogen concentration.

As is evident from the data presented in the foregoing discussion, radial growth is related to internal (leaf) nitrogen concentration as well as to the external (soil) supply. Although foresters are accustomed to think in terms of the latter, there is reason to believe that the effects of nitrogen on the physiological processes in trees can be more closely approximated by the use of internal concentrations.

The data summarized in Table 12 not only afford some

TABLE 12

INTERNAL (LEAF) NITROGEN CONCENTRATIONS DIVIDED INTO REGIONS ON THE BASIS OF THE GROWTH RESPONSE OF THE VARIOUS SPECIES

Nitrogen-Tolerance Group	*Species*	*N% of Leaves on Poorest Control Plot*	*Region of Minima*	*Working Region*	*Estimated Optimum N%*	*Region of Tension*
(1)	*(2)*	*(3)*	*(4)*	*(5)*	*(6)*	*(7)*
I	Red Oak	1.66	Up to 1.87	1.87 to 2.46-2.57	2.46 to 2.57	2.46 to 2.76
	White and Chestnut Oaks	2.00	Up to 2.22	2.22 to 2.72-2.80	2.72 to 2.80	2.72 to 2.88
	Trembling Aspen	1.81	Up to 2.00	2.00 to 2.64-2.77	2.64 to 2.77	2.64 to 2.93
	Red Maple	1.38	Up to 1.70	1.70 to 2.55-2.68	2.55 to 2.68	2.55 to 2.83
	Group I averages	*1.71*	*Up to 1.95*	*1.95 to 2.59-2.71*	*2.59 to 2.71*	*2.59 to 2.85*
II	Pignut Hickory	1.53	Up to 1.75	1.75 to 2.37-2.42	2.37 to 2.42	2.37 to 2.48
	Sugar Maple	1.38	Up to 1.75	1.75 to 2.77-2.85	2.77 to 2.85	2.77 to 2.94
	Beech	1.75	Up to 1.95	1.95 to 2.77-2.85	2.77 to 2.85	2.77 to 2.94
	Black Gum	1.55	Up to 1.83	1.83 to 2.75-2.85	2.75 to 2.85	2.75 to 3.02
	Group II averages	*1.55*	*Up to 1.82*	*1.82 to 2.67-2.74*	*2.67 to 2.74*	*2.67 to 2.85*
III	White Ash	1.58	Up to 2.01	2.01 to 2.80-2.86	2.80 to 2.86	2.80 to 2.97
	Yellow Poplar	1.70	Up to 2.15	2.15 to 2.97-3.02	2.97 to 3.02	2.97 to 3.08
	Basswood	1.90	Up to 2.32	2.32 to 3.12-3.15	3.12 to 3.15	3.12 to 3.16
	Group III averages	*1.72*	*Up to 2.16*	*2.16 to 2.96-3.01*	*2.96 to 3.01*	*2.96 to 3.07*
	Averages, all species	**1.66**	**Up to 1.96**	**1.96 to 2.72-2.80**	**2.72 to 2.80**	**2.72 to 2.91**

interesting comparisons which shed additional light on the fundamental differences between species of the three nitrogen-tolerance groups, but also aid in explaining the discrepancies the reader may have noted between the classification of species in Fig. 13 and the grouping of trees in Tables 11 and 12 according to nitrogen tolerance. As regards Fig. 13, discussion of which has been deferred to this point, it will be observed that the various trees are grouped according to the general shape of their $N_{\%}$ curves in relation to that for white and chestnut oaks, which have a significantly higher internal nitrogen concentration on the poorer sites than any of the other species. Thus basswood and yellow poplar are classed together since the $N_{\%}$ curves for these two species increase sharply, cross above the white oak-chestnut oak curve at relatively low nitrogen supplies, and attain maxima which are considerably higher than for the other species. According to this classification ash is not grouped with basswood and yellow poplar, as in Table 11, since the $N_{\%}$ curve for this species corresponds more closely to those for beech, sugar maple and black gum. The curves for these four species all cross above the white oak-chesnut oak curve, but at higher relative nitrogen supplies than those of basswood and yellow poplar. The $N_{\%}$ curve for aspen, which is quite similar to that for white and chestnut oaks but has a significantly lower point of origin, is classed alone. So is that for pignut hickory which, as shown in Fig. 13, is quite different from those of any of the other species. Red oak and red maple are classed together because of the similarity in their curves of average relationship, neither of which crosses the white oak-chestnut oak $N_{\%}$ curve.

In view of the relationships between internal nitrogen concentration and radial increment, the fact that at the higher nitrogen supplies basswood and yellow poplar have greater internal nitrogen concentrations than any of the other trees is in agreement with the growth response of these species to increments of nitrogen through this range of supplies. Similarly, the internal nitrogen concentrations attained by practically all of the other species at the higher levels of nitrogen supply are in keeping with their respective growth rates through this range of supplies, and hence with the relative nitrogen-tolerance groupings summarized in Table 11. But at the lower levels of nitrogen supply the order in which the various species rank as to internal nitrogen concentration has little or no relationship to their relative growth rates or, therefore, to their classification according to nitrogen tolerance. Basswood, for example, has been rated as nitrogen demanding because of its poor growth in nitrogen-deficient soils. Yet the internal nitrogen concentration of this species on the poorest control plot is second only to that of white and chestnut oaks. On the other hand trembling aspen, which is capable of relatively good growth under similar conditions, has an internal nitrogen concentration significantly less than basswood (Fig. 13).

As pointed out earlier in this discussion, these apparent discrepancies can be explained upon the basis of the data summarized in Table 12. It will be observed that on the poorest control plots the average internal nitrogen concentration of trees included in the nitrogen-tolerant group is significantly greater, in relation to the optimum internal concentration, than for any of the intermediate or nitrogen-demanding species of groups II and III. For example, nitrogen-tolerant trees like white and chestnut oaks growing in soils with a relative nitrogen supply of $x + 0$ have an internal nitrogen concentration of 2.00, which is 74% of the lower limit of the optimum internal concentration range of from 2.72 to 2.80, whereas such a nitrogen-demanding species as white ash growing on an equally poor site has an internal nitrogen concentration of 1.58, which is only 56% of that necessary for maximum growth of this species. Similarly, the internal nitrogen concentration of trembling aspen growing on a nitrogen-deficient site is 69% of the optimum (2.64) for the species as compared to 61% for basswood and 57% for yellow poplar, both of which are nitrogen-demanding, and 65%, 50%, 63% and 56%, respectively, for such intermediate species as pignut hickory, sugar maple, beech and black gum. Again, little or no distinction can be made between species of groups II and III as regards internal concentrations at the lower levels of nitrogen availability as compared to the optima for the various trees. However, in the upper ranges of nitrogen supply, both the average level of internal nitrogen concentration and the growth rate of the nitrogen-demanding trees are significantly greater than for any of the intermediate species.

It is apparent that in the lower ranges of nitrogen supply the order in which species rank in internal nitrogen concentration is not necessarily indicative of their relative nitrogen tolerance. On nitrogen-deficient sites the growth rate of trees with relatively high internal nitrogen concentrations may be less than that of species with lower internal concentrations. Hence, the only reliable basis for comparison, or index to nitrogen tolerance, is the degree to which trees growing on such sites approach, in internal nitrogen concentration, the experimentally determined optimum for the species.

Leaf Analysis

The method of leaf analysis has been used extensively to determine the suitability of soils to field and garden crop plants (Macy, 1936; Thomas, 1937, '39), fruit trees (Hardy *et al.,* 1935; Chandler, 1936; and Lilleland and Brown, 1938), forest trees (Mitchell, 1935; Mitchell and Finn, 1935) and coniferous seedlings (Gast, 1937; Mitchell, 1934, '39). Similarly, in the present study the experimentally determined relationships between nitrogen supply and the nitrogen content of the leaves of various indicator species were utilized to evaluate the relative nitrogen-supplying capacity of the six different sites on which series of variously fertilized plots were established, thus permitting coordination of data from all plots included in the experiment.

The method of leaf analysis is comparative. When considered alone, little or no significance can be attributed to the chemical composition of the leaves of plants grown in any single nutrient environment. As previously discussed (Mitchell, 1934, '35, '39), a standard of comparison is essential. Such a standard may be established experimentally for plants of a given species by growing them in substrates of varying nutrient availability and determining the chemical composition of the leaves periodically during the growing season. So far as deciduous trees are concerned, it is more practical to sample only the physiologically mature leaves (Mitchell, 1936).

In the present study nitrogen was varied by known amounts, and the growth and internal nitrogen concentration of the various tree species determined. For every species there was a high degree of correlation between the amount of nitrogen applied and the concentration of this element in the physiologically mature leaves. These relationships, which may be expressed by the Mitscherlich equation, can be used to evaluate, in relative terms, the nitrogen-supplying capacity of soils of unknown fertility. The procedure is illustrated by the data presented in Fig. 1 (B).

Let 2.22% be taken as the average nitrogen concentration of the leaves of red oaks growing on a site of unknown fertility. According to leaf analysis (see Fig. 1, B) the nitrogen-supplying capacity of this site is equivalent, *in effect,* to $x + 167$ pounds per acre on the relative nitrogen supply scale. Similar estimates may be made on the basis of the curves of average relationship for other species.

The range of relative nitrogen supplies established in the present experiment is a convenient and useful standard of comparison or reference scale. It should be remembered, however, that this artificially created range of supplies is relative rather than absolute. There is no true zero, since trees cannot survive in soils totally lacking in nitrogen. The x of the reference scale represents the unknown amount of this element supplied by the soil of the poorest control plot (*ON-0*). All other nitrogen supplies are expressed in relation to x—that is, $x + 25$ pounds of nitrogen per acre, $x + 50$, etc. The numerical equivalent of the constant x in pounds of nitrogen per acre is of little moment. Of primary importance is the effect, upon tree growth and internal nitrogen concentration, of known increments of nitrogen expressed quantitatively in any convenient units. But since the various nitrogen supplies are relative, so are site estimates evaluated upon this basis. Thus an internal concentration of 2.22% for red oaks does not indicate that the soil in which the trees are growing contains a total of 167 pounds of nitrogen per acre. Rather it indicates that the nitrogen-supplying capacity of this site is *equivalent,* in effect upon internal nitrogen concentration, to 167 pounds of water-soluble nitrogen added to an acre of the poorest soil used in the experiment here reported.

The fact that the reference scale is relative rather than absolute does not detract from its value. It is convenient to use in making quantitative comparisons of the nitrogen availability level of various sites *in terms of the requirements of forest trees.* The total nitrogen content of soils may be readily determined, in absolute terms, by direct chemical analysis. However, so far as tree nutrition is concerned, little or no significance can be attached to the results of such determinations.

The results of statistical studies indicate that estimates of nitrogen-supplying capacity by the method of leaf analysis are accurate to within about ± 10 pounds of nitrogen per acre on the relative nitrogen supply scale. When properly applied, the accuracy of the method is not affected by those variations in rainfall, depth and physical properties of soil, soil moisture, local climate, age of trees, elevation and exposure which were encountered during the present study. It may be well to emphasize that the geographic limits of these values will have to be determined by the same technique as here employed.

Root competition, as measured by basal area, is the only factor which appears to have any appreciable influence on the relationship between nitrogen supply and internal nitrogen concentration. Trees growing on plots in stands of high basal area tend to have low internal nitrogen concentrations. The opposite is true of stands of exceedingly low basal area. Hence the method of leaf analysis should be used with caution in comparing sites occupied by stands which differ greatly in this regard. However, inspection of the data here reported indicates that relative nitrogen availability ratings based upon the standard of comparison established during the present study can be considered reliable for sites occupied by stands within the basal area range of from 55 to 85 square feet per acre. Comparisons at greater extremes may be of questionable accuracy. The writers have worked out an apparently satisfactory method for correcting internal nitrogen concentrations for large differences in basal area. However, the reliability of this correction factor has not been tested sufficiently to justify reporting at this time.

The number of trees of the indicator species to sample on a given area will depend upon the deviation of the individual samples from the mean nitrogen concentration of the leaves of all trees sampled. On the basis of the average deviation of samples taken from some fifty different sites throughout the Northeast, it appears that a mean based upon the analysis of about ten trees scattered over an area of one-quarter to one acre is sufficient for a statistically significant estimate of nitrogen availability.

Discussion of Relative Merits of Leaf Analysis and Direct Soil Analysis

A direct analysis of the soil for available nutrients has been proposed and used by various workers in attempting to evaluate the potential productivity of a given soil. Such methods have some distinct disadvantages. The extracting solutions used constitute empirical procedures which do not necessarily simulate natural processes of absorption of nutrients by plants. These methods make no allowance for such biological factors as mycorrhizae, which may increase the absorption capacity of some species by as much as 300 percent for certain elements (Hatch, 1936, '37; Mitchell, Finn and Rosendahl, 1937; McComb, 1938), or for the fact that plants in general and forest trees in particular differ widely in their tolerance of unfavorable nutrient environments. Therefore, what may be termed "available nutrients" by a procedure of direct analysis will not necessarily be a good estimate of the quantitative value for nutrients which can be absorbed by a given plant from a given nutrient environment.

In the case of nitrogen, a large part of the available supply exists in a water-soluble form and is either leached from the soil or absorbed by plants rather rapidly. Soils which are known to accumulate nitrates to a considerable degree will often show an absence of nitrates in a water extract.

A good example of such a situation with forest soils has been presented by Wallihan (1938). In studying the amount of nitrogen as well as soil moisture available to vegetation on trenched and untrenched plots, he determined the amount of nitrate nitrogen in water extracts of the soils. In no case did he find more than 1 ppm present. Total water-soluble nitrogen also showed no correlation with treatment. But an analysis of the leaves of the ground vegetation on the plots showed an average increase in total nitrogen in the foliage on the trenched plots of 53 percent over that of the untrenched plots. This difference was consistent among the replicates and was statistically significant.

The distinct advantage of the method of leaf analysis is that by chemical analysis of the leaves we can obtain a more reliable estimate of the amount of the various nutritional elements which have been absorbed by, and therefore are available to, plants growing in a given soil. One therefore uses a natural biological rather than an artificial extraction method for estimating available nutrients.

Although used extensively, the method of leaf analysis has not been universally accepted by soil scientists. The chief disadvantage and source of criticism is the continually fluctuating chemical composition of the leaves of certain plants. To obtain satisfactory results the method must be used properly in regard to the physiological stage of development of the plants at the time of sampling. It is true that for herbaceous species the relationships between external supply and internal nutrient concentration are not so clear cut as with deciduous trees and other woody plants. This is due to the fact that the internal (leaf) nutrient concentration and the growth response of trees, which is largely vegetative, are seldom affected by withdrawals of nutrients such as are required in the more complicated fruiting metabolism of herbaceous plants (Blackman, 1919; Gregory, 1926; Armstrong and Albert, 1931; Eaton, 1931; and Mitchell, 1934, p. 44).

Woody plants, especially deciduous trees, offer an excellent opportunity to apply the method of leaf analysis. That the leaves depict rather accurately the relative supply of nutrients in the soil has been shown by the data presented in this report. To sample the leaves at a similar physiological stage is comparatively simple, since leaf size and chemical composition are relatively constant during the month just previous to yellowing. In the northeastern United States the sampling period is about August 20 to September 20. However, the time at which leaves start to yellow, after which they are worthless so far as leaf analysis is concerned, varies somewhat with species and environmental factors. These factors and the general subject of leaf sampling technique were discussed in detail in a previous report (Mitchell, 1936).

Because the method of leaf analysis is a natural biological method, because it has been shown to correlate well with soil nutrient levels and because of the ease of obtaining samples of similar physiological age, it was employed in the present study. It is recommended for use by forest ecologists, silviculturists and others interested in evaluating the chemical aspects of forest sites.

VARIATIONS IN THE NITROGEN-SUPPLYING CAPACITY OF REPRESENTATIVE FOREST SITES THROUGHOUT THE NORTHEAST

In the present study data were obtained on the internal nitrogen concentration and the diameter increment of various tree species supplied increasing amounts of nitrogen through an artificially created range of from $x + 0$ to $x + 1000$ pounds of nitrogen per acre. The magnitude of the growth response of certain species, which in some cases exceeded 300 percent (Fig. 16), clearly demonstrates the importance of nitrogen to tree nutrition. There can be no doubt that soils of the poorest sites studied are nitrogen deficient. But just how important this growth factor is to foresters depends upon the frequency distribution of forest sites of a given region when classified according to nitrogen-supplying capacity.

A preliminary survey, which was designed to supply information on the relative nitrogen availability of forest soils of the Northeast, was started in the summer of 1937. With the aid of various cooperating agencies fifty permanent and temporary sample plots were established in representative stands in different parts of six states. So far as time permitted, the following data were obtained for each plot: location, site quality, elevation, aspect, slope, topography, soil type, drainage, forest type, site index, stand composition and basal area, and the average age, height, diameter and diameter increment by species. In addition, over 1500 individual leaf samples, for chemical analysis, were taken from trees of twenty-two different species. The analytical results, summarized according to species and location of plot, are presented in Table 13.

Although the growth measurements as well as the analytical results and other data obtained during this preliminary survey of various sites of the Northeast have been freely drawn upon in those earlier sections of this report devoted to interpretation of data from the different series of fertilized plots, only the analytical results from the former study are included in Table 13.

The listing in Table 13 indicates that red oaks occur on a greater number of plots than any other tree. The lowest internal nitrogen concentration for this species on any site is 1.50, for plot E-19, and the highest is 2.68, for plot FS-2-B. Variations of this magnitude, when interpreted on the basis of data from the controlled experiment (Fig. 2), indicate that so far as nitrogen supply is concerned these two *unfertilized* sites differ sufficiently to account for highly significant differences in the growth rate of all trees studied, especially such nitrogen-requiring species as yellow poplar, basswood and white ash. The red oak, sugar maple and yellow poplar data for certain representative plots are compared in Fig. 19. Other species growing on the different plots show similar variations in internal nitrogen concentration (Table 13).

It is not certain that either the very best or the poorest forest sites in the Northeast were included in this survey. However, in view of the experimentally determined relationship between relative nitrogen supply and the internal nitrogen concentration of forest trees, it is evident from the data summarized in Table 13 that for those sites examined there are highly significant variations in nitrogen-supplying capacity. Just how the different sites rate in this regard may be determined by leaf analysis, using red oak as the indicator species. Following the technique previously described, estimates were made of the relative nitrogen supply of the thirty-six sites on which red oaks occurred. Then the various sites were grouped according to estimated nitrogen supply into classes which differed by fifty pounds of nitrogen per acre. The frequency distribution curve, based upon the resultant data, is shown in Fig. 20.

It appears that the frequency distribution of the soils thus classified is asymmetrical rather than normal, since the mean is significantly different from the median. Assuming that the sites examined are representative, the distribution curve indicates that the nitrogen supplies of some 20 percent of the soils of the Northeast are equivalent, in effect upon internal nitrogen concentration, to from $x—50$ to $x + 50$ on the relative nitrogen supply scale used to coordinate data from the controlled experiment. This range of supplies, which corresponds to the region of minima for nitrogen-tolerant trees, is highly unfavorable for intermediate and nitrogen-demanding species. Thus, so far as deciduous trees are concerned, around 20 percent of the forest sites of the Northeast may be classed as nitrogen deficient. Similarly, approximately 65 percent of the soils may be considered as average to good in this regard, since their nitrogen supplies

TABLE 13

The Nitrogen, Phosphorus and Potassium Content of Leaves from Forest Trees Growing on Various Sites Throughout the Northeast[1]

Location of Plot	Plot Number	Red Oak[2]	Spanish Oak[2]	Black Oak[2]	Post Oak[2]	Scarlet Oak[2]	White Oak[2]	Chestnut Oak[2]	Sugar Maple[2]	Red Maple[2]	Black Birch[2]	Paper Birch[2]	Yellow Birch[2]	Beech[2]	Yellow Poplar[2]	White Ash[2]	Pignut Hickory[2]	Basswood[2]	Beech[2]	Black Gum[2]	Trembling Aspen[2]	Large-toothed Aspen[2]	Ironwood[2]
Bartlett Experimental Forest (Northeastern For. Expt. Sta., U.S.F.S.) near Bartlett, N. H.[3]	FS-1-A	....	....	....	....	....	....	....	**1.60***[4] 0.15 *1.42*	**1.85***[4] 0.14 *1.53*	....	....	**2.23***[4] 0.15 *1.92*	**2.21***[4] 0.13 *1.71*	....	....	....	....	....	....	....	....	....
	FS-1-B	....	....	....	....	....	....	....	**1.47*** 0.10 *1.14*	**2.01*** 0.11 *1.44*	....	**1.87*** 0.10 *1.58*	....	**2.22*** 0.12 *1.65*	....	....	....	....	....	....	....	....	....
Chenango Experimental Forest (Northeastern For. Expt. Sta., U.S.F.S.) near Smyrna, N. Y.[3]	FS-2-A	**2.64*** 0.21 *1.58*	....	....	....	....	....	....	**1.80** 0.25 *1.85*	....	....	....	....	....	....	....	....	....	....	....	....	....	....
	FS-2-B	**2.68*** 0.21 *1.96*	....	....	....	....	....	....	**1.77*** 0.34 *1.96*	....	....	....	....	....	....	....	....	....	....	....	....	....	....
Green Bank State Forest, New Jersey[5]	FS-3-A	....	**2.18‡** 0.12 *1.29*	**1.97** 0.13 *1.27*	**2.09‡** 0.17 *1.45*	....	**2.15** 0.16 *1.44*	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....
Bass River State Forest, New Jersey[5]	FS-3-B	....	....	**1.98*** 0.10 *1.09*	....	....	**2.04** 0.14 *1.46*	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....
Lebanon State Forest, New Jersey[5]	FS-4-A	**1.83*** 0.13 *1.54*	....	....	....	....	**1.91*** 0.18 *1.57*	**1.78** 0.16 *1.83*	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....
	FS-4-B	**1.82*** 0.12 *1.59*	....	....	....	....	**1.92*** 0.19 *1.57*	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....
Belleplain State Forest, New Jersey[5]	FS-5-A	....	....	**1.81*** 0.10 *1.38*	....	**1.78*** 0.10 *1.17*	**2.04*** 0.13 *1.35*	....	....	**1.64‡** 0.12 *0.89*	....	....	....	....	....	....	....	....	....	....	....	....	....
	FS-5-B	....	....	**1.64*** 0.11 *1.35*	....	**1.81*** 0.10 *1.36*	**2.12*** 0.14 *1.45*	....	....	**1.58‡** 0.11 *1.05*	....	....	....	....	....	....	....	....	....	....	....	....	....
Stokes State Forest, New Jersey[5]	FS-6-A	**1.97*** 0.18 *1.61*	....	....	....	**2.07‡** 0.20 *1.62*	**2.26** 0.25 *1.67*	**1.94*** 0.22 *1.89*	....	....	**2.22*** 0.27 *1.51*	....	....	....	**1.93*** 0.21 *1.46*	**1.59‡** 0.31 *1.90*	**1.73‡** 0.16 *1.34*	....	....	....	....	....	....
	FS-6-B	**2.17*** 0.20 *1.68*	....	....	....	**1.98*** 0.16 *1.40*	**2.21‡** 0.21 *1.50*	**2.07*** 0.20 *1.67*	....	**1.65‡** 0.27 *1.74*	**2.24*** 0.26 *1.87*	....	....	....	....	....	....	....	....	....	....	....	....
Jenny Jump State Forest, New Jersey[5]	FS-7-A	**2.07** 0.18 *2.14*	....	**1.89‡** 0.16 *1.62*	....	....	**2.01‡** 0.21 *1.40*	**2.05** 0.19 *1.50*	**1.64‡** 0.55 *2.02*	**1.77‡** 0.37 *1.67*	**2.22‡** 0.27 *2.10*	....	....	**2.02‡** 0.17 *1.49*	**2.07‡** 0.31 *1.61*	**1.64‡** 0.23 *1.81*	**1.55‡** 0.16 *1.19*	....	....	....	....	....	....
	FS-7-B	**2.21*** 0.21 *1.69*	....	....	....	....	....	**1.86‡** 0.15 *1.62*	....	....	....	....	....	....	....	**1.83‡** 0.25 *1.80*	**1.63** 0.17 *1.73*	....	....	....	....	....	....
Near Almond, New York[6]	FS-8-A	....	....	....	....	....	....	....	**1.39*** 0.29 *1.75*	....	....	....	....	**2.27*** 0.22 *1.44*	....	**1.98*** 0.29 *2.23*	....	....	....	....	....	....	**1.71*** 0.17 *1.34*
	FS-8-B	....	....	....	....	....	....	....	**1.42*** 0.30 *1.52*	**1.81*** 0.18 *1.64*	....	....	....	**2.07*** 0.25 *1.61*	....	**1.92*** 0.23 *2.02*	....	....	....	....	....	....	....
Missouri Branch, West Virginia[7]	FS-9-A	**2.32** 0.15 *1.75*	....	....	....	....	....	....	....	**1.72‡** 0.11 *1.65*	....	....	....	**2.27‡** 0.14 *0.98*	....	**1.88‡** 0.12 *1.22*	**2.12‡** 0.14 *1.52*	....	....	....	....	....	....
	FS-9-B	**2.22** 0.12 *1.41*	....	....	....	....	....	....	**2.01‡** 0.12 *1.28*	....	....	....	....	**2.22‡** 0.12 *1.19*	**2.33‡** 0.15 *1.33*	....	**2.14‡** 0.13 *1.50*	....	....	....	....	....	....
Harvard Forest, Petersham, Mass.[8]	FS-10-A	**2.09*** 0.15 *1.30*	....	....	....	....	....	....	....	**1.48*** 0.13 *1.54*	....	....	**2.14‡** 0.16 *1.46*	....	....	**1.95** 0.14 *1.80*	....	....	....	....	....	....	....
	FS-10-B	**2.24*** 0.21 *1.30*	....	....	....	....	....	....	....	**1.76‡** 0.31 *2.12*	....	**2.19‡** 0.21 *1.41*	**2.39‡** 0.23 *1.81*	**2.17‡** 0.21 *1.35*	....	....	....	....	....	....	....	....	....
	FS-10-C	**2.35*** 0.22 *1.32*	....	**1.95‡** 0.21 *1.17*	....	....	....	....	....	**1.68** 0.49 *2.27*	....	**2.10** 0.27 *1.99*	....	**2.12‡** 0.25 *1.44*	....	....	....	....	....	....	....	....	....
New York State College of Forestry Experiment Station, South of Syracuse, N. Y.[9]	FS-11-A	....	....	....	....	....	....	....	....	....	....	....	....	....	**1.93‡** 0.26 *2.05*	....	....	....	....	....	....	....	....
	FS-11-B	....	....	....	....	....	....	....	....	....	....	....	....	....	**2.22‡** 0.19 *1.56*	....	....	....	....	....	....	....	....
Cove type (*cf.* 1, Raup's (1938) Section A), Black Rock Forest[10]	E-1	**2.06*** 0.16 *1.23*	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....
Lower slope site (*cf.* Raup's type 2, Section A), Black Rock Forest[10]	E-2	**2.08*** 0.18 *1.27*	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....
Upper slope site (*cf.* Raup's type 3, Section A), Black Rock Forest[10]	E-3	**1.86*** 0.17 *1.20*	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....
White Oak—Hickory type (*cf.* 4, Raup's Section A), Black Rock Forest[10]	E-4	**2.10*** 0.19 *1.37*	....	....	....	....	**2.20*** 0.22 *1.62*	....	....	....	....	....	....	....	....	....	**1.69*** 0.18 *1.12*	....	....	....	....	....	....
Upper slope site (*cf.* Raup's type 2, Section AA), Black Rock Forest[10]	E-5	**1.91*** 0.13 *1.36*	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....
Cove type (*cf.* 4, Raup's Section AA) Black Rock Forest[10]	E-6	**2.12*** 0.20 *1.80*	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....
White Oak type (*cf.* 4, Raup's Section F), Black Rock Forest[10]	E-7	**1.99*** 0.17 *1.12*	....	....	....	....	**2.36*** 0.24 *1.57*	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....
Red Maple swale (about 3, Raup's Section F), Black Rock Forest[10]	E-8	**2.01*** 0.16 *1.35*	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....
Cove type near intersection of White-oak Trail and Bog Meadow Road (*cf.* map, Raup, 1938), Black Rock Forest[10]	E-9	**2.14*** 0.17 *1.57*	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....
Cove type near intersection of Canterbury Brook and Hulse Road (*cf.* map, Raup, 1938), Black Rock Forest[10]	E-10	**2.20*** 0.16 *1.36*	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....
Mid-slope site above Frog Hill, Black Rock Forest[10]	E-11	**2.14*** 0.22 *1.63*	....	....	....	....	....	....	....	**1.49** 0.47 *2.43*	....	....	....	....	....	....	....	....	....	....	....	....	....
Ridge site above Clark Lot, Black Rock Forest[10]	E-12	**1.89*** 0.19 *1.17*	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....
Mid-slope site above Clark Lot, Black Rock Forest[10]	E-13	**1.89*** 0.18 *1.51*	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....
Mid-slope site above Clark Lot, Black Rock Forest[10]	E-14	**1.92*** 0.21 *1.18*	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....
Lower slope site above Aleck Meadow Reservoir, Black Rock Forest[10]	E-15	**1.73*** 0.16 *1.42*	....	....	....	....	**1.96*** 0.24	**2.04*** 0.23	**1.55** 0.33 *1.57*	**1.60** 0.28	....	....	....	....	....	**1.53** 0.30	**1.60** 0.18	....	....	**1.61** 0.23	....	....	....
Mid-slope site below Frog Hill, Black Rock Forest[10]	E-16	**1.66*** 0.15 *1.79*	....	....	....	....	**2.00** 0.18	**1.99** 0.15	**1.38*** 0.20	**1.38** 0.18	....	....	....	....	**1.70*** 0.14	**1.74*** 0.25	**1.53** 0.12	**2.03** 0.19	....	**1.55** 0.19	....	....	....
Private woodlot near Mountainville, N. Y.[11]	E-17	**2.22*** 0.17 *2.02*	....	....	....	....	....	**2.25** 0.21	**2.09‡** 0.36 *1.84*	....	....	....	....	....	**2.28*** 0.28	**2.13** 0.34	....	**2.46‡** 0.28	....	....	....	....	....
Private woodlot near Cornwall-on-Hudson, N. Y.[11]	E-18	....	....	....	....	....	....	....	**2.23*** 0.14 *0.85*	....	....	....	....	....	....	**2.30*** 0.17	**2.14** 0.16	....	....	....	....	....	....
Private Estate near Pittsburgh, Pa.[11]	E-19	**1.50*** 0.17 *0.79*	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....
Grounds of New York Military Academy, Cornwall-on-Hudson, N. Y.[11]	E-20	....	....	....	....	....	....	....	**1.65*** 0.18 *0.63*	....	....	....	....	....	....	....	....	....	....	....	....	....	....
Private estate near Newburgh, N. Y.[11]	E-21	....	....	....	....	....	....	....	**1.88*** 0.14 *0.69*	....	....	....	....	....	....	....	....	....	....	....	....	....	....
Private estate near Cornwall-on-Hudson, N. Y.[11]	E-22	....	....	....	....	....	**2.26‡** 0.14 *0.76*	**2.22‡** 0.16 *1.05*	**1.76‡** 0.24 *0.80*	**1.85‡** 0.23 *0.56*	....	....	....	....	....	....	**2.01‡** 0.12 *1.08*	....	....	....	....	....	....
Mid-slope site below Frog Hill, Black Rock Forest[10]	E-23	**2.09*** 0.14 *1.77*	....	....	....	....	**2.15‡** 0.17	**2.44‡** 0.15	**1.69‡** 0.32 *1.34*	**1.68‡** 0.23	....	....	....	....	**2.06** 0.15	**1.87** 0.18	**2.17‡** 0.16	....	....	....	....	....	....
Mid-slope site east of Continental Road, Black Rock Forest[10]	E-24	**2.02*** 0.18 *1.31*	....	....	....	....	....	**2.15*** 0.23	**1.52*** 0.41 *1.44*	**1.64‡** 0.43	**1.96‡** 0.36	....	....	....	**1.82‡** 0.20	**1.68** 0.31	**1.96‡** 0.19	**2.07*** 0.28	**1.94‡** 0.14	....	....	....	....
Cove site near Sands Bridge, Black Rock Forest[10]	E-25	**2.00*** 0.19 *2.21*	....	....	....	....	**2.21** 0.26	**2.29*** 0.22	**1.68** 0.49 *1.51*	**1.53‡** 0.39	**2.40‡** 0.34	....	....	....	....	**1.57*** 0.30	**1.75** 0.18	....	....	**1.72‡** 0.37	**1.69** 0.17	....	....
Arnot Forest near Ithaca, N. Y.[12]	C-1	**1.69‡**	....	....	....	....	**1.97‡**	....	**1.55***	**1.53**	**1.93**	....	....	....	....	**1.85**	....	**2.11***	**2.03***	....	**2.20‡**	**2.04**	**1.91** ....
Arnot Forest near Ithaca, N. Y.[12]	C-2	....	....	....	....	....	....	....	....	**1.40***	....	....	....	....	....	....	....	**1.90**	**1.78**	....	**1.81***	....	....

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[1] Analytical results (N, P and K) presented in this table are distinguished as follows: nitrogen, in **bold-faced** type, at the head of each three-entry column; phosphorus, in roman type, directly beneath; and potassium, in *italics*, third. All analytical data are expressed as percentages of dry matter.

[2] Scientific equivalents of common names are given in Table 1.

[3] Plots established and leaf samples collected by the Northeastern Forest Experiment Station of the U. S. Forest Service; chemical analysis by the Black Rock Forest Laboratory.

[4] An asterisk (*) at the head of a column indicates that each analytical result ($N_{\%}$, $P_{\%}$, $K_{\%}$) is based upon the analysis of leaf samples from 10 or more trees; a dagger (‡) is used to identify results based upon the analysis of leaves from 4 trees or less.

[5] Plots established and leaf samples collected by the New Jersey Department of Conservation and Development; chemical analysis by the Black Rock Forest Laboratory.

[6] Plots established and leaf samples collected by the Division of Lands and Forests, New York Conservation Department, in cooperation with the C. C. C.; chemical analysis by the Black Rock Forest Laboratory.

[7] Plots established and leaf samples collected by the West Virginia Department of Conservation; chemical analysis by the Black Rock Forest Laboratory.

[8] Plots established and leaf samples collected under the direction of Dr. P. R. Gast, Harvard Forest; chemical analysis by the Black Rock Forest Laboratory.

[9] Leaf samples collected by Professor E. F. McCarthy, New York State College of Forestry; chemical analysis by the Black Rock Forest Laboratory.

[10] Permanent and temporary sample plots of the Black Rock Forest.

[11] Plots established and leaf samples collected and analyzed by Mr. H. L. Mitchell in connection with consulting work on private estates.

[12] Plots established and leaf samples collected and analyzed by Dr. Robert F. Chandler, Jr., Cornell University.

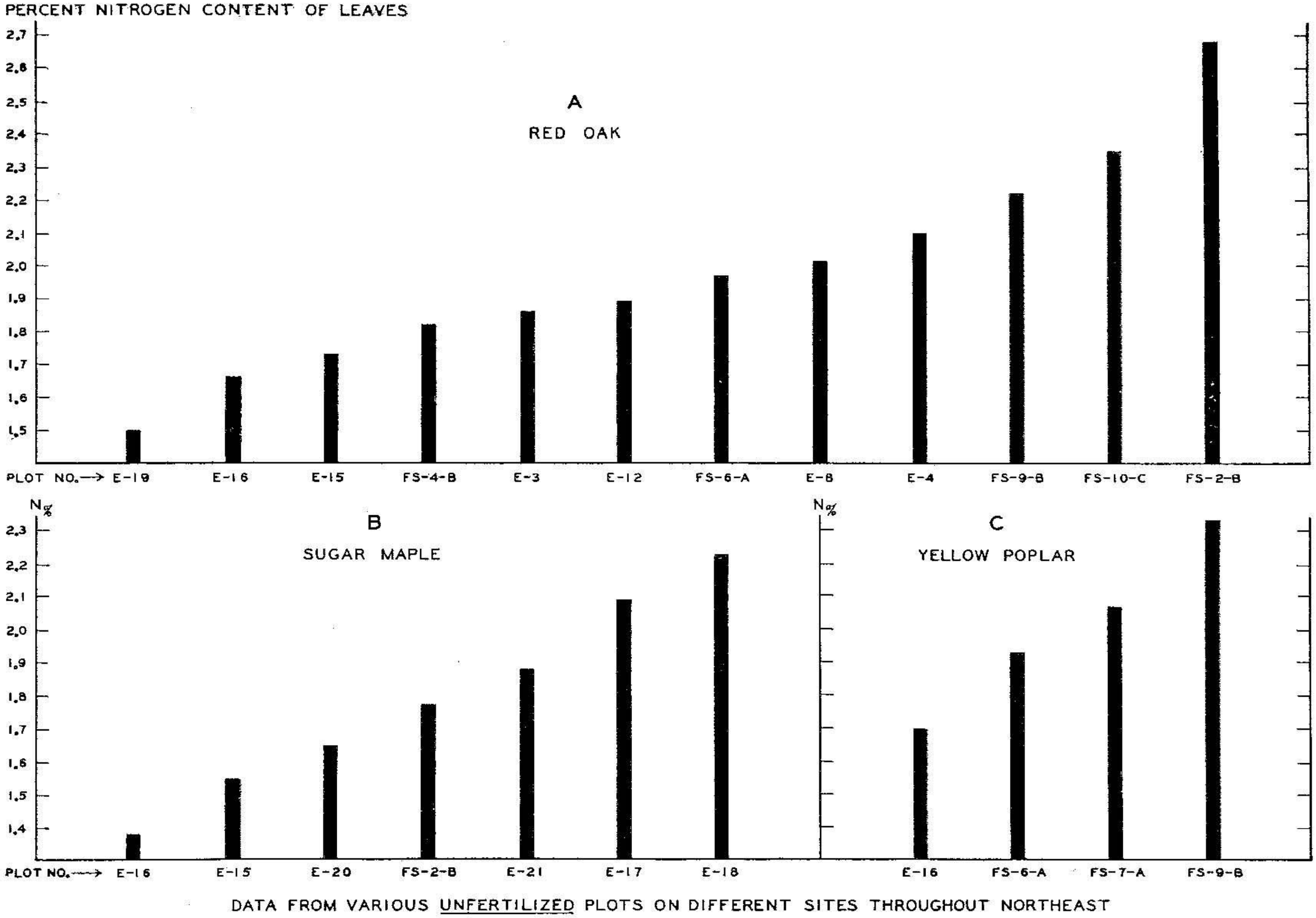

FIG. 19.—Graphs showing the variation in the nitrogen content of leaves from trees growing on various unfertilized sample plots located on different sites throughout the Northeast.

Plots are arranged on the abscissae of the above graphs according to the nitrogen content of the leaves of trees growing thereon. Basic data are from Table 13. Any correlation between plot number and nitrogen supply, as indicated by the nitrogen content of the leaves, is entirely accidental, since plot numbers were arbitrarily assigned without regard to site quality.

are equivalent in effect to from $x + 50$ to $x + 400$ on the relative nitrogen supply scale. It is evident from the frequency curve that only some 15 percent of the soils can be classed as very good to excellent in this regard—that is, with nitrogen supplies equivalent in effect to the optimum range of from $x + 400$ to $x + 600$ on the relative nitrogen supply scale. Although there may be somewhat better sites than the best of those examined, it is doubtful if *fully stocked* stands of even the most nitrogen-tolerant species can exist on sites with a relative nitrogen supply of $x - 50$ or less. No such sites could be found during the present study. This is given as the reason for the skewed distribution of the data presented in Fig. 20.

The Phosphorus and Potassium Requirements of Forest Trees

Leaf samples taken from the fifty different plots throughout the Northeast were analyzed for phosphorus and potassium as well as for nitrogen. The analytical data are summarized in Table 13. It will be observed that the various species differ considerably in both internal phosphorus and potassium concentration. This suggests that forest trees vary in their phosphorus and potassium as well as their nitrogen requirements.

However, the minimal, working and optimal ranges of potassium and phosphorus supply, and their associated internal concentrations for various trees, have not been accurately determined by experiment. Only negative results were obtained from preliminary potassium fertilizer studies at the Black Rock Forest. Nine deciduous species growing on a series of plots supplied varying quantities of potassium fertilizer showed a correlation between the amount of this element applied and the internal potassium concentration, but little or no growth response was observed. This suggests that the soils of the Black Rock Forest are well supplied with potassium,

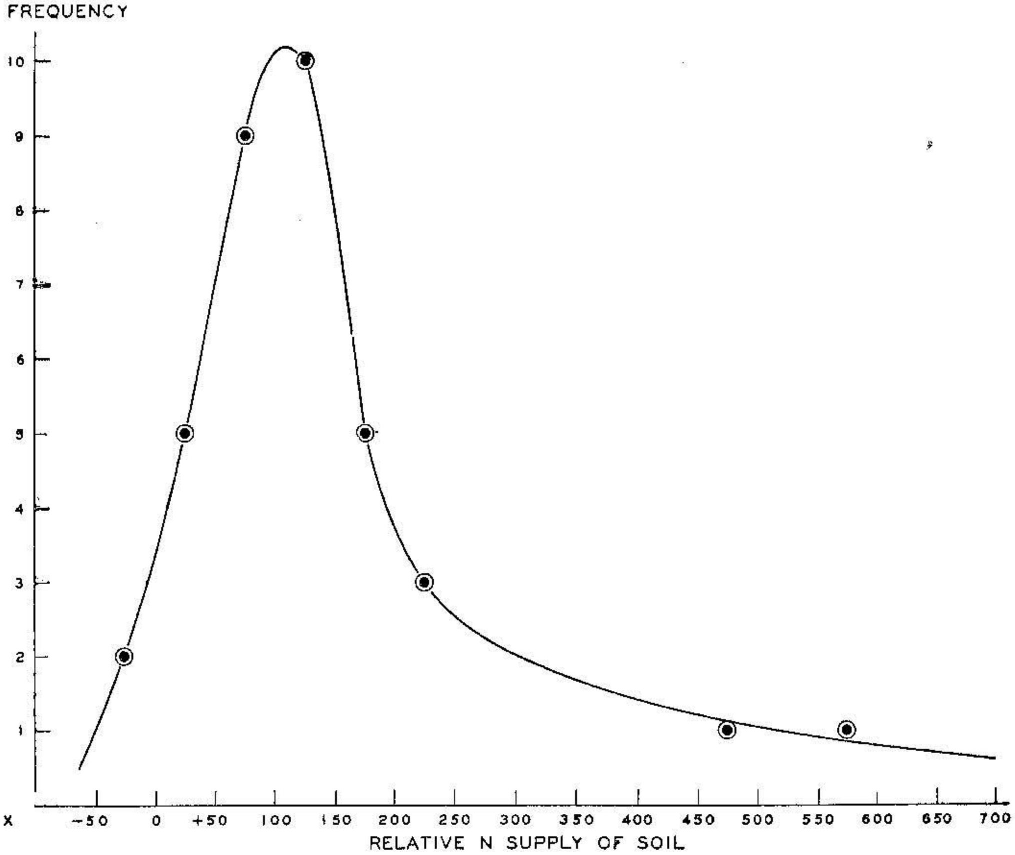

FIG. 20.—The frequency distribution of 36 forest sites of the Northeast classified according to relative nitrogen supply.

a conclusion which agrees with the results of pot culture tests of these soils (Mitchell, 1934). The role of potassium in tree nutrition remains to be worked out on some potassium-deficient site.

As regards phosphorus, a total of twenty quarter-acre plots supplied varying amounts of this element have been established on the Black Rock Forest. Analytical data for trees on these plots indicate that, as with nitrogen and potassium, there is a good correlation between the amount of phosphorus applied and the concentration of this element in the leaves of the trees studied. However, since complete growth data are not yet available, only tentative conclusions can be drawn regarding the phosphorus requirements of the various species.

That the fifty sites examined differ greatly in phosphorus and especially potassium availability is evidenced by the variations in the analytical results for red oak and sugar maple, which are common to the greatest number of sites (Table 13). How important these differences are to tree growth and distribution are questions which cannot be answered until reliable data are available on the phosphorus and potassium requirements of the various species.

DISCUSSION OF DATA IN RELATION TO SILVICULTURE

THE frequently observed tendency to minimize the importance of the chemical aspect of site is believed attributable to the dearth of information in forestry literature on the comparatively unexplored field of tree nutrition. No one will deny that, in the majority of cases, historical factors (Raup, 1938) and such factors as climate, soil profile, and especially soil moisture, are relatively more important than mineral nutrition in determining the distribution and growth of forest stands and the elements of which they are composed. However, in view of the experimental evidence presented in this report it is believed that the chemical aspects of site, especially nitrogen supply, often play a more important role than heretofore supposed.

An inspection of the stands in which the various permanent and temporary plots were located reveals that, in general, the frequency of incidence of the nitrogen-demanding species varies with the soil nitrogen supply.[1]

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[1] In the majority of cases a fairly reliable estimate of the composition of the stands examined can be obtained from the data summarized in Table 13. As a rule, samples were taken from at least ten trees of each primary species of the stand, and from as many of the secondary species as occurred on an area of from one-fourth to one acre. Thus, if the analytical results for a given species are marked with an asterisk (*), indicating that ten or more trees were sampled, the species is usually a primary element of the stand; if marked with a dagger (†), indicating that four or less trees were sampled, the species may be considered as relatively infrequent. There are a few exceptions. In some cases only trees of a single ''indicator'' species were sampled. In others a special effort was made to include samples from an adequate number (10 if possible) of all nitrogen-demanding species, even though they were relatively infrequent. This necessitated increasing the plot area to as much as five acres in certain instances. However, all statements in the above discussion concerning the frequency of incidence of the various species were carefully checked against detailed notes on the composition of each stand.

Of the fifty different stands examined, basswood, yellow poplar and white ash were in no case found on sites with a relative nitrogen supply, as determined by foliar diagnosis, equivalent to less than $x + 0$. And in only two instances, plots E-16 and C-2, were these species found on sites of such low nitrogen-supplying capacity. Although basswood occurred on plot C-2, and all three nitrogen-demanding species occurred on plot E-16, they were in each case infrequent, secondary elements of the stand, their growth rate was poor in comparison with that of the nitrogen-tolerant species, and very poor in comparison to that of which they are capable at higher levels of nitrogen supply. On the other hand the nitrogen-demanding species were found in relative abundance, in many cases as primary elements of the stands, on practically all sites with nitrogen supplies equivalent to $x + 150$ or better. And on all such sites the growth rate of these trees was much better, in relation to that of the nitrogen-tolerant species, than on nitrogen-deficient sites.

The relationship between nitrogen supply and the occurrence of the nitrogen-demanding species is too consistent to be disregarded. No matter how favorable climate, soil profile and soil moisture may be it is believed that, so far as these species are concerned, nitrogen is a critical factor on sites with a relative nitrogen supply equivalent to $x + 0$ or less—as indicated by internal concentrations of 1.50, 1.70 and 1.90 or less for white ash, yellow poplar and basswood, respectively. Although nitrogen-tolerant trees occur and are capable of sustaining growth in somewhat poorer soils, the nitrogen-demanding species apparently pinch out at about this level of nitrogen availability. Hence it is probably just as poor silviculture to plant, or otherwise favor during cultural operations, ash, yellow poplar or basswood on such a site as it would be to underplant a birch-beech-maple stand with a light-demanding tree like larch. So far as nitrogen supply is concerned these species cannot be expected to compete effectively with other trees or make anywhere near the growth of which they are capable except on sites with a nitrogen supply equivalent to $x + 75$ or more—as evidenced by internal concentrations of 2.01, 2.15 and 2.32 or more for white ash, yellow poplar and basswood, respectively, or, if these species are lacking, 1.96 for red oak and 1.90 for sugar maple.

From the standpoint of site improvement it is important to know how the various species compare as to the quantity of nutrients returned each year to the soil in the form of litter. In the present study nitrogen and other essential elements were considered only in terms of external supply and percentage composition of the physiologically mature leaves. Hence little or no conclusive evidence was obtained on the absolute quantity of nutrients absorbed by, contained in or returned to the soil by the different species. The data suggest, however, that forest trees vary in nutrient-absorptive capacity, and possibly in the quantity of nutrient elements deposited on the forest floor each year in the form of litter. These possibilities should be investigated further.

SUMMARY AND CONCLUSIONS

THE experiments herein reported were devised to study the nitrogen nutrition and the growth of certain deciduous forest trees of the northeastern United States. Series of from three to six quarter-acre plots were established in stands of mixed hardwoods on each of six different sites. One plot of each series served as a control, and the others were supplied varying amounts of nitrogenous fertilizer. Near the end of the same growing season that the fertilizer was applied, leaf samples, for chemical analysis, were taken from dominant and codominant trees on each plot. The average radial increment of trees on the variously fertilized plots was determined by means of increment borings.

The results of the present experiment established some definite and reproducible relationships between soil nitrogen supply, the concentration of this element in the foliage, and the radial increment of each of the species studied. Both the growth and the foliage nitrogen content of the trees increased with nitrogen supplements through a range of nitrogen supplies equivalent in effect to those of poor to good natural soils. Further additions of nitrogen resulted in successively smaller increases in radial increment and internal (leaf) nitrogen concentration. These relationships may be expressed algebraically with the Mitscherlich formula, which provides a basis for graphical fitting of the data.

On the fertilized plots the leaves of all species were from 30 to 150 percent greater in size and much darker green in color than those of trees on the control plots.

The various species were found to differ considerably in their nitrogen requirements. Red, white and chestnut oaks, red maple and aspen made fairly satisfactory growth in nitrogen-deficient soils, and approached maximum radial increment at a significantly lower relative nitrogen supply than any of the other trees studied. These species were classed as ''nitrogen-deficiency tolerant.'' Beech, sugar maple, pignut hickory and black gum appeared to be intermediate in the scale of nitrogen-deficiency tolerance. Such species as yellow poplar, white ash and basswood, which were infrequent or absent on the poor sites, made poor growth in nitrogen-deficient soils and approached maximum growth only at very high levels of nitrogen availability, were considered as ''nitrogen demanding'' or ''nitrogen requiring.''

To facilitate comparisons and discussion, the range of relative nitrogen supplies established during the present experiment was divided, on the basis of the growth response of trees of each of the nitrogen-deficiency-tolerance groups, into the following regions: (1) the ''region of minima,'' which includes definitely limiting supplies; (2) the ''working region,'' which includes supplies equivalent in effect to those of average to good natural soils; (3) the ''optimum region,'' which is what the name implies; and (4) the ''region of tension,'' through which range of supplies increments in nitrogen result in little or no increase in tree growth. The various range divisions for species of each of the nitrogen-deficiency-tolerance groups are summarized in Table 11.

A high degree of correlation was observed between tree growth and internal (leaf) nitrogen concentration. Such a relationship is to be expected within critical ranges of nitrogen availability since internal nitrogen concentration, which is a function of the external (soil) supply, is the more precise measure of the nitrogen which enters into or otherwise influences the physiological processes that control growth. Thus the *internal* nitrogen concentration ranges for the various species may be similarly divided, on the basis of growth response, into regions which correspond almost exactly to those into which the external supplies were separated. The species are so characterized, individually and according to nitrogen-deficiency-tolerance groups, in Table 12.

The observed ability of the nitrogen-deficiency-tolerant species to sustain growth in soils of low nitrogen availability is believed attributable to the fact that, on such sites, the internal nitrogen concentration of these trees is significantly greater, in relation to their respective optima, than for the intermediate or nitrogen-demanding species.

Because of the high degree of correlation between soil nitrogen supply and foliage nitrogen content, the method of leaf analysis was used to evaluate the relative nitrogen-supplying capacity of soils on which the different series of plots were located. The resulting estimates of soil nitrogen supply provided a basis for the comparison and coordination of data from all plots studied. That the leaf analyses of both the fertilized and unfertilized plots from all series could be fitted to a common Mitscherlich curve indicated the correctness of the projected relationships between nitrogen supply and foliage nitrogen content.

The experimental data herein reported are offered as a tentative standard of comparison for use in evaluating soil nitrogen supply by the method of leaf analysis. The relative merits of leaf analysis and direct soil analysis are discussed.

Using the method of foliar diagnosis, estimates were made of the relative nitrogen-supplying capacity of fifty representative forest sites throughout the northeastern United States. The various sites were classified according to relative nitrogen supply, and a frequency distribution curve fitted to the resultant data. It appears that 20 percent of the sites of the Northeast may be classed as nitrogen-deficient, 65 percent as fair to good, and only 15 percent as very good to excellent in this regard.

Inspection of stands on sites thus evaluated revealed not only a growth relationship but a high degree of correlation between soil nitrogen supply and the frequency of incidence of the nitrogen-requiring species. These data are discussed in relation to silvicultural practices in stands on sites of low nitrogen availability.

BIBLIOGRAPHY

Armstrong, G. M. and Albert, W. B. 1931. A Study of the Cotton Plant with Especial Reference to Its Nitrogen Content. Jour. Agri. Research **42**:689-703.

Blackman, V. H. 1919. The Compound Interest Law of Plant Growth. Ann. of Bot. **33**:353-360.

Chandler, Robert F., Jr. 1936. Absorption, Distribution and Seasonal Movement of Potassium in Young Apple Trees and the Effect of Potassium Fertilizer on Potassium and Nitrogen Content and Growth of Trees. Jour. Agri. Research **53**:19-42.

———1938. The Influence of Nitrogenous Fertilizer Applications upon Seed Production of Certain Deciduous Forest Trees. Jour. of Forestry **36**:761-766.

Denny, Charles S. 1938. Glacial Geology of the Black Rock Forest. Black Rock Forest Bul. 8.

Eaton, Frank M. 1931. Root Development as Related to Character of Growth and Fruitfulness of the Cotton Plant. Jour. Agri. Research **43**:875-883.

Gast, P. R. 1937. Studies on the Development of Conifers in Raw Humus. III. The Growth of Scots Pine (*Pinus Silvestris* L.) Seedlings in Pot Cultures of Different Soils under Varied Radiation Intensities. Meddel. fr. Statens Skogsförsöksanstalt **29**:587-682.

Gregory, F. G. 1926. The Effect of Climatic Conditions on the Growth of Barley. Ann. of Bot. **40**:1-26.

Hardy, F., McDonald, J. A. and Rodriquez, G. 1935. Leaf Analysis as a Means of Diagnosing Nutrient Requirements of Tropical Orchard Crops. Jour. Agri. Sci. **25**:610-627.

Hatch, A. B. 1936. The Role of Mycorrhizae in Afforestation. Jour. of Forestry **34**:22-29.

———1937. The Physical Basis of Mycotrophy in Pinus. Black Rock Forest Bul. 6.

Heiberg, S. O. 1937. Nomenclature of Forest Humus Layers. Jour. of Forestry **35**:36-39.

Lilleland, O. and Brown, J. G. 1938. The Potassium Nutrition of Fruit Trees. II. Leaf Analyses. Proc. Amer. Soc. Hort. Sci. **36**:91-98.

Macy, P. 1936. The Quantitative Mineral Nutrient Requirements of Plants. Plant Physiology **11**:749-764.

McComb, A. L. 1938. The Relation between Mycorrhizae and the Development and Nutrient Absorption of Pine Seedlings in a Prairie Nursery. Jour. of Forestry **36**:1148-1154.

Mitchell, Harold L. 1934. Pot Culture Tests of Forest Soil Fertility. Black Rock Forest Bul. 5.

———1935. A Method for Determining the Nutrient Needs of Shade Trees with Special Reference to Phosphorus. Black Rock Forest Papers **1**:1-4.

———and Finn, R. F. 1935. The Relative Feeding Power of Oaks and Maples for Soil Phosphorus. Black Rock Forest Papers **1**:5-9.

———and Hosley, N. W. 1936. Differential Browsing by Deer on Plots Variously Fertilized. Black Rock Forest Papers **1**:23-27.

———1936. Trends in Nitrogen, Phosphorus, Potassium and Calcium Content of the Leaves of Some Forest Trees During the Growing Season. Black Rock Forest Papers **1**:29-44.

———Finn, R. F. and Rosendahl, R. O. 1937. The Relation between Mycorrhizae and the Growth and Nutrient Absorption of Coniferous Seedlings in Nursery Beds. Black Rock Forest Papers **1**:58-73.

———1939. The Growth and Nutrition of White Pine (*Pinus Strobus* L.) Seedlings in Cultures with Varying Nitrogen, Phosphorus, Potassium and Calcium. Black Rock Forest Bul. 9.

Newlin, J. A. and Wilson, T. R. C. 1919. The Relation of the Shrinkage and Strength Properties of Wood to Its Specific Gravity. U. S. Dept. Agri. Bul. 676.

Paul, Benson H. 1930. The Application of Silviculture in Controlling the Specific Gravity of Wood. U. S. Dept. Agri. Tech. Bul. 168.

Raup, Hugh M. 1938. Botantical Studies in the Black Rock Forest. Black Rock Forest Bul. 7.

Romell, L. G. and Heiberg, S. O. 1931. Types of Humus Layer in the Forests of Northeastern United States. Ecology **12**:567-608.

Scholz, Harold F. 1931. Physical Properties of the Cove Soils on the Black Rock Forest. Black Rock Forest Bul. 2.

Snedecor, George W. 1937. Statistical Methods. Collegiate Press, Ames, Iowa.

Thomas, Walter 1937. Foliar Diagnosis: Principles and Practice. Plant Physiology **12**:571-600.

———1939. Control of Crop Nutrition by the Method of Foliar Diagnosis. Pennsylvania Agri. Expt. Sta. Bul. 378.

Wallihan, Ellis F. 1938. Light, Soil Moisture, and Nutrients as Factors Affecting the Response of Forest Vegetation to Trenching. Cornell Univ. Abstracts of Theses for 1938, pp. 398-402.