THE BLACK ROCK FOREST

BULLETIN No. 9

HENRY H. TRYON, *Director*

THE GROWTH AND NUTRITION OF WHITE PINE (*Pinus Strobus* L.) SEEDLINGS IN CULTURES WITH VARYING NITROGEN, PHOSPHORUS, POTASSIUM AND CALCIUM

With Observations on the Relation of
Seed Weight to Seedling Yield

By
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FOREWORD

THE experiments described in this report are a continuation of the series of studies initiated by the writer at the Black Rock Forest in 1932. This program of research derived from and was designed to complement the series of silvical investigations originated by Professor P. R. Gast of the Harvard Forest.

The writer is particularly indebted to Dr. Gast for inspiration and guidance in planning the cooperative Black Rock Forest experiments, for advice on technical problems, for critical suggestions regarding the interpretation of data, and for giving freely of his time to the preparation of this report. For these and many other favors the writer wishes to express his sincere appreciation.

Assistance was also received from Dr. A. B. Hatch, School of Forestry, University of Idaho. While working with the author during the summers of 1932-'33, Dr. Hatch aided in planning the studies herein described and took many of the photographs reproduced in this and previous reports. His part in these studies, to which reference is made in the text, was published in Black Rock Forest Bulletin No. 6.

For valuable suggestions regarding the presentation and discussion of data here reported, acknowledgment is made to the following: Dr. Robert F. Chandler, Jr., Cornell University; Dr. T. J. B. Stier, Harvard University; Dr. Hardy L. Shirley, Lake States Forest Experiment Station; and Dr. A. J. Riker, University of Wisconsin.

Credit is also due to Messrs. Raymond F. Finn and Russell O. Rosendahl, Research Assistants. The former aided with observations, weighing, computations and the chemical analysis of data from the 1933 and subsequent experiments. Mr. Rosendahl assisted with the 1936-'37 nursery studies, to which reference is made in this report.

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October, 1938

TABLE OF CONTENTS

PAGE

INTRODUCTION 1

DETAILS OF EXPERIMENTAL METHOD 4

Pots, Sand and Watering Technique 4

Seeds and Planting 6

Replacements 7

Protection 7

Solar Radiation Control and Measurement 9

Nutrient Solutions 9

Harvesting and Analysis 12

CORRECTION FOR THE INFLUENCE OF SEED WEIGHT UPON THE YIELD OF SCOTS, CORSICAN AND WHITE PINE SEEDLINGS 14

Seed-Size Correction for Scots Pine 16

Seed-Size Correction for Corsican Pine 17

Seed-Size Correction for White Pine 23

Method 1 23

Method 2 31

Other Methods 35

Refinements in Technique 36

NUTRIENT-SAND CULTURE EXPERIMENTS 40

The Yield of White Pine Seedlings Grown in Nutrient-Sand Cultures of Varying Nitrogen, Phosphorus, Potassium and Calcium Concentration 40

The Relation Between Nitrogen Supply and Seedling Yield 40

The Relation Between Phosphorus Supply and Seedling Yield 50

The Relation Between Potassium Supply and Seedling Yield 54

The Relation Between Calcium Supply and Seedling Yield 59

PAGE

Root/Shoot Ratio Variations 64

Root Extension and Development in Different Nutrient Environments 67

Needle Color as an Index to Nutrient Deficiency . . . 74

The Relationships Between the External (Solution) Concentration of Nitrogen, Phosphorus, Potassium and Calcium and the Internal (Seedling) Content of these Elements 75

The Relation Between Nitrogen Supply and the Nitrogen Content of Seedlings 75

The Relation Between Phosphorus Supply and the Phosphorus Content of Seedlings 80

The Relation Between Potassium Supply and the Potassium Content of Seedlings 82

The Relation Between Calcium Supply and the Calcium Content of Seedlings 84

The Nitrogen, Phosphorus, Potassium and Calcium Content of the Shoots of White Pine Seedlings 86

The Relationships Between Internal Concentration of Nitrogen, Phosphorus, Potassium and Calcium and Seedling Yield 91

Adjustment of the External Nutrient Supply 102

DISCUSSION OF DATA IN RELATION TO CURRENT NURSERY PRACTICE 107

Mineral Nutrient Requirements 108

Estimating Chemical Fertility 109

Timing of Application and Fertilizer Source 112

Practical Considerations 121

SUMMARY AND CONCLUSIONS 125

BIBLIOGRAPHY 133

INTRODUCTION

PLANT physiologists have directed their attention more to field or garden crop plants and fruit trees than to forest trees, largely because of the greater economic value of the former. As a result comparatively little is known of the physiology, especially the nutrition, of shade and timber tree species. This lack of silvical data is particularly noticeable in forest nurseries, where the use of fertilizers is, as a rule, more haphazard and less effective than the methods applied in agriculture. It is true that there have been many partially controlled field experiments regarding the effect of various fertilizer treatments upon the growth and development of tree seedlings planted in seedbed soils of undetermined nutrient-supplying powers. The results of such studies have proved of value in guiding subsequent practice in a particular nursery. But the usual field experiments, largely because they lack precision in the control of nutritional and other factors, have not yielded much in the way of fundamental and therefore more widely applicable data regarding the mineral nutrient requirements of tree species. It is believed that the desired information can be obtained more surely and efficiently from carefully controlled cultural experiments, followed and confirmed rather than preceded by field studies.

The so-called nutrient-sand technique, essentially similar to that previously used (Mitchell, 1934; Gast, 1937), was again employed in the experiments which this report describes. This experimental method, although not completely satisfactory, probably provides the best means thus far developed for determining certain fundamental relationships between nutritional factors and the growth and development of tree seedlings. It is clearly recognized, however, that because of the artificiality of the technique, conclusions based solely upon data so obtained may or may not be useful in their application to growth in the nursery seed bed or the forest. Thus, the fundamental relationships discovered in the carefully controlled cultural experiment, a somewhat artificial environment, do not necessarily constitute a sound basis for the broad interpretations and generalizations which are the aim of all fundamental research—that is, not until these relationships are thoroughly tested and confirmed under the more complex conditions found in nature. Such testing is the proper and logical function of the controlled and the uncontrolled field experiment. Accordingly, all of the nutrient elements varied in the cultural experiments reported in full in this paper were also varied individually and in several combinations in a series of field studies carried out during the summers of 1934, '35, '36 and '37 at the Black Rock Forest experimental nursery (see Mitchell, Finn and Rosendahl, 1937). These studies, which were designed primarily to test under nursery conditions the conclusions drawn from the carefully controlled cultural experiments, are not here discussed in detail. However, the more pertinent data from the field studies are used freely in that section of this report in which certain fundamental relationships—discovered in cultural studies and confirmed with field trials—are interpreted and discussed in relation to current nursery practice.

Experience with agricultural crops has shown that the experimental procedure of maintaining at a constant level all growth factors except the one studied—which is varied by known amounts—is particularly useful in preliminary studies with species of undetermined nutrient requirements. In this way it is possible to separate the effects of a single nutrient element. Nitrogen was varied individually in the present study in order to elaborate and confirm previous observations regarding the relationship of this highly important element to the growth and development of white pine seedlings. Phosphorus and potassium, frequently deficient in seed-bed and forest soils, and calcium, an important plant constituent, were also varied in individual series. Little or nothing is known of the physiological responses of tree species to varying supplies of the latter three elements. Until the critical ranges of supply of all of the more important essential elements are delimited with a fair degree of accuracy, as a result of such studies, it is difficult if not impossible to devise precise experiments to study the highly important but complex problem of physiological balance. The same applies, although to a lesser degree, to studies of interactions such as the effects of varied nutrition at different levels of some other environmental factor, *i.e.*, radiation, temperature, moisture supply, etc.

The results of the 1933 white pine experiment, herein reported for the first time, will be referred to in the discussion as the M-'33 data. Frequent reference is also made to certain other investigations with various species of *Pinus*. These experiments, some of which are entirely distinct from the series of the writer, include the following: the 1929 nutrient-sand culture experiment of Aldrich-Blake (1930); the 1931 nutrient-sand culture experiment of Gast and Mitchell (see Mitchell, 1934; Gast, 1937); the 1932 nutrient-sand culture experiment of Mitchell (*loc. cit.*); the 1934, '35, '36 and '37 nursery experiments of Mitchell (reported in part by Mitchell, 1936, '37); and the 1930, '32 and '34 nutrient-sand culture experiments of Gast (*loc. cit.*). Reference to these experiments may be simplified by using the following abbreviations: A-B-'29, G M-'31, M-'32, '34, '35, '36, '37 and G-'30, '32, '34, respectively[1] (see Gast, 1937, Table A).

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[1] The initials A-B, G and M refer to Aldrich-Blake, Gast and Mitchell, respectively; '29, '30 etc. are the years of the experiments and should not be confused with publication dates, according to which citations are made to published reports included in the bibliography.

DETAILS OF EXPERIMENTAL METHOD

THE experimental methods employed in this study were essentially the same as those used in previous studies, described in detail in the reports on the G-'30, '32, '34, G M-'31, and M-'32, '34 experiments. The important details of the slightly modified procedure followed in the 1933 white pine experiment are outlined briefly below, chiefly for the benefit of those not familiar with the previous reports.

POTS, SAND AND WATERING TECHNIQUE

In the M-'33 experiment glazed clay pots containing the sand mixture were placed inside of 8-quart metal pails. Monel metal screens, which react only slightly with the solutions used, prevented the sand from running through the hole in the bottom of the pot into the pail. The pails, which were 9.5 inches in diameter at the top, 7.5 inches at the bottom and 8 inches deep, were given several coats of acid-resistant asphalt paint. Each was fitted with a metal bung near the bottom. A glass T-tube inserted in this bung connected the pail with a 1-gallon jug which served as a reservoir for the nutrient solution. Solutions were forced from the jug reservoir into the pail by applying pressure (with hand pump) to the former. The pail-pot-jug arrangement is shown in detail in Plate I.

Two kinds of sand, both 99.89% pure silica, were used. Pots were filled to a depth of 5 inches with No. 4 Columbia silica, which is angular in shape and rather coarse. A mixture of 2 parts (by volume) of the Columbia silica and 3 parts of Ottawa, which is finer and nearly spherical, was used in the upper part of the pots. Drainage experiments proved this to be the best combination. The size-class distribution of the two sands was discussed in detail in the report on the M-'32 experiment.

When the pots, pails and supply jugs were in position, shown in Plate I, exactly 4.5 liters of distilled water were poured evenly over the sand in each pot and allowed to drain free into the jug reservoir. The level in the jug was then marked, and since the sand would always retain the same amount of water, the volume of the solution was kept constant throughout the summer by keeping the water level in each jug up to the mark. The water lost by transpiration and evaporation

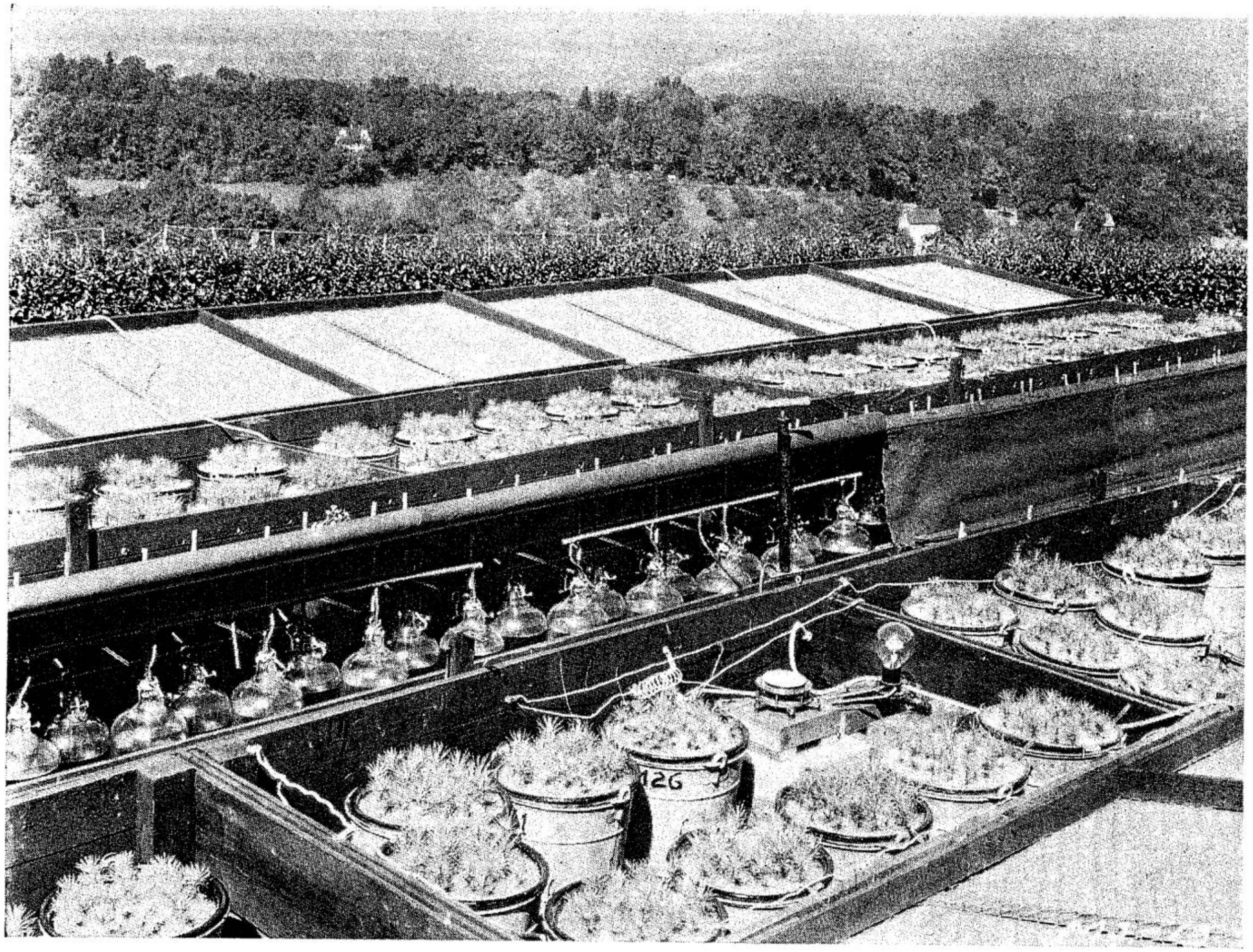

PLATE I.—ARRANGEMENT OF POTS, PAILS AND SUPPLY BOTTLES DURING EXPERIMENT.

Multiple pumping device is shown with pump attached. Supply bottles are covered by cloth shades to protect nutrient solutions from sun. Shades can be raised or lowered as shown. Pyrheliometer (right) and photronic cell are mounted in near box.

was made up each day by the addition of distilled water. Flushing the solution into the pots was greatly facilitated by the use of the multiple pumping arrangement shown in Plate I. This consists of a brass tube connecting five or more jugs so that air (from hand pump) can be forced into all of them in one operation. Each day at 8 A.M. the pots were flooded and then allowed to drain free immediately thereafter. Between 11 A.M. and 12 noon—depending on air temperature, wind velocity, etc.—the pots were again flooded. This time the solutions were kept at approximately half height during the hottest part of the day, after which they were allowed to drain free. Except on cool, cloudy days the pots were again flooded at 5 P.M. and then drained immediately. This watering schedule proved entirely satisfactory.

The arrangement just described has the following advantages: (1) there can be no loss of nutrients as in the Hesselman method (see Mitchell, 1934, p. 12), (2) even distribution of the solution is assured, (3) the volume of the solution, and hence the concentration of the various nutrient elements in solution, is easily controlled, (4) a large volume of solution may be used, and (5) seedlings can be watered more quickly and with better volume control than with many of the other methods in use.

The chief disadvantage is in the lack of temperature control. Evaporation from the surface of the unglazed pots used in the M-'32 experiment tended to lower the temperature in these pots. But to prevent possible loss of nutrients in the porous walls, glazed pots were substituted in the 1933 experiment, reported here. The glaze undoubtedly precludes nutrient loss, but Hatch (personal communication) found that on extremely hot days the temperature within the glazed pots is sometimes as much as 7° F. higher than in the porous pots. It is doubtful, however, if the temperature in either type of pot was ever sufficiently high to have any direct deleterious effect on seedling growth. This is evidenced by the fact that the M-'32 and M-'33 nutrient-sand culture results were almost identical (see Fig. 8A) even though different pots were used.

In the G-'34 and subsequent experiments (Gast, 1937) the pot and pail combination was discarded in favor of bottomless, stoneware, gallon jugs with an acid-proof glaze. These were placed (inverted) in racks above the nutrient-supply jugs and were packed in sphagnum moss which was kept moist. Since the moss prevents excessive fluctuations in pot temperature, and the hard glaze precludes the possibility of nutrient loss, this arrangement is believed to be the most satisfactory yet devised.

SEEDS AND PLANTING

Seeds used in this experiment were separated on the basis of fresh weight into 1.0-milligram classes. This permitted correction of plant weights at the time of harvesting for the amount of food reserves with which they started.

Seeds were obtained from a single tree growing on the Pack Demonstration Forest, Warrensburg, New York. After weighing, seeds of the various classes were sterilized for one minute in 0.1% solution of bichloride of mercury, rinsed in sterile water, stratified in moist filter paper contained in sterile flasks and stored at a constant temperature of + 5° C. for six weeks before planting. On May 19, 1933, the end of the storage period, the seeds were planted in washed sand contained in wooden flats (see Plate II, Mitchell, 1934). The sand was treated with acetic acid as recommended by Doran (1932)—1.5 pints of 0.8% acetic acid per square foot of seed bed at time of planting—and no damping off was noted. By June 18 the seeds had germinated and shed seed coats. At this time all seedlings, except those to be used to determine seed-size correction factors, were transplanted to the sand culture pots. Twenty-seven seedlings, from seed of a *single* weight class, were placed in each. The planting dibble, previously described, assured even spacing. The remaining seedlings, from seed of the various weight classes, were taken from the flats on June 29. The discarded seed coats were also gathered at this time.

REPLACEMENTS

Whenever a seedling died, it was immediately replaced so that there were always the same number competing for the available water and nutrients in each pot. When such replacements were made, a waxed thread was attached to the seedling and it was discarded at the end of the summer.

PROTECTION

Pots were shielded from rains with wooden frames covered with Cello Glass, previously described (Mitchell, 1934). This was necessary because of the possibility of contamination by fixed atmospheric nitrogen brought down by rain, and because of the necessity for accurate volume control of the nutrient solutions. The Cello Glass screens were hinged to the racks, as shown in Plate I, to facilitate opening and closing. Since birds often pull up newly-transplanted seedlings, the racks containing the pots were covered with quarter-inch mesh wire screens during the two weeks following transplanting (see Plate VII, Mitchell, *loc. cit.*). Nutrient solution supply jugs were shaded with heavy cloth screens (window shades) as shown in Plate I. This prevented excessive temperatures, and effectively stopped the growth of algae, which otherwise thrive on the nutrient solutions and frequently clog the glass connections.

TABLE 1

KEY TO 1933 NUTRIENT-SAND CULTURE SERIES

Nitrogen Series [1]		*Phosphorus Series* [1]		*Potassium Series* [1]		*Calcium Series* [1]	
Number of Pots [2]	*Nitrogen Concentrations in ppm N*	*Number of Pots* [2]	*Phosphorus Concentrations in ppm P*	*Number of Pots* [2]	*Potassium Concentrations in ppm K*	*Number of Pots* [2]	*Calcium Concentrations in ppm Ca.*
1	0	1	0	1	0	1	0
1	25	2	50	2	50	2	50
1	50	1	100	1	100	2	100
1	75	2	200	2	200	2	300
1	100	2	300	2	319	2	600
..	...	2	400	2	400	1	900
..	...	1	500	1	500	..	...
..	...	1	600	1	600	..	...
..	...	1	700	1	700	..	...
..	...	1	800	1	800	..	...
..	...	1	900	1	900	..	...

[1] Essential nutrient elements other than the one varied were supplied in constant and approximately optimum amounts to all pots of each series.

[2] Twenty-seven seedlings were planted in each pot.

SOLAR RADIATION CONTROL AND MEASUREMENT

White pine seedlings cannot be exposed to full sunlight immediately after transplanting (Mitchell, 1934). For this reason they were covered during the first week with wooden slats (lath) spaced so that the radiation intensity was reduced to about 40% of full sunlight. The spacing was gradually increased during the next two weeks until all slats were removed. Thereafter the seedlings received full sunlight. Experiments have demonstrated conclusively that, if other factors are not limiting, white pine seedlings make their best growth when exposed to full sunlight during the greater part of the initial growing season (Mitchell, 1936; Gast, 1937).

Solar radiation was measured with an Eppley Weather Bureau Type Pyrheliometer registering on a Leeds and Northrup two-point recording potentiometer (Micromax, equipped with special integrating device). These instruments and the general subject of radiation measurement are discussed in detail by Gast (1937). One pyrheliometer is shown in Plate I (right). The instrument to the immediate left is a photronic cell which, although enclosed in a weather-proof mounting, proved very unsatisfactory (see Gast, *loc. cit.*). For this reason no record of total *illumination* was obtained.

Measurements of *total solar radiation* (visible plus infra-red) with the Eppley pyrheliometer and recorded as in this experiment are believed by Gast (*loc. cit.*) to be accurate within ± 3%. The cumulative radiation received by the seedlings from the time they were transplanted to the pots (June 18) until they were harvested on October 4 was found to be 38.1 kilogram calories per square centimeter. This is an average of 353 gram calories per square centimeter per day. Since the pyrheliometer was placed at the plant level among the pots, which were shaded during the first three weeks and covered with Cello Glass screens during rains, the total radiation value (38.1 kg. cal.) is somewhat lower than that actually received in this locality during the period of the experiment.

NUTRIENT SOLUTIONS

The nutrient solutions used in the 1933 experiment were discussed in the report on the 1932 white pine experiment (Mitchell, 1934). The various combinations and associated pH values were presented in detail in Tables 1, 2, 3, 4, 6 and 11 of that report. This tabular material is not repeated here.

Briefly, nitrogen, phosphorus, potassium and calcium were varied in individual series as indicated in Table 1. Essential nutrient elements other than the one varied were supplied in constant and approximately optimum amounts to all pots of each series. The basic solutions were based upon the results of previous experiments (Aldrich-Blake, 1930;

TABLE 2

CALCIUM SERIES NUTRIENT SOLUTIONS AND APPLICATION SCHEDULES[1]
1933 SAND CULTURE EXPERIMENT

Calcium Concentrations Used

Calcium Concentration in ppm Ca	*Source*	*Milligrams of Source per Liter*	*Milligrams Source per Pot (4.5 Liters)*
0	$CaCl_2 \cdot 6H_2O$	0	0
50	"	273.31	1,229.89
100	"	546.63	2,459.83
300	"	1,639.89	7,379.50
600	"	3,279.78	14,759.01
900	"	4,919.67	22,138.51

Calcium Application Schedule

Final Calcium Concentrations in ppm Ca to be Attained	0	50	100	300	600	900
Milligrams $CaCl_2 \cdot 6H_2O$ per Application						
	Applied June 24 →	1229.89	1229.89	1229.89	1229.89	1229.89
		June 29 →	1229.89	1229.89	1229.89	1229.89
			July 11 →	4919.66	4919.66	4919.66
				July 15 →	7379.50	7379.50
					July 19 →	7379.50
					Total[2]	22138.40

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[1] Figures beyond those significant were retained in this table for convenience in machine calculation.
[2] The totals of columns in the application schedule should check with the values given in column 4 above.

TABLE 2—*(Continued)*

Basic Nutrient Solution Supplied to All Pots in Calcium Series

Source	*Milligrams of Source per Liter*	*Milligrams per Pot (4.5 Liters)*	*Concentration of Nutrient Elements in ppm (Milligrams per Liter)*						
			Ca	N	P	K	S	Fe	Mg
$CaCl_2 \cdot 6H_2O$	Varied	Varied	Varied	......	......	......	......	...	......
KH_2PO_4	1111.98	5003.91	......	......	253.37	319.37	......	...	......
NH_4NO_3	857.16	3857.22	......	300.00	......	......	......	...	......
$MgSO_4 \cdot 7H_2O$	1780.00	8010.00	......	......	......	......	231.50	...	175.60
Ferric Citrate	20.00	90.00	......	......	......	......	......	3.40	......

Basic Solution Application Schedule

Source	*NH_4NO_3*	*KH_2PO_4*	*$MgSO_4$ $7H_2O$*	*Ferric Citrate*
Date of Application	*Milligrams of Source per Application*			
June 1	500.01	648.65	1335.00	90.00
June 24	785.73	1019.32	1335.00	....
July 11	1285.74	1667.97	2670.00	....
July 19	1285.74	1667.97	2670.00	....
Totals[1]	3857.22	5003.91	8010.00	90.00

[1] These totals should check with values given in column 3 of the basic solution table.

Mitchell, 1934; Gast, 1937). The concentration in parts per million (ppm)—milligrams per liter—of the different elements in the basic solutions were as follows:[1]

N	P	K	Ca	Mg	Fe	S
300	253	319	244	176	3.4	231

These concentrations, with the exception of calcium which is somewhat lower, are essentially the same as those used in previous studies. The chief difference is that the total volume of each solution was maintained at 4.5 liters throughout the growing season, whereas the greatest volume previously used was 3.5 liters. All solutions were made by dissolving chemically pure salts in distilled water.

Solutions used in the calcium series are given in detail in Table 2. These data, which have not been discussed previously, illustrate methods of preparation and application similar in principle to those used for solutions of the N, P and K series. It will be observed (see application schedules, Table 2) that the concentration of all nutrient elements in each solution was increased gradually, and that the maximum (final) concentrations given in Table 2 were not attained until four weeks after the seedlings were transplanted to the pots. This gradual increase was necessary because of the fact that the basic solution used, although approximately optimum for older and larger seedlings, is sufficiently concentrated to have a definitely toxic effect upon white pine seedlings in the early stages of their development. Attention is also called to the calcium application schedule of the calcium series, as shown in Table 2. Calcium concentrations above 50 ppm were attained gradually, and for the same reason. Similar precautions were observed with solutions of series in which N, P, and K were varied (see Tables 1 and 6, Mitchell, *loc. cit.*).

HARVESTING AND ANALYSIS

Seedlings of the 1933 white pine experiment were harvested on October 4, 108 days from the time they were transplanted to the pots. After lifting, the seedlings were washed with a small stream of water to remove sand particles. Each was examined under a microscope, and records of various features of the root systems were made. Seedlings were then measured, cut into two portions, root and shoot for

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[1] Minor elements such as boron, manganese, zinc and copper, small amounts of which are known to be essential to the normal growth and development of certain plants (see Brenchley, 1936), were not included in the basic solutions. Tests have shown that culture-grown one-year-old white pine seedlings do not benefit by supplements of these elements, probably because all are present in the seed, chemicals or sand in minute but sufficient amounts.

ratio determinations, each part placed in a labeled glassine envelope, dried at +70°C. and weighed to ±0.1 milligram.

A representative seedling from each pot was preserved for reference, photographs and morphological study. The dried specimens, after weighing, were ground in a Wiley mill to pass through a 0.55 mm. mesh screen. Chemical analyses of the ground samples were made according to methods previously described (Mitchell, 1934 and 1936).

CORRECTION FOR THE INFLUENCE OF SEED WEIGHT UPON THE YIELD OF SCOTS, CORSICAN AND WHITE PINE SEEDLINGS

THE studies of Aldrich-Blake (1930), Champion (1933, and references cited), Mitchell (1934) and Gast (1937) indicate that seed weight exerts an important control on the early cumulative dry weight of several species of pine. During the initial growing period seedling yield is proportional to seed weight or some equivalent measure of food reserves in the embryo and endosperm. Just how much longer differences in "seed capital" are reflected in the growth rate is as yet unknown. It is certain, however, that the distribution of weights in an average sample of *Pinus* seeds includes a range sufficient to account for large variations in the yield of one-year-old seedlings. Differences of ±35% from the mean are possible.

Deviations of this magnitude may affect adversely the significance of experimental data. Therefore, in experiments where a high degree of precision is required and physical limitations preclude the use of a large number of seedlings, it is necessary either to: (1) eliminate variations in seed size, or (2) separate seeds into appropriate weight classes so that the resulting seedlings may be corrected at the time of harvesting for differences in original food reserves. The latter procedure, which is usually the more practical, was followed in the present ('33) as well as previous studies of the series. The following discussion is concerned primarily with the derivation of seed-size correction factors used to convert to a common basis the weights of seedlings grown in the nutrient-sand cul-

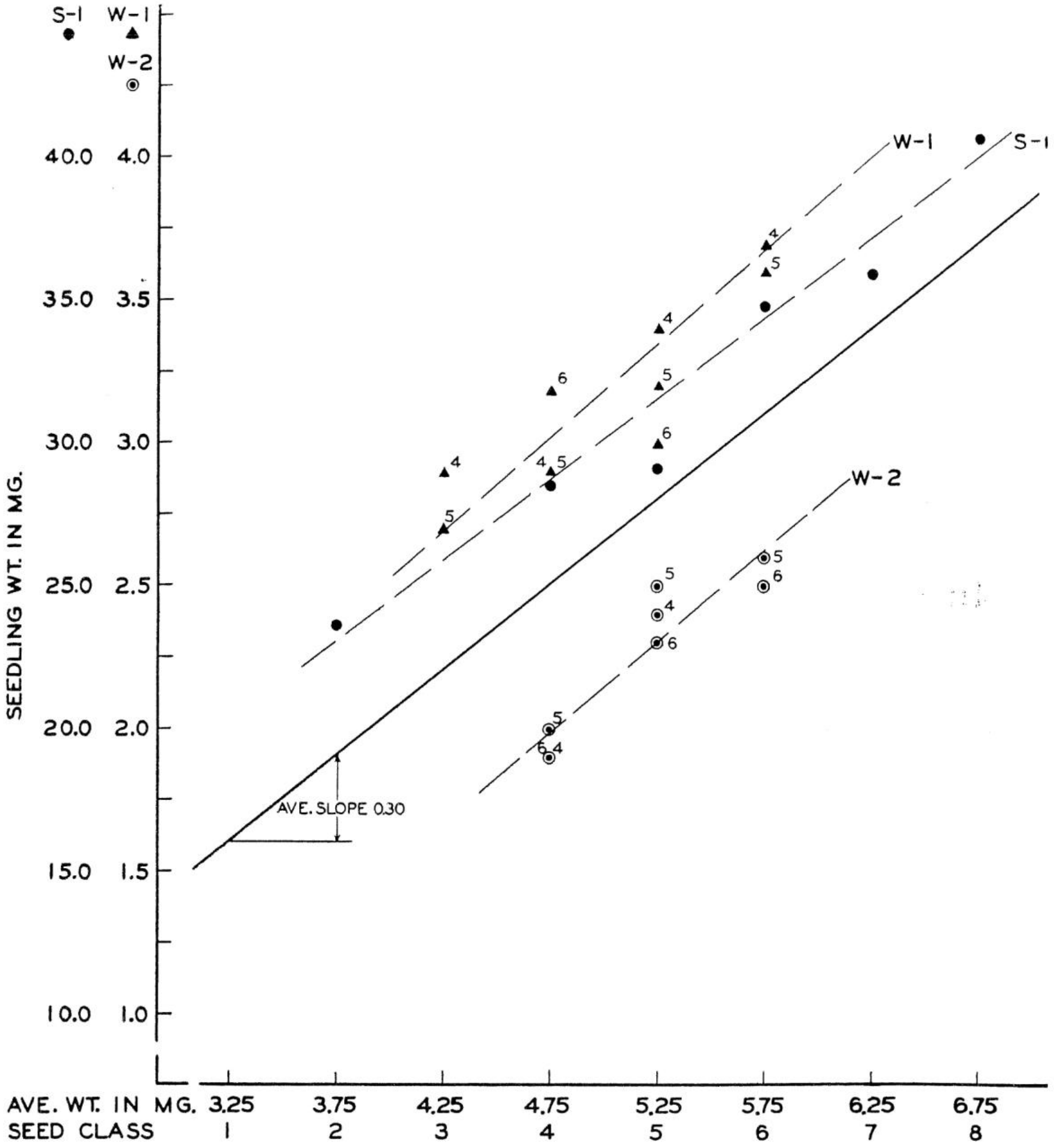

Fig. 1.—THE DRY WEIGHTS OF SCOTS PINE SEEDLINGS GROWN FROM SEEDS OF VARIOUS FRESH WEIGHTS. DATA: S-1, W-1 FROM GAST, 1930 EXPERIMENT; W-2 FROM GAST AND MITCHELL, 1931 EXPERIMENT.

The small figures near each point indicate the number of primary cotyledons (see discussion, Mitchell, 1934, p. 31).

ture series of the 1933 white pine experiment. Certain previously reported observations regarding Scots and Corsican as well as white pine are drawn upon for illustrations and as a background for discussion of seed weight data obtained from the M-'33 and subsequent experiments.

SEED-SIZE CORRECTION FOR SCOTS PINE
(*Pinus silvestris* L.)

Seed-size correction factors were derived and applied for the first time to data from the G-'30 Scots pine experiment. The methods which have since been developed were a result of Gast's study of data from his own 1930-'31 and the A-B-'29 experiments. Their application to the G M-'31 Scots pine experiment has been described (Mitchell, 1934). The fundamental facts are illustrated by the data presented in Fig. 1. In this case correction ratios were derived from the calculated average relationship between fresh weight of seeds, separated into 0.5-milligram classes, and the dry weight of resulting seedlings grown for varying periods in pure sand to which no nutrients were added.

It will be observed (Fig. 1) that the S-1 data were plotted against a reduced ordinate scale. Although it is not apparent when all data are plotted against the same scale, Fig. 1 illustrates and calculation shows that the characteristic slope of the curve based upon the S-1 data is essentially the same as that of the two W series even though the former seedlings, which grew longer, attained a weight approximately ten times greater than the latter. This is highly significant since it indicates that, during the first year, the *ratio* between the weights of seedlings from seed of different size is unaffected by variations in the period of growth. Neither is this ratio affected by variations in environmental factors, as will be demonstrated later in this discussion with white and Corsican pine data.

The heavy line in Fig. 1 represents the average slope of the three series of data. From this average relation coefficients were derived for converting the weights of seedlings from seeds of various size to the equivalent of seedlings from seeds of a single size. Thus, the weights of seedlings from seed class 4 can be converted to weights equivalent to seedlings grown from seed class 5 (the median class) by multiplying by 1.130, from class 6 to class 5 by multiplying by 0.896 and from class 7 to class 5 by multiplying by 0.812. These are the factors used by Mitchell (1934) and Gast (1937) to reduce to a comparable basis the yield of Scots pine grown from seeds of various weight in the same or different nutrient environments.

Seed-Size Correction for Corsican Pine
(*Pinus laricio* Poir.)

The Corsican Pine data of Aldrich-Blake (1930, Table 14) may be similarly treated. His results, as plotted in Fig. 2 A, show the relation between fresh weight of seeds (2-mg. classes) and the yield of seedlings grown for the same length of time in nutrient-sand cultures of different nitrogen concentration ($N = 0$, $N = 1$, $N = 2$ etc.). The lines of average relation (Fig. 2) were fitted[1] to each set

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[1] The regression lines plotted in Fig. 2 A are expressed by the following equations:

(For $N = 0$) $y = 8.40\ x + 99.0$
1 $y = 19.70\ x + 31.0$
2 $y = 19.45\ x + 165.2$
4 $y = 30.60\ x + 105.0$
8 $y = 37.70\ x + 166.5$
16 $y = 33.50\ x + 546.0$

in which $x =$ fresh weight of seed (independent variable), $y =$ dry weight of resultant seedlings (dependent variable) and N ($N = 0$, $N = 1$ etc.) refers to the amount of nitrogen in the nutrient solution. Equation constants were derived according to the method of least squares (see above) from data reported by Aldrich-Blake (1930, Table 14).

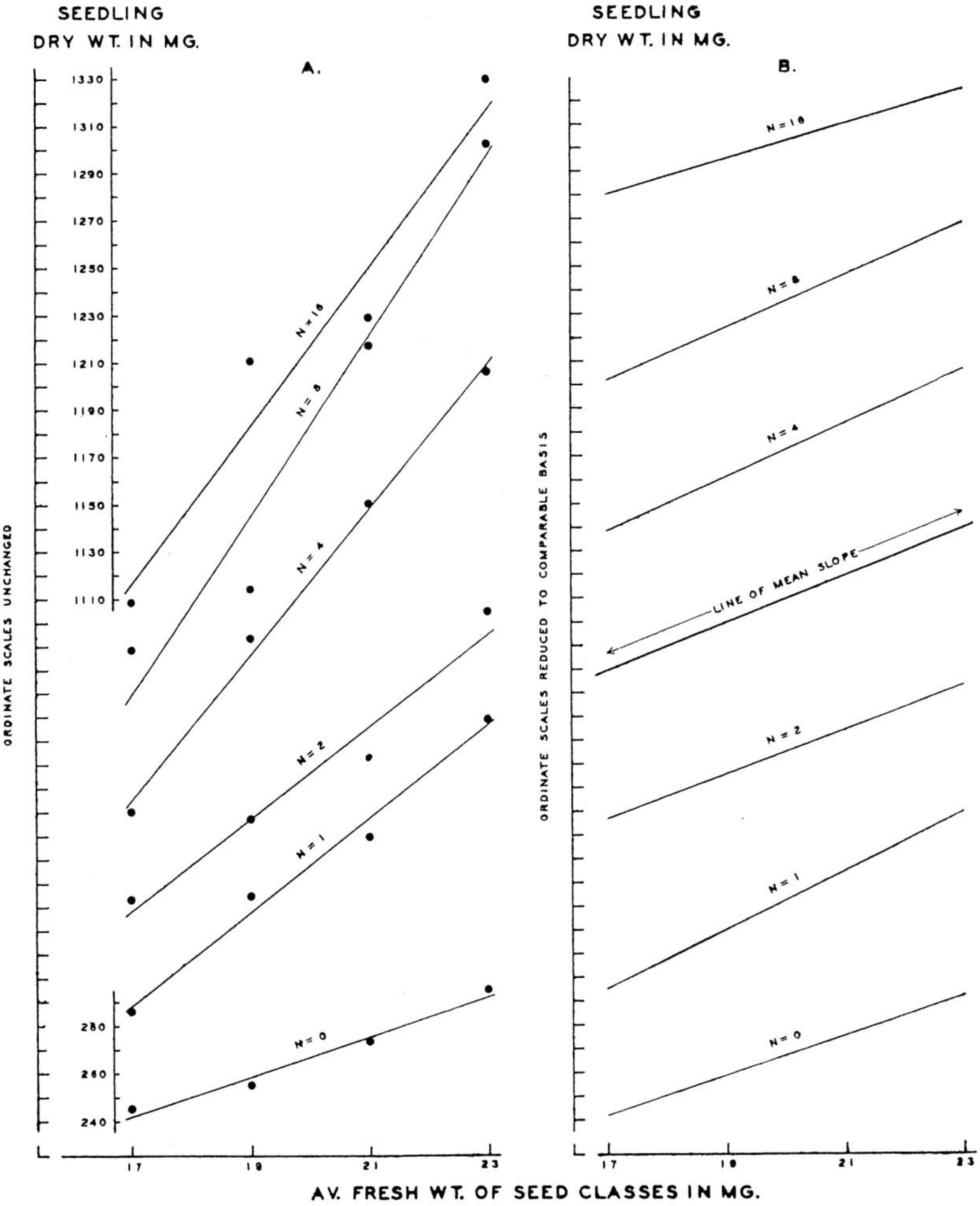

FIG. 2.—THE DRY WEIGHTS OF CORSICAN PINE SEEDLINGS GROWN FROM SEEDS OF VARIOUS FRESH WEIGHTS IN NUTRIENT-SAND CULTURES OF DIFFERENT NITROGEN CONCENTRATION. DATA FROM ALDRICH-BLAKE, 1930, TABLE 14.

of data by the method of least squares (Bruce and Schumacher, 1935). The family of curves in Fig. 2 A indicate that, when plotted against the same ordinate scale, the actual slope of the regression lines increases with nitrogen supply. Aldrich-Blake (1935) has stated that, because of this fact, correction ratios derived from the linear relation between seed weight and the resultant weight of seedlings grown in sand devoid of nutrients, ''cannot yield accurate results'' when applied to seedlings grown in more favorable nutrient environments, as in the G M-'31 and the M-'32 experiments. But Aldrich-Blake is mistaken, as the following discussion of his Corsican pine data demonstrates.

The regression lines (Fig. 2 A) do vary in *actual slope* with nitrogen supply, but in such a manner that the *ratios* between seedlings from seeds of different size remain unchanged. For this reason correction factors based on data from seedlings which received no nitrogen are equally applicable to those grown in the highest, or any other nitrogen supply. For example, the average (calculated) yields of seedlings from seed classes 17 and 23 are 241.8 and 292.2, respectively, for those supplied no nitrogen ($N = 0$), and 1115.5 and 1316.5 for those supplied the greatest amount of nitrogen ($N = 16$). The resulting ratios are:

$$\frac{292.2}{241.8} = 1.208 \ (N = 0), \text{ and } \frac{1316.5}{1115.5} = 1.180 \ (N = 16).$$

These ratios (correction factors), although derived from observation at the two extremes of nitrogen supply, are the same within limits of experimental error. If anything, the characteristic slope (rate of increment) of the $N = 0$ data is the greater.

In Fig. 2 B the various regression lines are shown plotted against ordinate scales which have been reduced by statistical procedures to a comparable basis. It is apparent from this illustration, and it can be demonstrated

TABLE 3

COMPARISON OF SEED WEIGHT CORRECTION VALUES FOR CORSICAN PINE

Fresh Wt. of Seed	*Factors for converting the yields of seedlings from seed of a given size (Col. 1) to a weight equivalent to those grown from 20-mg. seed, the median weight used in the Aldrich-Blake experiment*	
	Gast [1]	*Mitchell*
(1)	(2)	(3)
17	1.127	1.126
19	1.039	1.039
21	0.965	0.964
23	0.902	0.899

[1] See Table 8 (1) and discussion pp. 623-631, Gast, 1937.

mathematically, that these regression lines have essentially the same rate of increment and that this rate is independent of nitrogen supply. The heavy "line of mean slope" is expressed by the equation

$$y = 9.97\,x + 67.6,^{1}$$

in which $x =$ fresh weight of seed and $y =$ dry weight of resultant seedlings. Yields corresponding to any two values of x may be multiplied (the same effect as increased nitrogen supply or period of growth) or divided by any single amount without changing their relationship to each other. From yields calculated in this way were derived the correction factors 1.126, 1.039, 0.964, and 0.899, with which to convert seedlings from seeds weigh-

---

[1] This formula represents the average relationship between fresh weight of seed and the dry weight of the resultant seedlings, as based on the six series of data shown in Fig. 2. The constants were derived from the following regression equations:

$$\begin{array}{rl}
(\text{For } N = 0) & y = 8.40\,x + 99.0 \\
1 & y = 12.38\,x + 19.5 \\
2 & y = 9.37\,x + 79.6 \\
4 & y = 11.39\,x + 39.1 \\
8 & y = 10.93\,x + 48.3 \\
16 & y = 7.35\,x + 119.9
\end{array}$$

which express, on a *comparable basis,* the relation between seed size and seedling yield for each series.

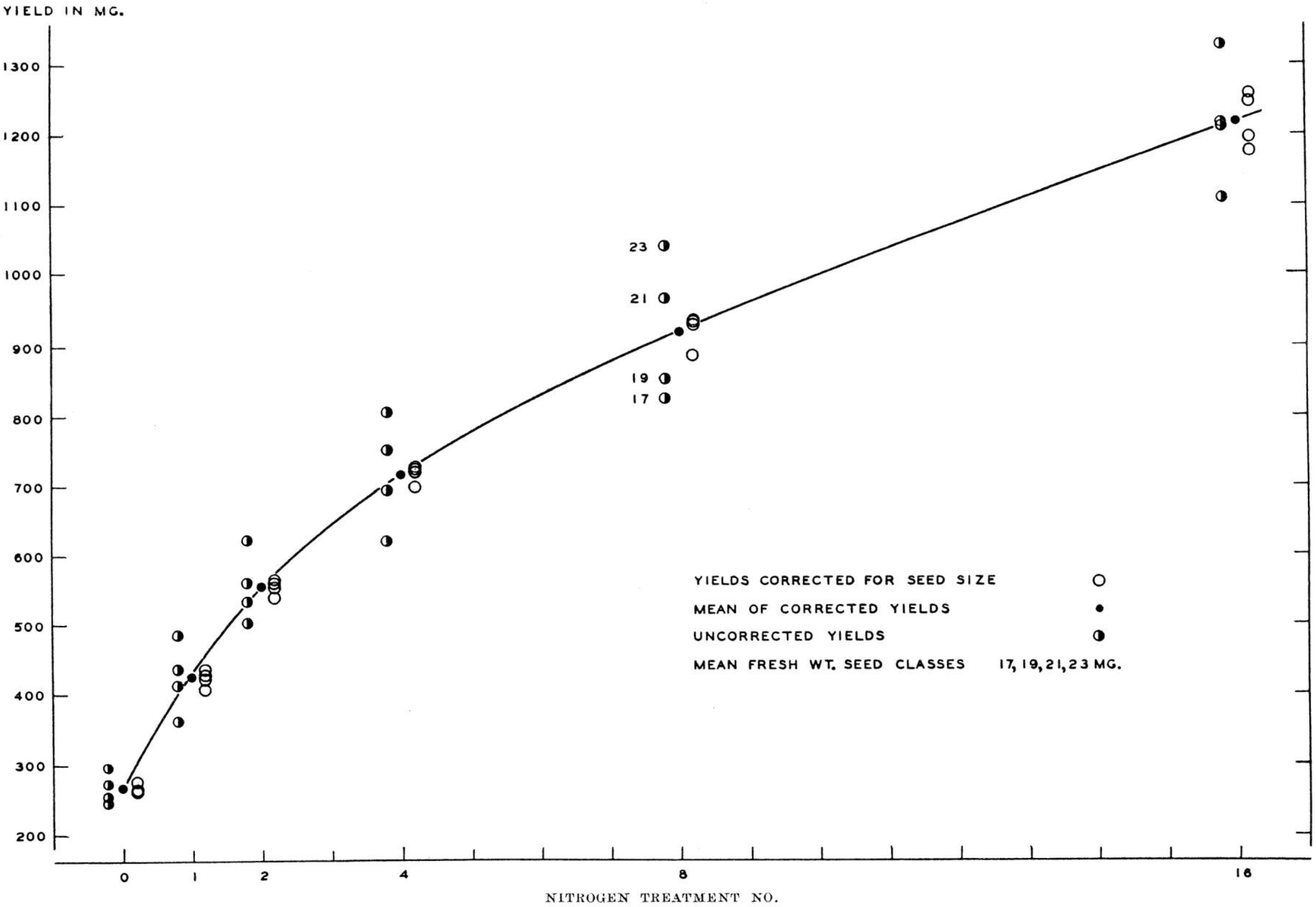

FIG. 3.—THE RELATION BETWEEN NITROGEN SUPPLY AND THE YIELD OF CORSICAN PINE SEEDLINGS FROM SEED OF DIFFERENT FRESH WEIGHT. BASIC DATA AFTER ALDRICH-BLAKE, 1930, TABLE 14.

Seedling yields corrected for the influence of seed weight, and expressed as from 20 mg. seeds, the median weight, are plotted to the right of the mean corrected yield at each nitrogen supply. Uncorrected yields from each seed weight class (17, 19, 21, 23) are plotted to the left. See discussion in text.

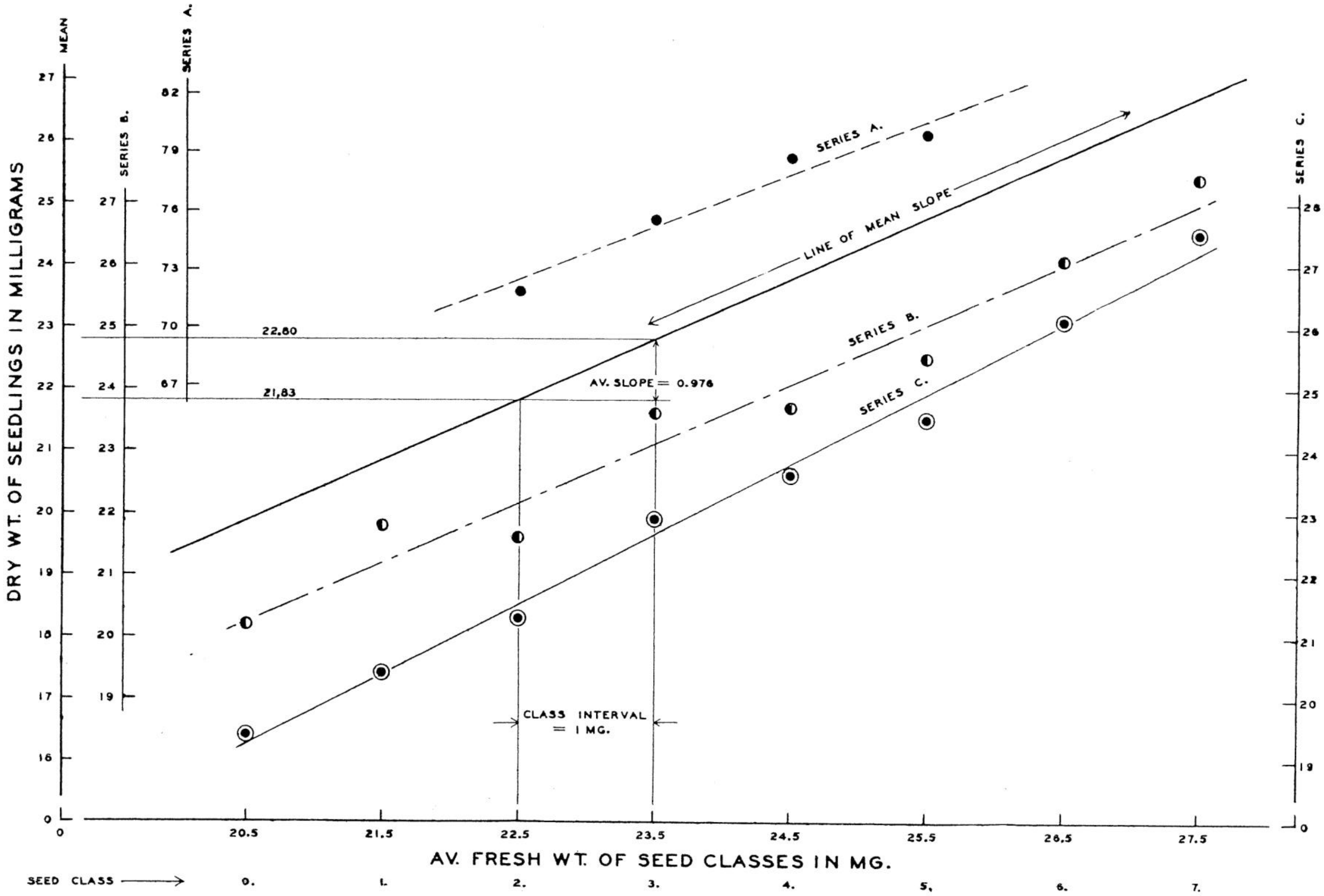

FIG. 4.—THE DRY WEIGHTS OF WHITE PINE SEEDLINGS GROWN FROM SEEDS OF VARIOUS FRESH WEIGHTS.

ing, respectively, 17, 19, 21 and 23 mg., to a weight equivalent to 20 mg. seeds, the median size used in the A-B-'29 experiment. There can be little doubt of their validity since almost identical correction factors were derived by Gast by an entirely different method, and he further substantiated the estimates thus obtained by a multiple correlation calculation. These values are compared in Table 3. The "scatter" or deviation of the A-B-'29 data from the yield curve of average relation is greatly reduced when seedling weights are corrected, with the above factors, for the influence of seed size. This is shown in Fig. 3 (*cf.* Gast's Fig. 10 C.).

SEED-SIZE CORRECTION FOR WHITE PINE (*Pinus strobus* L.)

Method 1.—The procedure used to calculate correction factors for Scots and Corsican pine is equally applicable to white pine. As shown in Fig. 4, the yields of white pine are also linearly related to the fresh weight of the seeds.

Seeds of each series were separated on the basis of fresh weight into 1-milligram classes, as indicated in Fig. 4. All were planted in washed sand contained in wooden flats. They received no mineral nutrients other than the small amounts present in the sand and the tap water with which the sand was kept moist. The series A seedlings, from seed used in the M-'32 white pine experiment, were grown for fifty-one days after seed coats were shed. The series B seedlings, grown the following year (1933) from the same lot of seed, were harvested on the eleventh day. The series C seedlings, from seed of another source, were also grown in 1933 and harvested on the eleventh day. Basic data on series A, B and C are presented in Tables 4, 5, and 6 respectively, and the results of statistical analyses are summarized in Table 7.

TABLE 4

The Dry Weight and Reserve Dry Weight of Seeds, and the Dry Weight of Seed Coats and Seedlings from White Pine Seeds of Various 1-Milligram Fresh Weight Classes

Seed Series A[1]

Seed Class	*Av. Fresh Wt. of Class in Mg.*	*Dry Wt. of Seed Coats in Mg.*		*Dry Wt. of Seeds in Mg.*		*Reserve Dry Wt.*[4] *in Mg. (6) — (4) = (7)*	*Dry Wt. of Seedlings in Mg.*[5]	
		Determined by Experiment	*Estimated from Regression Equation* [2]	*Determined by Experiment*	*Estimated from Regression Equation* [3]		*Determined by Experiment*	*Calculated* [6]
(1)	*(2)*	*(3)*	*(4)*	*(5)*	*(6)*	*(7)*	*(8)*	*(9)*
0	20.5	6.75±0.03[7]	6.62	18.88±0.06[7]	19.05	12.43	....	66.07
1	21.5	7.06±0.04	6.95	19.78±0.05	19.89	12.94	....	69.03
2	22.5	7.20±0.02	7.29	20.90±0.05	20.73	13.44	71.83±0.53[7]	71.93
3	23.5	7.40±0.03	7.62	21.74±0.07	21.57	13.95	75.62±0.93	74.89
4	24.5	7.68±0.04	7.96	22.60±0.02	22.42	14.46	78.67±0.84	77.85
5	25.5	8.55±0.04	8.29	23.52±0.11	23.26	14.97	79.82±1.03	80.81
6	26.5	8.83±0.05	8.63	24.07±0.09	24.10	15.47	....	83.71
7	27.5	8.71±0.08	8.96	24.77±0.11	24.94	15.98	....	86.67

[1] Seed of the same lot used in the 1932 white experiment (see Mitchell, 1934, Table 17).

[2] These values calculated with equation I, Table 7.

[3] These values calculated with equation II, Table 7.

[4] Reserve dry weight, as defined by Gast, is the material available for the development of the embryo, and is equal to the dry weight of the seed minus the dry weight of the seed coat (see Baldwin, 1936 and Gast, 1937).

[5] Seedlings grown for 51 days in sand to which no nutrients were added.

[6] These values calculated with equation IV, Table 7; yields calculated with equation III are essentially the same.

[7] Standard error of mean.

TABLE 5

THE DRY WEIGHT AND RESERVE DRY WEIGHT OF SEEDS, AND THE DRY WEIGHT OF SEED COATS AND SEEDLINGS FROM WHITE PINE SEEDS OF VARIOUS 1-MILLIGRAM FRESH WEIGHT CLASSES

SEED SERIES B[1]

Seed Class	Av. Fresh Wt. of Class in Mg.	*Dry Wt. of Seed Coats in Mg.*		*Dry Wt. of Seeds in Mg.*		Reserve Dry Wt.[4] in Mg. (6) — (4) = (7)	*Dry Wt. of Seedlings in Mg.*[5]	
		Determined by Experiment	*Estimated from Regression Equation*[2]	*Determined by Experiment*	*Estimated from Regression Equation*[3]		*Determined by Experiment*	*Calculated*[6]
(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
0	20.5	7.19±0.32[7]	7.12	18.88±0.06[7]	19.04	11.92	20.30±0.28[7]	20.24
1	21.5	7.22±0.11	7.40	19.78±0.05	19.89	12.49	21.88±0.20	21.20
2	22.5	7.73±0.14	7.68	20.90±0.05	20.74	13.06	21.67±0.37	22.16
3	23.5	8.18±0.15	7.96	21.74±0.07	21.58	13.62	23.64±0.29	23.11
4	24.5	8.37±0.18	8.24	22.60±0.02	22.43	14.19	23.79±0.35	24.07
5	25.5	8.80±0.14	8.52	23.52±0.11	23.28	14.76	24.52±0.39	25.04
6	26.5	8.82±0.14	8.79	24.07±0.09	24.12	15.33	26.18±0.41	26.00
7	27.5	9.02±0.16	9.07	24.77±0.11	24.97	15.90	27.43±0.35	26.96

[1] Data from series A seed (see Table 3) after one year of storage.

[2] These values calculated with equation V, Table 7.

[3] These values calculated with equation VI, Table 7.

[4] Reserve dry weight, as defined by Gast, is the material available for the development of the embryo, and is equal to the dry weight of the seed minus the dry weight of the seed coat (see Baldwin, 1936 and Gast, 1937).

[5] Seedlings grown for 11 days in sand to which no nutrients were added.

[6] These values calculated with equation VIII, Table 7; yields calculated with equation VII are essentially the same.

[7] Standard error of mean.

TABLE 6

THE DRY WEIGHT AND RESERVE DRY WEIGHT OF SEEDS, AND THE DRY WEIGHT OF SEED COATS AND SEEDLINGS FROM WHITE PINE SEEDS OF VARIOUS 1-MILLIGRAM FRESH WEIGHT CLASSES

SEED SERIES C[1]

Seed Class	*Av. Fresh Wt. of Class in Mg.*	*Dry Wt. of Seed Coats in Mg.*		*Dry Wt. of Seeds in Mg.*		*Reserve Dry Wt.[4] in Mg. (6) — (4) = (7)*	*Dry Wt. of Seedlings in Mg.[5]*	
		Determined by Experiment	*Estimated from Regression Equation [2]*	*Determined by Experiment*	*Estimated from Regression Equation [3]*		*Determined by Experiment*	*Calculated [6]*
(1)	*(2)*	*(3)*	*(4)*	*(5)*	*(6)*	*(7)*	*(8)*	*(9)*
0	20.5	6.63±0.07[7]	6.50	19.11±0.09[7]	19.16	12.66	19.40±0.41[7]	19.24
1	21.5	6.84±0.12	6.82	20.28±0.14	20.04	13.22	20.42±0.20	20.38
2	22.5	7.24±0.10	7.14	20.80±0.12	20.91	13.77	21.37±0.31	21.50
3	23.5	7.44±0.17	7.46	21.98±0.08	21.79	14.33	22.91±0.20	22.64
4	24.5	7.61±0.07	7.78	22.41±0.14	22.67	14.89	23.61±0.33	23.78
5	25.5	8.08±0.18	8.10	23.70±0.23	23.55	15.45	24.55±0.25	24.92
6	26.5	8.65±0.33	8.41	....	24.42	16.01	26.13±0.22	26.06
7	27.5	8.79±0.18	873	....	25.30	16.57	27.59±0.50	27.21

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[1] Seed from a single tree and of the lot used in the 1933 white pine experiment, reported in this paper.

[2] These values calculated with equation IX, Table 7.

[3] These values calculated with equation X, Table 7.

[4] Reserve dry weight, as defined by Gast, is the material available for the development of the embryo, and is equal to the dry weight of the seed minus the dry weight of the seed coat (see Baldwin, 1936 and Gast, 1937).

[5] Seedlings grown for 11 days in sand to which no nutrients were added.

[6] These values calculated with equation XII, Table 7; yields calculated with equation XI are essentially the same.

[7] Standard error of mean.

TABLE 7

STATISTICAL ANALYSIS OF DATA PRESENTED IN TABLES 4, 5 AND 6

Seed Series (1)	*Independent Variable (x)* (2)	*Dependent Variable (y)* (3)	*Number of Observations* (4)	*Regression Equation* [1] (5)	*Correlation Coefficient* [2] (6)	*Standard Error of Estimate* [2] (7)
A	Fresh Wt. Seeds	Dry Wt. Seed Coats	160	$y=0.335x-0.25$ I	.97	0.03
	Fresh Wt. Seeds	Dry Wt. Seeds	201	$y=0.842x+1.79$ II	.96	0.05
	Fresh Wt. Seeds	Dry Wt. Seedlings	412	$y=2.702x+11.63$ III	.98	0.71
	Reserve Dry Wt. Seeds	Dry Wt. Seedlings	412	$y=5.803x-6.06$ IV	.98	0.70
B	Fresh Wt. Seeds	Dry Wt. Seed Coats	210	$y=0.278x+1.42$ V	.94	0.13
	Fresh Wt. Seeds	Dry Wt. Seeds	200	$y=0.847x+1.69$ VI	.93	0.06
	Fresh Wt. Seeds	Dry Wt. Seedlings	614	$y=0.961x+0.54$ VII	.97	0.40
	Reserve Dry Wt. Seeds	Dry Wt. Seedlings	614	$y=1.690x+0.09$ VIII	.98	0.47
C	Fresh Wt. Seeds	Dry Wt. Seed Coats	1155	$y=0.318x-0.02$ IX	.96	0.11
	Fresh Wt. Seeds	Dry Wt. Seeds	421	$y=0.877x+1.18$ X	.94	0.09
	Fresh Wt. Seeds	Dry Wt. Seedlings	514	$y=1.136x-4.05$ XI	.99	0.24
	Reserve Dry Wt. Seeds	Dry Wt. Seedlings	514	$y=2.036x-6.53$ XII	.97	0.24
Average	Fresh Wt. Seeds	Dry Wt. Seedlings	1540	$y=0.976x-0.13$ ...... XIII[3]	..	...
	Reserve Dry Wt. Seeds	Dry Wt. Seedlings	1540	$y=1.838x-2.84$ ...... XIV[3]	..	...

[1] Each formula expresses the average relation between the two variables entered in columns 2 and 3 of the same line. Equation constants were calculated according to the method of least mean squares (see Bruce and Reineke, 1931 and Bruce and Schumacher, 1935). Regression lines representing the various relationships are plotted in Figs. 4, 5 and 6.

[2] The correlation coefficient expresses the degree of relationship between two variables, and the standard error of estimate is a measure of curve accuracy (Mills, 1931; Bruce and Reineke, 1931 and Bruce and Schumacher, 1935).

[3] The constant which determines "rate of increment" in formula XIII is the arithmetic mean of similar constants in equations VII and XI, and in the equation $y = 0.8313\,x + 3.58$. The latter expresses the A series relationship when the yields are reduced, by dividing by 3.25, to the exact mean (at seed class 2) of the B and C series seedlings, which grew for a shorter period. The other constant (-0.13) in equation XIII is such that the value on the "line of mean slope" corresponding to the median seed class (class 2) will equal the mean weight of the series B and C seedlings from seed of the same class. Constants for formula XIV were similarly derived, using equations VIII and XII, and the equation $y = 1.788\,x - 1.89$, which expresses the relation between reserve dry weight and the yield of series A seedlings on a reduced basis.

As with Scots pine, the period of growth has no appreciable effect on the ratios between seedlings grown from seed of different size. It will be observed (Fig. 4) that, when reduced to a comparable basis, the characteristic slopes of the three series of data are almost identical even though the series A seedlings grew for a much longer period. Compare, for example, the ratio between the yields of series A seedlings from seed classes 2 and 5 (calculated yields given in Table 4, col. 9) with similar ratios based on either the B or C series data (Tables 5 and 6, col. 9). The differences are within the limits of experimental error.

The experimentally determined average relationship, based on the three series of data, is expressed by equation XIII (Table 7)) and is represented in Fig. 4 by the heavy "line of mean slope." Correction factors in Table 8 are merely ratios between yields calculated according to the average relation between the two variables. This is illustrated by data presented in Fig. 4. Seedlings grown from class 2 seeds weigh 21.83 mg., whereas 22.80 mg. is the yield corresponding to seed-class 3. The ratio between the yields,

$$\frac{21.83}{22.80} = 0.957,$$

is the factor by which to convert seedlings from class 3 seed to a weight equivalent to those from seed class 2. Other factors in Table 8 were similarly computed. If correction factors for smaller or larger class intervals are desired, they may be derived from yields obtained by solving equation XIII for correspondingly larger or smaller fresh weight values.

The results of various tests indicate that the correction factors in Table 8, which are based on numerous and consistent data, are applicable within reasonable limits of seed-size distribution. They may be applied with almost equal accuracy to the yields of seedlings from seed

TABLE 8

SEED-SIZE CORRECTION FACTORS FOR WHITE PINE[1]

Seed Class	*Av. Fresh Wt. of Class in Mg.*	*Dry Wt. of Seedlings in Mg.*[2]	*Factors for converting the weight of a seedling grown from seed of a given size (Col. 1) to a weight equivalent to that from seed of any one of the arbitrary sizes listed above Cols. 4 to 11*[3]							
			Class 0	*1*	*2*	*3*	*4*	*5*	*6*	*7*
(1)	*(2)*	*(3)*	*(4)*	*(5)*	*(6)*	*(7)*	*(8)*	*(9)*	*(10)*	*(11)*
0	20.5	19.88	1.000	1.049	1.098	1.147	1.196	1.245	1.294	1.344
1	21.5	20.85	0.953	1.000	1.047	1.094	1.141	1.188	1.234	1.281
2	22.5	21.83	0.911	0.955	1.000	1.044	1.089	1.134	1.179	1.224
3	23.5	22.80	0.872	0.914	0.957	1.000	1.043	1.086	1.129	1.171
4	24.5	23.78	0.836	0.877	0.918	0.959	1.000	1.041	1.082	1.123
5	25.5	24.76	0.803	0.842	0.882	0.921	0.960	1.000	1.039	1.079
6	26.5	25.73	0.773	0.810	0.848	0.886	0.924	0.962	1.000	1.038
7	27.5	26.71	0.744	0.781	0.817	0.854	0.890	0.927	0.963	1.000

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[1] Because these factors were derived according to method 1 (see text), they are not necessarily applicable to seedlings other than those grown the same season from any one of the lots of seed used in these experiments.

[2] These weights, from which the correction factors (yield ratios) were derived, were calculated with equation XIII, Table 6. This equation expresses the average relation between fresh weight of seed and the dry weight of seedlings adjusted for relative values, as determined by the three series of data shown in Fig. 4.

[3] Read vertically.

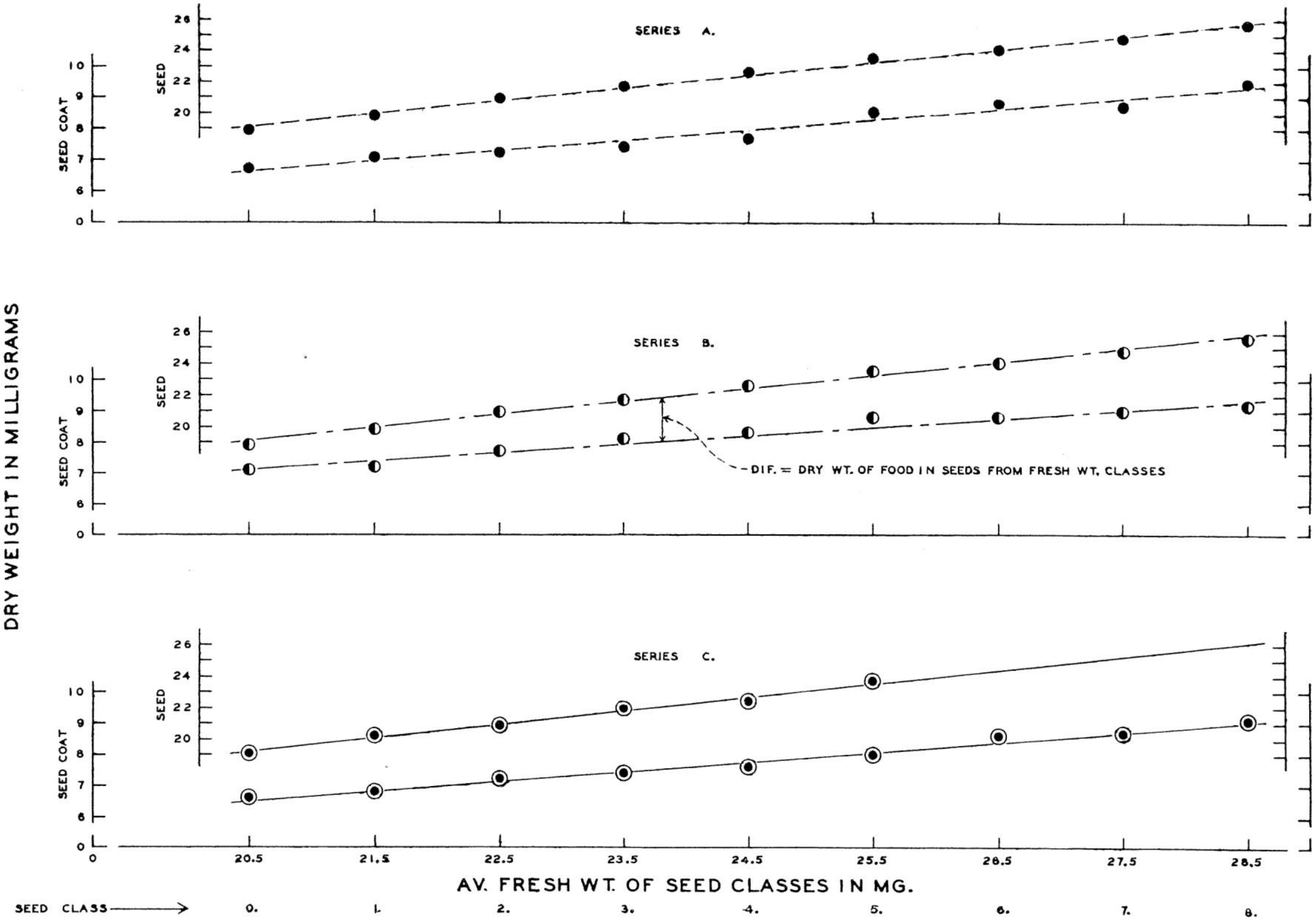

FIG. 5.—THE DRY WEIGHTS OF WHITE PINE SEEDS AND SEED COATS FROM SEEDS OF VARIOUS FRESH WEIGHTS.

of any *one* of the three series (A, B or C) used in these experiments. But it should be emphasized that neither these factors nor any factors similarly derived (such as those for Scots and Corsican pine, discussed above) can be relied upon to reduce to a comparable basis the yields of seedlings from seeds of different source or the same source in different years. The reason is that fresh weight is not necessarily a reliable measure of food reserves, the seed-size factor which influences seedling yield during the initial season.

It is known that the amount of food reserves (''effective weight'') in seeds of identical fresh weight varies not only with seed source, but from year to year in the same sample. For example, the series A and B data were obtained in 1932 and 1933, respectively, from seed of the same lot. As shown in Tables 4 and 5 (cols. 7), identical fresh-weight classes of A and B differ significantly in food reserves, due probably to chemical changes during storage (see Gast, 1937, Table 10 and discussion). And neither the A nor the B series data agrees with that of corresponding fresh-weight classes of series C. Food reserves, expressed as dry weight (see Tables 4, 5 and 6), are the dry weight of the seed minus the dry weight of the seed coat. This quantity, which has been termed ''reserve dry weight'' by Gast, represents the material available for the development of the embryo (see Baldwin, 1936, p. 42).

Method 2.—It is frequently necessary to reduce to a common basis the data obtained in different years from seeds of varied source. Factors for making such corrections can be based on reserve dry weight, with which seedling yield is highly correlated. Yield is almost directly proportional to reserve dry weight. This relationship, as based on the M-'32 data only, and the derivation of correction ratios therefrom, were discussed by Mitchell (1934) and Gast (1937). Ratios calculated on this basis are unaffected by variations in seed origin,

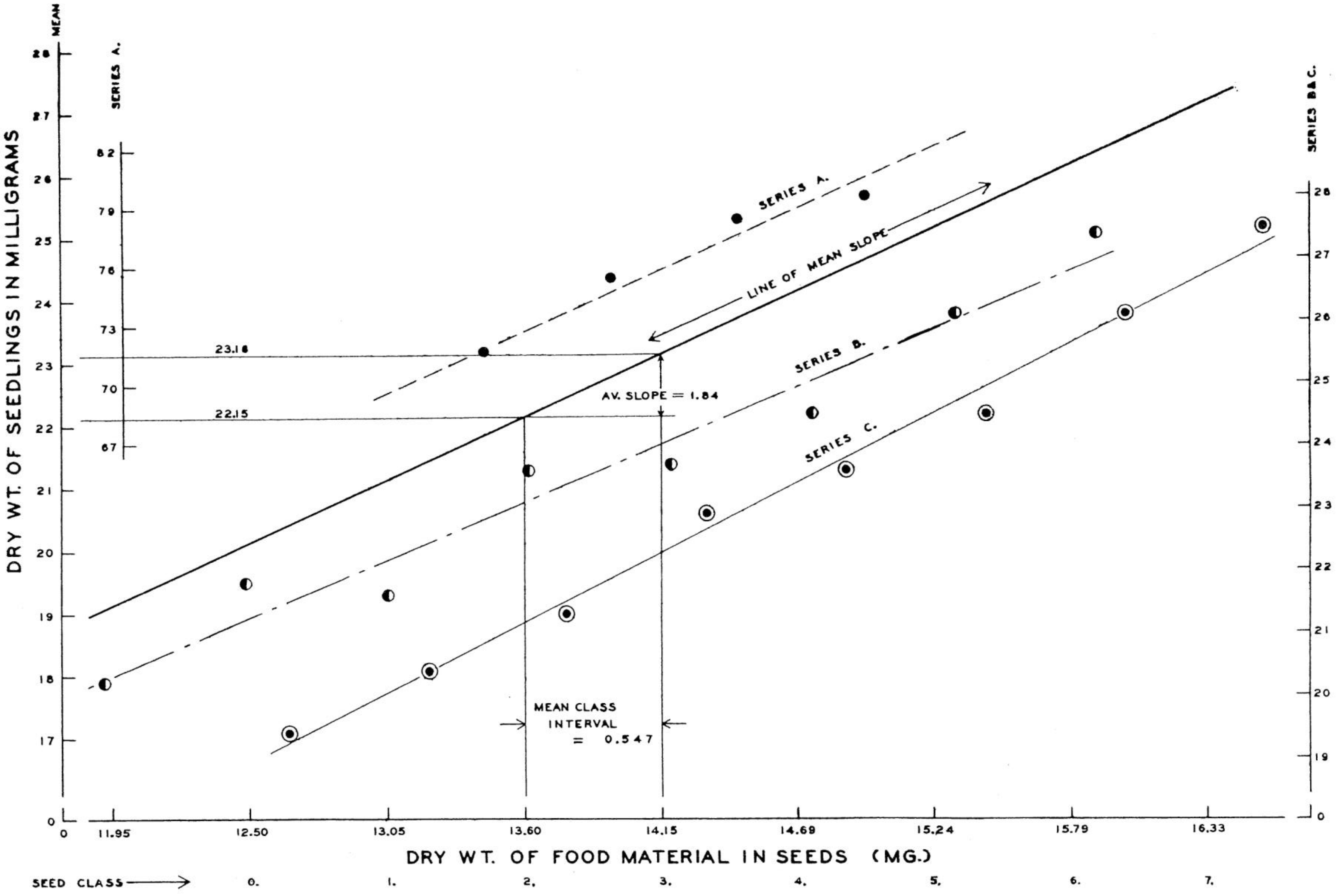

FIG. 6.—THE DRY WEIGHTS OF WHITE PINE SEEDLINGS GROWN FROM SEEDS OF VARIOUS RESERVE DRY WEIGHTS.

seed-coat thickness, moisture content or changes during storage, the factors which limit the application of correction ratios derived from the relation between fresh weight of seed and seedling yield.

The dry seed and seed-coat weights of the three series of data are shown plotted over the corresponding fresh-weight classes in Fig. 5 (data from cols. 3 and 5, Tables 4, 5 and 6). In each instance the difference between the seed and seed-coat weight (calculated values used in subtractions) is taken as the reserve dry weight of the corresponding fresh-weight class. The reserve dry weights of the various fresh-weight classes are entered in column 7 of Tables 4, 5 and 6, and the relation between these values and seedling yield is shown, for each series, in Fig. 6.[1]

The average relation between the two variables, as based on the three series of data, is expressed by regression equation XIV (Table 7) and is shown in Fig. 6 as the heavy "line of mean slope." This illustration was simplified by arbitrarily assigning seed class numbers (0, 1, 2 etc.) to reserve dry weight values which differed by 0.547, the mean class interval of the three series of data. Seed class numbers (based on fresh weight) correct for any one series of data do not correspond to those of the other series because of variations in reserve dry weight, the independent variable in Fig. 6. But these differences have no influence upon correction factors since the line of mean slope represents a rate of increment (average of regression lines A, B and C), and yield ratios derived therefrom can be related to actual differences in reserve dry weight. Thus, as shown in Fig. 6, if the reserve dry weights of two lots of seed are 13.60

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[1] It will be noted (Fig. 6, Tables 5 and 6) that the yields of seedlings from series C seed are somewhat lower than those from series B seed of equal reserve dry weight, although seedlings from both lots of seed were grown for the same length of time during the same season. This lack of perfect agreement is attributed to slight differences in mineral nutrition, since seeds of the two lots were planted in sand from two different sources.

and 14.15, the resulting seedlings will weigh 22.15 mg. and 23.16 mg. respectively. The correction factor is, therefore, the ratio between the yields,

$$\frac{23.16}{22.15} = 1.045.$$

Or, since the ratio between the two reserve dry weights,

$$\frac{14.15}{13.60} = 1.040,$$

is essentially the same as that between the yields, it is probable that correction factors may be based on either criterion. Gast (1937) has used the ratios between reserve dry weight.

Fresh-weight classes 0, 1, 2, 3 and 4 of the series C seed were used in the 1933 nutrient-sand culture experiments reported in this paper. The reserve dry weights corresponding to these fresh-weight classes are: 12.66, 13.22, 13.77, 14.33 and 14.89, respectively (data from Table 6, col. 7). Seedling yields corresponding to these reserve dry weights (calculated with equation XIV, Table 7) are: 20.43, 21.46, 22.47, 23.50 and 24.53, respectively. The correction factors 1.100, 1.047, 0.956 and 0.916 (yield ratios) can be used to convert the final yields of seedlings from series C seed classes 0, 1, 3 and 4, respectively, to weights equivalent to seed class 2, the median class. All basic data (Tables 9, 13, 15 and 17) are expressed as of seed class 2 (reserve dry weight = 13.77 mg.).

In the discussion which is to follow, it is necessary to compare the 1932 white pine data (Mitchell, 1934, Table 19), obtained from seed of series A, with the 1933 data from seed of series C. The former were expressed as of seed class 5, which had a reserve dry weight of 14.97. The reserve dry weight of the series C fresh-weight class 5 is 15.45. This is a very significant difference for which method 1 makes no provision, since the *fresh weights* are identical. But, as discussed above, the final yield of seedlings from the different experiments can be reduced to a common basis by either the ratio between their respective reserve dry weights, or that between corresponding seedling weights calculated by equation XIV. Thus, to convert the 1932 data (series A seed class 5) to weights equivalent to those of the 1933 seedlings (expressed as of series C seed class 2, reserve dry weight = 13.77), the former are multiplied by 0.911. This factor is the ratio between yields (calculated by equation XIV) corresponding to the reserve dry weights of the median classes (2 and 5) of the two seed sources. By the same method, the yields of seedlings from seeds of different origins can be reduced to a common basis. Reserve dry weights, since they are necessary for such comparisons, should be considered as essential data.

Other Methods.—Because of variations in the ratio of mass to volume, differences in seed-coat thickness, changes in moisture content and oxidation of food reserves during storage, final seedling yield corrections based on seed volume rather than mass (weight) are of questionable accuracy even when confined to data obtained from a single lot of seed. For the same reasons, factors so derived certainly cannot be used to convert to a common basis the final weights of seedlings from seed of varied source. That is, not in carefully controlled experiments involving a limited number of observations and requiring a high degree of precision.

Addoms (1937) attempted to eliminate the seed-size factor by transplanting to culture solutions only seedlings which had been carefully selected from germination beds on the basis of ''uniformity of size and general appearance.'' But relatively large variations (*loc. cit.*, Figs. 1 and 2) in the size of plants grown for several months in identical culture solutions seem to have convinced Addoms ''that such selection is not sufficient.'' Others have arrived at the same conclusion.

Refinements in Technique

It sometimes happens that seedlings from smaller seeds are heavier than those from larger seeds, even when all are grown for the same length of time and in apparently identical environments. Such results, which are relatively infrequent, are in part due to mistakes, such as the mixing of seed classes, or to differences in environment—nutrient supply, light, soil moisture etc.—which escape observation. An unusual genetic constitution is possibly the explanation for a limited number of exceptionally large or small seedlings.

There is another factor, however, which may account for small inconsistencies. In the case of white pine, for example, the seeds were separated on the basis of fresh weight into 1-milligram classes, and the mid-point of the class interval was in each instance taken as the mean weight of seeds falling within the established limits of the class (see Figs. 4 and 5). Thus, 20.5 mg. was assumed to represent the mean weight of seeds falling (by random selection) in the group comprised of seeds weighing from 20.0 mg. to 20.99 mg. Means for other groups were similarly determined. But, theoretically at least, the true mean weight and the mid-point of the class interval are seldom identical. This is illustrated by data presented in Fig. 7.

The data plotted in this figure, although not complete for any single lot of seed, are sufficient to show that the frequency distribution of weights in any given lot is approximately normal, and that this distribution is best represented by a symmetrical, bell-shaped curve. Such a curve was fitted by statistical procedures to the series A data, the most complete of the three series. Areas under this curve, between ordinates erected at any two points on the abscissa scale, are proportional to the number of seeds falling between these values. Thus, the number of class 0 seeds falling between 20.5 mg. and

20.99 mg. (represented by crosshatched area) is greater than the number falling between 20.0 mg. and 20.5 mg. (represented by stippled area). The arithmetic mean weight of all seed in class 20.0 mg. to 20.99 mg. is, therefore, slightly greater than 20.5 mg., the mid-value of the class. For classes with lower limits greater than the point of highest frequency (see class 6, Fig. 7), the mean weight is slightly less than the mid-point of the class.

Absolute accuracy is impossible unless each seed weight is recorded separately. Such a procedure is highly impractical. But errors due to this factor can be reduced considerably by lowering the class interval. For example, the 0.5-mg. class limit used for Scots pine,

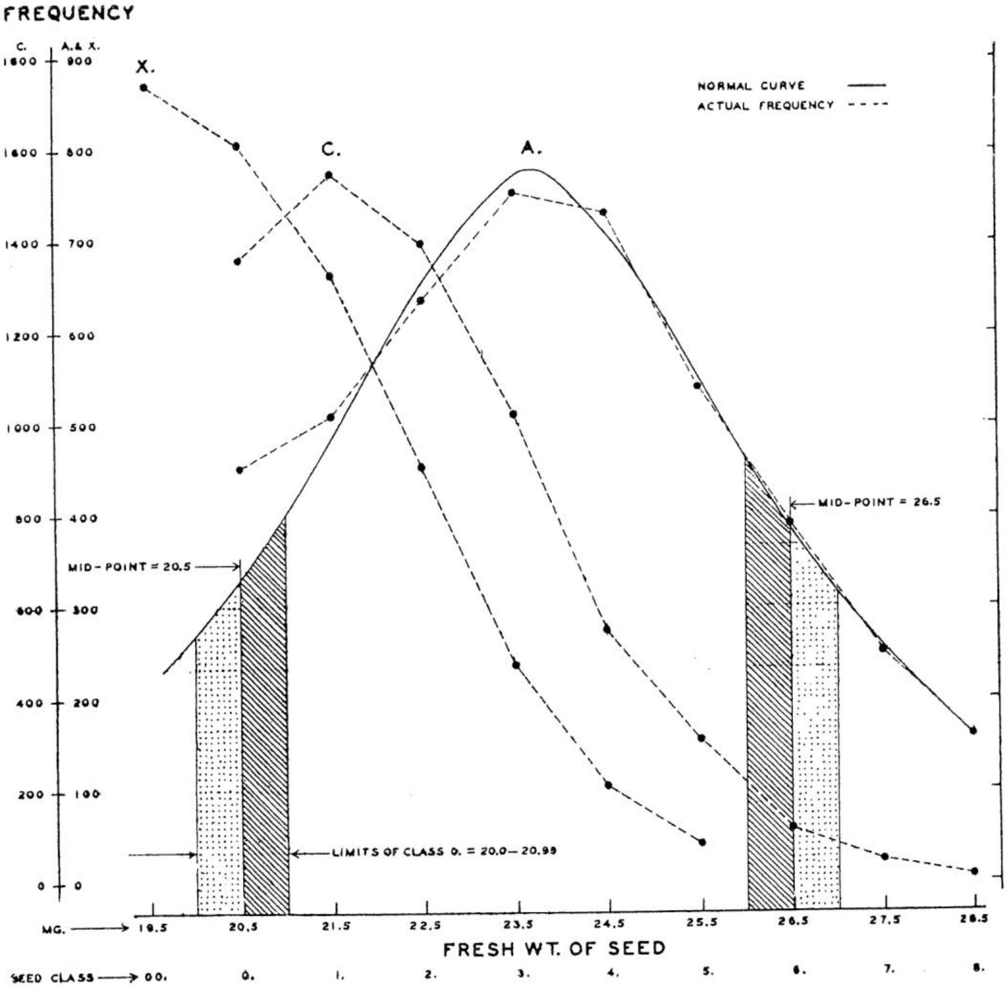

FIG. 7.—THE FREQUENCY DISTRIBUTION OF WEIGHTS IN THREE DIFFERENT LOTS OF WHITE PINE SEED.

which is approximately 10% of the mean weight of the median seed class (5.0 mg.), is undoubtedly too high. It should be lowered in future work to at least 5% of the fresh weight value (similar to white pine) and possibly to 2%, as recommended by Gast (1937). The 1-mg. class interval used for white pine, which is approximately 5% of the weight of the median class, appears to be satisfactory. Because of factors discussed in the following paragraph, it is doubtful if further reduction would result in much improvement.

Gast *(loc. cit.)* found significant differences between the theoretical and the actual mean weight of random samples from groups of Scots pine seed separated into 0.5-mg. classes on the basis of fresh weight. These he attributed to moisture loss and inaccuracy in weighing, two factors which must be considered. To minimize such errors, Gast recommends fast, accurate weighing with a precise balance, and that the seed sample used during weighing be returned immediately thereafter to the stock container, in which an atmosphere of constant moisture content should be maintained. If these precautions are observed, and if the class interval is kept within 5% of the weight of the median seed class, it is believed that the mid-value of any given class can be considered as a sufficiently accurate estimate of the mean weight of seeds falling within the limits of the class. Further refinements are probably beyond the accuracy of the majority of balances now in use in laboratories where this type of work is done.

It would be desirable in experiments like this to use pure lines of seed. This, however, is usually impossible. But the influence of genetic factors can be reduced if all seeds have at least one parent in common. Where comparisons are possible, it is evident that the average deviation of data from seed from a single tree is significantly less than that of seedlings produced by seeds from many different seed trees growing in the same locality. If the sample contains seeds from trees growing in widely separated regions, the variation is still greater. Such variation is attributable to differences in age and condition of seed tree, and in environmental and climatic factors, as well as to genetic differences. However, in every lot of plants are found individuals of exceptional vigor, which is probably the result of a favorable inherited constitution.

NUTRIENT-SAND CULTURE EXPERIMENTS

THE YIELD OF WHITE PINE SEEDLINGS GROWN IN NUTRIENT-SAND CULTURES OF VARYING NITROGEN, PHOSPHORUS, POTASSIUM AND CALCIUM CONCENTRATION

IN THE 1933 nutrient-culture experiment, four elements —nitrogen, phosphorus, potassium and calcium—were varied in individual series, as summarized in Table 1. For each series, all essential elements other than the one varied were supplied in constant and approximately optimum amounts. Data obtained from the different nutrient series of this experiment are presented in separate sections of the following discussion. Where possible and of interest, these data are compared with the results of other investigations regarding the nutrient requirements of the same and different species of *Pinus*.

The Relation Between Nitrogen Supply and Seedling Yield

The total dry weights of white pine seedlings grown during the 1932 and 1933 experiments in nutrient-sand cultures of different nitrogen concentration, but with constant and approximately optimum supplies of P, K, Ca, S, Mg and Fe, are shown plotted in Fig. 8 A (data from Tables 9 and 10). Conditions of moisture supply, solar radiation and basic nutrient solution were approximately equal during the two experiments. When correction is made for differences in seed source and size, the duplication is almost exact.

Seedlings of the 1932 experiment were grown from

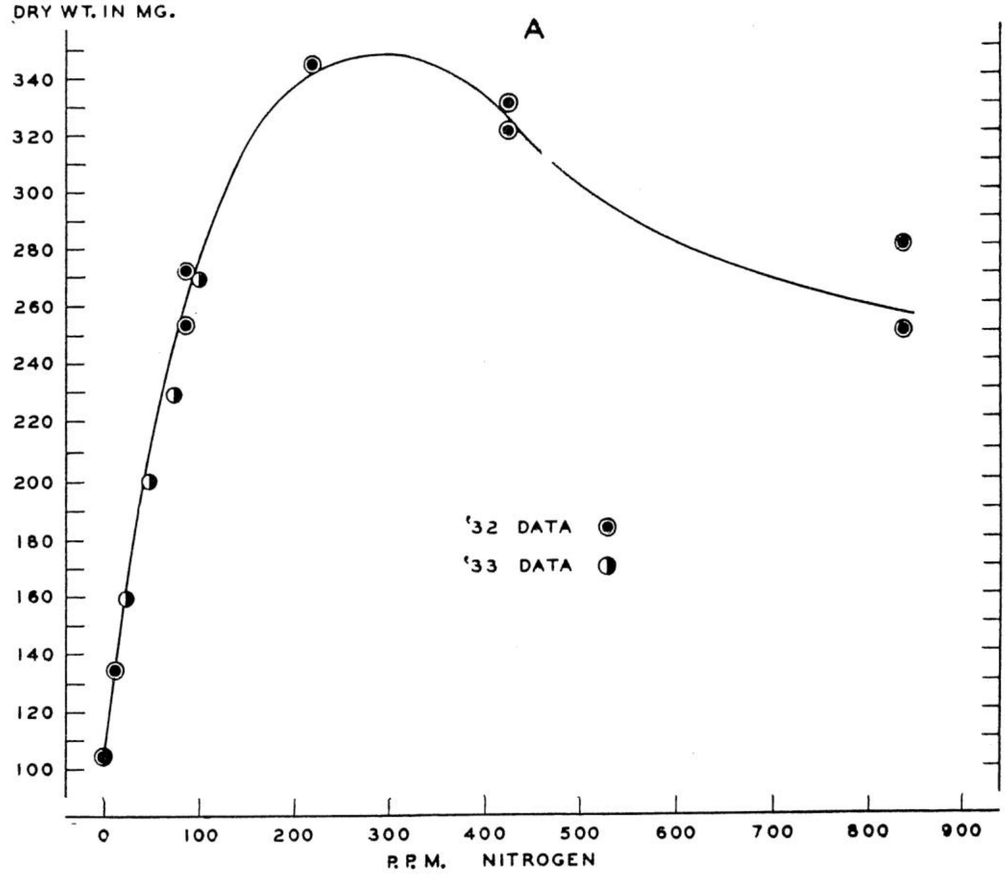

FIG. 8-A.—THE DRY WEIGHTS OF WHITE PINE SEEDLINGS GROWN FOR ONE SEASON IN NUTRIENT-SAND CULTURES OF VARIED NITROGEN CONCENTRATION.

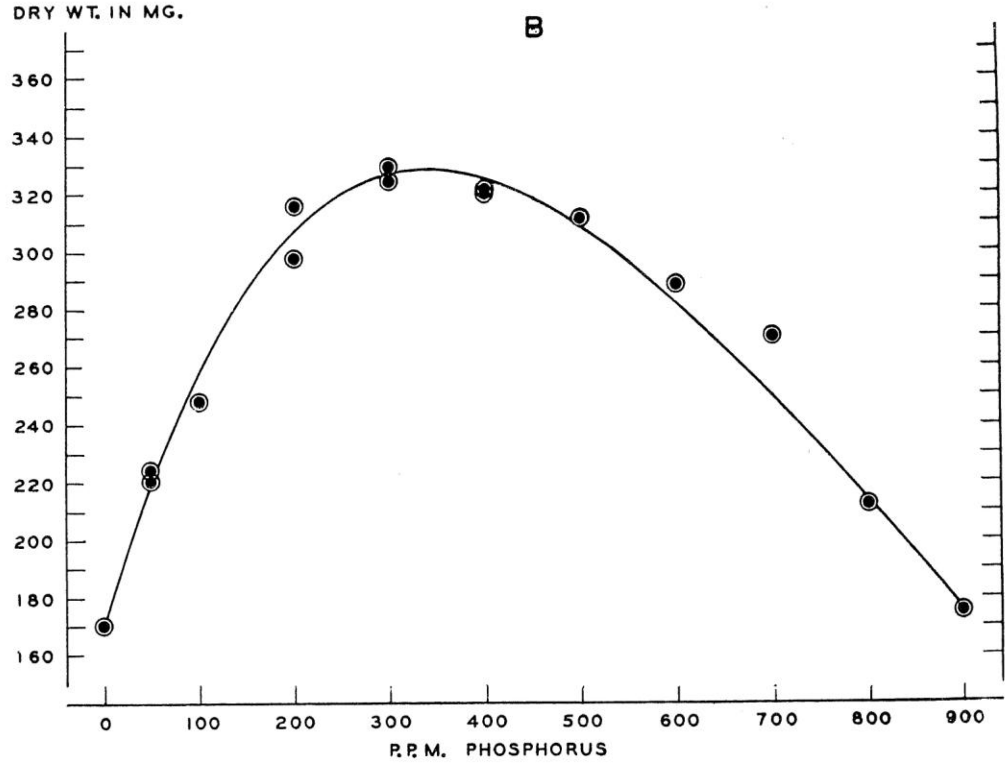

FIG. 8-B.—THE DRY WEIGHTS OF WHITE PINE SEEDLINGS GROWN FOR ONE SEASON IN NUTRIENT-SAND CULTURES OF VARIED PHOSPHORUS CONCENTRATION.

TABLE 9

DRY WEIGHTS, ROOT/SHOOT RATIOS AND NITROGEN CONTENTS OF WHITE PINE SEEDLINGS FROM NUTRIENT-SAND CULTURES OF VARIED NITROGEN CONCENTRATION

						Nitrogen Content		
						Seedlings		*Shoots Only*
Nitrogen Concentration ppm N	*Seed Class Used* [1]	*Dry Wt. of Seedlings in Mg.*	*No. of Seedlings* [2]	*Dry Wts. Corrected as from Series C Seed Class 2* [3]	*Root/Shoot Ratio*	*% Dry Wt. ($N_{\%}$)*	*Milligrams* [4] *(N_{mg})*	*% Dry Wt.*
(1)	*(2)*	*(3)*	*(4)*	*(5)*	*(6)*	*(7)*	*(8)*	*(9)*
1932 EXPERIMENT								
0	5	115.2 ± 3.6[5]	25	104.9	0.78	0.72	0.76	1.13
12.9	5	147.8 ± 3.6	27	134.6	0.81	0.81	1.09	1.07
88.3	5	299.6 ± 13.0	18	272.9	0.78	1.77	4.83	2.05
	5	276.8 ± 18.1	17	252.2	0.74	1.87	4.72	2.15
219.4	5	379.9 ± 12.1	24	346.1	0.64	2.71	9.38	2.97
425.9	5	363.7 ± 14.4	18	331.3	0.42	3.69	12.23	3.94
	5	351.9 ± 20.0	17	320.6	0.45	3.63	11.64	4.01
838.9	5	308.2 ± 15.4	22	280.8	0.31	4.53	12.72	4.31
	5	273.3 ± 9.4	22	249.0	0.34	4.42	11.01	4.24
1933 EXPERIMENT								
0	4	113.8 ± 1.3	16	104.2	0.61	0.73	0.76	1.01
25	4	173.5 ± 4.0	18	158.9	0.65	1.05	1.66	1.39
50	4	229.2 ± 9.1	23	209.9	0.62	1.34	2.81	1.67
75	4	249.0 ± 4.5	22	228.1	0.72	1.79	4.08	2.00
100	4	292.5 ± 9.9	24	267.9	0.62	1.92	5.14	2.10

[1] Series A seeds (see Table 4) were used in the 1932 experiment, and series C seeds (see Table 6) in the 1933 experiment.

[2] Number of harvested seedlings after discarding replacements and those whose weights deviated from the mean by more than 3 × std. dev.

[3] All yields in this column are expressed as from series C seed class 2 (reserve dry weight = 13.77 mg.). Seed size correction factors are discussed in text.

[4] $N_{\%}$ (col. 7) × seedling yield (col. 5) = N_{mg}.

[5] Standard error of mean.

TABLE 10

CALCULATED COMPARED WITH EXPERIMENTALLY DETERMINED YIELDS AND NITROGEN CONTENTS OF WHITE PINE SEEDLINGS FROM NUTRIENT-SAND CULTURES OF VARIED NITROGEN CONCENTRATION [1]

Nitrogen Concentration ppm N	*Dry Wt. of Seedlings in Mg.*[2]		*Nitrogen Content of Seedlings*			
			% Dry Wt. ($N_{\%}$)		*Milligrams* (N_{mg})	
	Experimentally Determined	*Calculated* [3]	*Experimentally Determined*	*Calculated* [4]	*Experimentally Determined*	*Calculated* [5]
(1)	*(2)*	*(3)*	*(4)*	*(5)*	*(6)*	*(7)*
0	**104.2** [6]	104.7	**0.73** [6]	0.70	**0.76** [6]	0.70
0	104.9	104.7	0.72	0.70	0.76	0.70
12.9	134.6	137.4	0.81	0.87	1.09	1.41
25.0	**158.9**	164.9	**1.05**	1.03	**1.66**	2.02
50.0	**209.9**	212.4	**1.34**	1.33	**2.81**	3.23
75.0	**228.1**	249.3	**1.79**	1.60	**4.08**	4.34
88.3	272.9	265.6	1.77	1.74	4.83	4.88
	252.2	265.6	1.87	1.74	4.72	4.88
100.0	**267.9**	278.4	**1.92**	1.85	**5.14**	5.32
150.0	....	317.1	....	2.30	....	7.06
219.4	346.1	342.8	2.71	2.80	9.38	8.94
250.0	....	346.7	....	2.99	....	9.58
300.0	....	347.5	....	3.26	....	10.48
350.0	....	342.4	....	3.49	....	11.19
425.9	331.3	328.0	3.69	3.76	12.23	11.93
	320.6	328.0	3.63	3.76	11.64	11.93
500.0	....	*303.0*	....	3.97	....	12.37
600.0	....	*282.5*	....	4.18	....	12.59
700.0	....	*268.0*	....	4.33	....	12.51
838.9	280.8	*257.5*	4.53	4.47	12.72	12.02
	249.0	*257.5*	4.42	4.47	11.01	12.02
900.0	....	*252.3*	....	4.52	....	11.71

[1] Basic data from Table 9.

[2] Yields expressed as from series C seed class 2; reserve dry weight = 13.77 mg. (see Table 6).

[3] Calculated with the Mitscherlich yield equation (constants given in Table 12) up to 450 ppm N; interpolated (see text) from smooth curve (Fig. 8 A) the remainder of the range.

[4] Calculated with the Mitscherlich equation (constants given in Table 20) over the entire range of N concentrations.

[5] Calculated with the Mitscherlich equation (constants given in Table 21) over the entire range of N concentrations.

[6] The 1933 data are in bold-face type; all other data are from the 1932 experiment (see Table 9).

series A seed (Table 4), and the final yields were expressed as of seed class 5 (reserve dry weight = 14.97 mg.), the median class of the group (see Mitchell, 1934, Tables 14 and 17). Those of the 1933 experiment were from series C seed (Table 6), and are expressed as of seed class 2, with a reserve dry weight of 13.77 mg. By using the appropriate seed-size correction factor, *r*, the dry weights of seedlings from the two experiments may be converted to a comparable basis. In Fig. 8 A they are expressed as from the median seed class used in 1933, as are all other data reported in this paper. In this case *r* has a value of 0.911, which is the ratio between yields (calculated with equation XIV, Table 7), corresponding to the reserve dry weights of the median classes (2 and 5) of the seed used in the two experiments.

As shown in Fig. 8 A, seedling yield is almost directly proportional to nitrogen supply up to a concentration of about 300 ppm; and at supplies greater than 300 ppm dry weights decrease as the nitrogen concentration increases. To facilitate discussion, the entire range of concentrations can be arbitrarily divided into four regions, as suggested by Gast (1937). Concentrations up to 50 ppm, which are lower, in terms of effect upon seedling growth, than the available nitrogen supply of a good natural soil, can be termed ''the region of minima.'' Concentrations from 50 ppm and increasing up to 175 to 200 can be called the ''working range.'' That region in which increases in nitrogen supply result in little or no change in dry weight increase can be termed the ''region of tension,'' and greater concentrations, the ''toxic region.'' The various range divisions are summarized in Table 11.

The Mitscherlich equation was used to calculate the curve shown in Fig. 8 A. The literature is replete with reports regarding the biological significance of this formula, its limitations and its usefulness in expressing the

TABLE 11

EXTERNAL CONCENTRATIONS OF N, P, K AND Ca DIVIDED INTO REGIONS ON THE BASIS OF SEEDLING YIELD RESPONSE [1]

Element	*Region of Minima*	*Working Region*	*Optimum Concentration (Calculated)*	*Region of Tension*	*Toxic Region*
Nitrogen	0-50	50-200	300	200-350	350 +
Phosphorus	0-50	50-200	350	200-400	400 +
Potassium	0-25	25-100	150	100-200	200 +
Calcium	0-25	25-100	200	100-350	350 +

[1] Curves of average relationship between external supplies of N, P, K and Ca (as ppm) and seedling yield are shown in Figs. 8 A, 8 B, 10 A and 10 B respectively.

results of pot and field experiments with various crop plants (Mitscherlich and Dühring, 1928; Niklas and Hock, 1934; Spillman and Lang, 1924; Willcox, 1930; Spillman, 1933; Lundegårdh, 1934). The applicability of the Mitscherlich curve to silvical data was discussed in previous reports (Mitchell, 1934; Gast, 1937), and only a brief review will be presented here.

The normal Mitscherlich yield equation is

$$y = A\ (1 - 10^{-c\,[x+b]}),$$

in which $y =$ the yield, $x =$ a growth factor (in this case, nitrogen), $A =$ the maximum theoretical yield that may be obtained with any amount of x, $c =$ the "efficiency" constant for the growth factor, and $b =$ the "x" equivalent contained in seed, soil, or both. If, as in the present experiment, sufficient nitrogen (or any other nutrient element) is supplied so that the effect upon yield is toxic, a "depression constant," k, must be added to the normal equation, which then becomes

$$y = A\ (1 - 10^{-c\,[x+b]}) \cdot 10^{-kx^2}.$$

Numerical values for the various constants, based upon data from the 1932 experiment, are entered in Table 12. The Mitscherlich yield curve, calculated according to these constants, fits the 1932 data over a nitro-

TABLE 12

STATISTICAL INDEXES AND CONSTANTS FOR MITSCHERLICH EQUATIONS EXPRESSING THE RELATIONSHIPS BETWEEN EXTERNAL (SOLUTION) CONCENTRATIONS OF N, P, K OR CA AND THE DRY WEIGHTS OF WHITE PINE SEEDLINGS[1]

Independent Variable[2] *(x)*	*Dependent Variable (y)*[3]	*Number of Observations*[4]	*Mitscherlich Equation Constants*[5]				*Concentration Range*[6]	*Correlation Index*[7]	*Standard Error of Estimate*[7]
			A	*b*	*c*	*k*			
(1)	*(2)*	*(3)*	*(4)*	*(5)*	*(6)*	*(7)*	*(8)*	*(9)*	*(10)*
Nitrogen . . .	Yield	293	438.26	33.29	0.00397	0.000000434	0 to 450	0.991	10.44
Phosphorus . .	Yield	341	437.07	118.72	0.00180	0.000000470	0 to 900	0.990	7.69
Potassium . . .	Yield	331	458.10	31.03	0.00449	0.000002195	0 to 320	0.991	6.85
Calcium	Yield	219	384.20	32.90	0.00842	0.000000240	0 to 300	0.995	6.81

[1] Calculated and experimentally determined yields are compared in cols. 2 and 3, Tables 10, 14, 16 and 18.

[2] Solution concentration of N, P, K and Ca as parts per million.

[3] Seedling dry weights in milligrams.

[4] These numbers are sums of harvested seedlings from all pots of each series.

[5] See text for a discussion of the Mitscherlich formula. Except for the nitrogen series data, all equation constants were derived from yields expressed as from series C seed class 2. Nitrogen series yields calculated according to the above constants, which were derived from data expressed as from series A seed class 5 (see Mitchell, 1934), can be converted to a comparable basis—*i. e.*, as from series C seed class 2—with the seed size correction factor 0.911 (see text).

[6] The range of concentrations (of N, P, K and Ca) over which yields calculated with the Mitscherlich equation agree with the observed data. In cases where the estimating formula is not applicable over the entire range, "calculated" yields at the higher concentrations are interpolated from smooth curves fitted by statistical procedures to the experimental data.

[7] These indexes were computed from observed data and curve values calculated (and/or interpolated, see footnote 6) over the entire concentration range.

gen concentration range of from 0 to 450 ppm. By introducing the appropriate seed-size correction factor *(r)* into the equation, which becomes

$$y = r \cdot A\ (1 - 10^{-c\,[x+b]}) \cdot 10^{-kx^2},$$

it may be used to express the experimentally determined relationship between nitrogen supply and the yield of white pine seedlings from seed of any given reserve dry weight. Thus the calculated yield values (curve) in Fig. 8 A, like the 1932 data on which the equation constants are based, were converted, with an r equal to 0.911, to a basis comparable to the 1933 data.

The statistical indexes in Table 12 evaluate the degree of association between the two variables, nitrogen supply and yield, and the precision of predictions based upon the calculated curve of average relationship. Calculated and experimentally determined yields are compared in Table 10. It is apparent that the Mitscherlich curve is in close agreement with the observed data over a nitrogen concentration range of from 0 to 450 ppm. A method for calculating yields at higher concentrations in the toxic region (up to 2490 ppm) was discussed in the report on the M-'32 experiment. But the effects of such high concentrations, since they are never found in nature, are of little practical importance.

As Gast (1937, Fig. 11) demonstrated, yields calculated with the Mitscherlich formula are linearly related to nitrogen supplies of the minimal and working ranges when both variables are plotted on logarithmic axes (see Fig. 9). In these ranges, which are the most interesting from the practical standpoint, the logarithmic relation is equally precise and provides a much simpler estimating formula than that of Mitscherlich. The chief advantage of the latter equation is that it is applicable through the region of tension and into the toxic range, whereas the simpler logarithmic relation is adaptable only to the minimal and working regions of nitrogen supply.

The results of the 1932 and the 1933 white pine experiments, presented in Fig. 8 A, are similar in many respects to data from comparable studies with Corsican pine, as reported by Aldrich-Blake (1930), and with both Scots and white pine, as reported by Gast (1937). Data from the various experiments are compared in Gast's Fig. 11, reproduced here as Fig. 9. It is significant that in every case yields of both Scots and white pine are proportional to nitrogen supply through the minimal and working regions, and that the point of maximum yield is approximately the same for both species. Nitrogen concentrations greater than 250 to 300 ppm result in little change in total dry weight, or are definitely toxic. But Corsican pine, which grow to a much greater size than Scots or white pine in solutions of equal nitrogen supply, show no signs of retarded growth in concentrations as high as 485 ppm. Apparently this species benefits by supplies considerably higher than the optimum for Scots and white pine.

According to Gast (*loc. cit.,* see Fig. 14), the physiological effects of increasing nitrogen concentration, as reflected in seedling yield, are conditioned and therefore frequently limited by solar radiation. Evidence of this may also be found in Fig. 9. It will be observed that yields of a single species, even though grown in solutions of similar nitrogen supply and expressed as from seed of a single size, are not always the same for the different experiments. Data from the M-'32 and M-'33 experiments, in which seedlings were exposed to approximately the same cumulative solar radiation (38.9 and 38.1 kg. cal. cm.$^{-2}$, respectively), are in almost perfect agreement.[1] The yields of seedlings from the G-'32 white pine experiment, in which the cumulative radiation for the

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[1] The cumulative solar radiation received from June through August was greater during 1932 than 1933. Consequently the 1933 experiment was allowed to continue longer, so that the cumulative radiation would be approximately equal for the two experiments (see discussion, Mitchell, 1934, pp. 66-67).

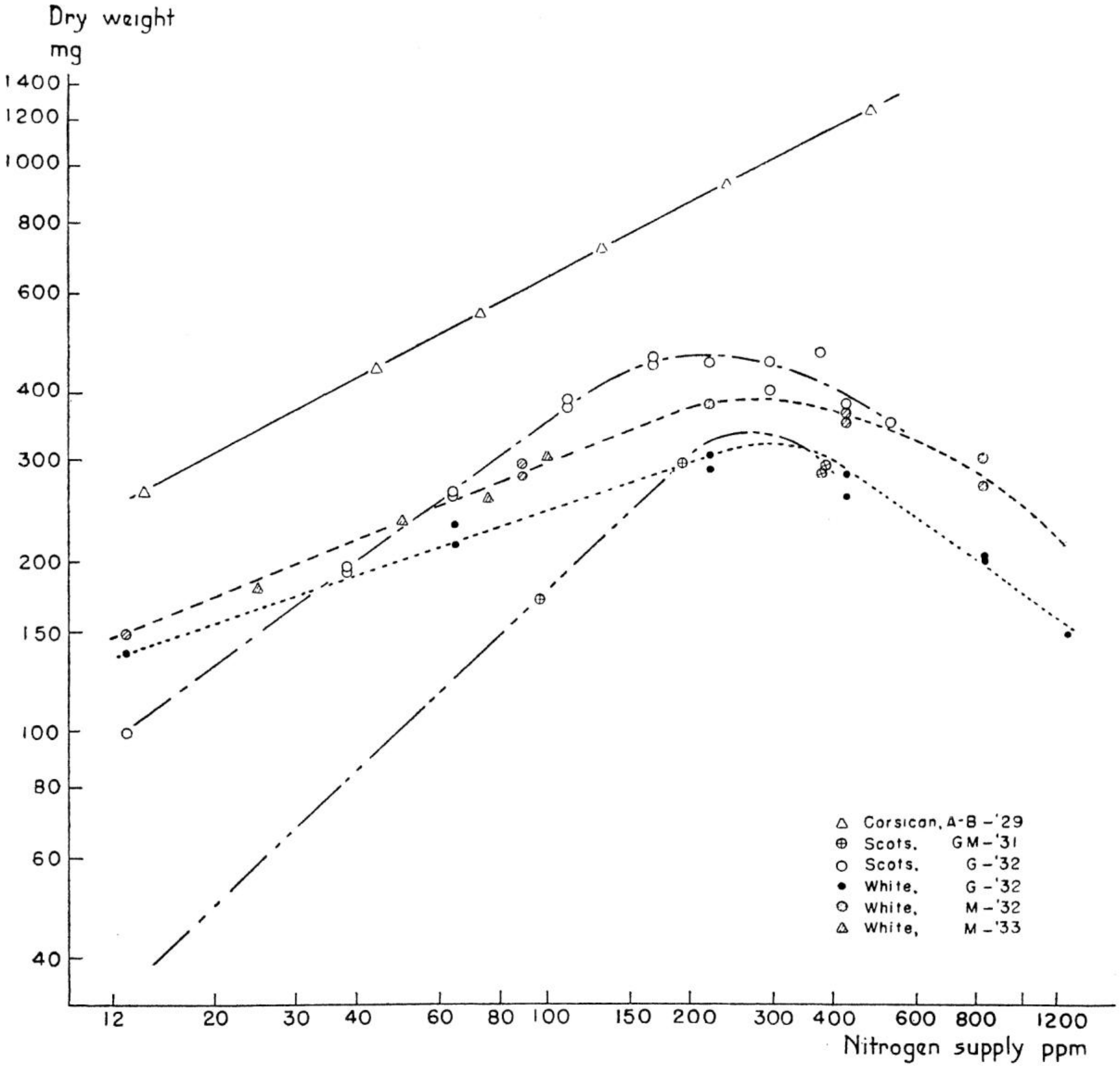

Fig. 9.—THE DRY WEIGHTS OF SCOTS, WHITE AND CORSICAN PINE SEEDLINGS GROWN FOR ONE SEASON IN NUTRIENT-SAND CULTURES OF VARIED NITROGEN CONCENTRATION. YIELD AND NITROGEN CONCENTRATION ON LOGARITHMIC: LOGARITHMIC AXES. DATA FROM VARIOUS EXPERIMENTS BY GAST, MITCHELL AND ALDRICH-BLAKE, AS INDICATED IN THE LEGEND.

From Gast (1937, Fig. 11).

growing period was only 32.5 kg. cal. cm.$^{-2}$, are significantly lower than those grown in the M-'32 and M-'33 experiments. This difference can be attributed to the variation in cumulative radiation, with which seedling yield is known to be highly correlated (Gast, 1937, p. 642; Mitchell, 1934, 1936).

After making due allowance for differences in cumulative radiation, it is still apparent from data presented in Fig. 9 that responses of the three species of *Pinus* to equal increases in nitrogen supply are not identical. This is evidenced by considerable differences in the slope of the various yield curves, some being steeper than others. The reaction of Scots pine, for example, to equivalent increments in nitrogen concentration, is significantly greater than that of either Corsican or white pine. Apparently the former are more efficient in the use of nitrogen. According to a method devised by Gast (*loc. cit.*, Fig. 19), whereby the relative efficiencies of the various species in the use of nitrogen can be evaluated upon a comparable basis, Scots pine are the most efficient, white pine the least efficient and Corsican intermediate.

The Relation Between Phosphorus Supply and Seedling Yield

The dry weights of white pine seedlings grown during the 1933 experiment in nutrient-sand cultures of different phosphorus concentration, but with constant supplies of all other essential nutrient elements, are shown in Fig. 8 B (data from Tables 13 and 14). The yields plotted in this figure are of seedlings from series C seed, expressed as from size class 2, as are the nitrogen series data in Fig. 8 A.

As shown in Fig. 8 B, seedling yield is almost directly proportional to phosphorus concentration up to about 200 ppm, where the yield curve starts to flatten; the point of maximum yield is between 300 and 350, approximately

TABLE 13

DRY WEIGHTS, ROOT/SHOOT RATIOS AND PHOSPHORUS CONTENTS OF WHITE PINE SEEDLINGS FROM NUTRIENT-SAND CULTURES OF VARIED PHOSPHORUS CONCENTRATION

1933 EXPERIMENT

						Phosphorus Content		
						Seedlings		*Shoots Only*
Phosphorus Concentration ppm P	*Seed Class Used*[1]	*Dry Wt. of Seedlings in Mg.*	*No. of Seedlings*[2]	*Dry Wts. Corrected as from Series C Seed Class 2*[3]	*Root/Shoot Ratio*	*% Dry Wt.* ($P_{\%}$)	*Milligrams* (P_{mg})[4]	*% Dry Wt.*
(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
0	0	154.6± 4.6[5]	25	170.1	.332	0.10	0.18	0.09
50	1	210.5±15.1	22	220.4	.330	0.30	0.65	0.26
	0	203.7±15.4	22	224.1	.338	0.27	0.61	0.24
100	1	236.2± 9.6	22	247.3	.342	0.38	0.94	0.34
200	0	270.0± 9.0	25	297.0	.415	0.58	1.73	0.53
	1	302.1±12.3	22	316.3	.429	0.57	1.80	0.52
300	0	298.7±12.5	25	328.6	.443	0.62	2.05	0.59
	1	310.0± 8.6	19	324.6	.395	0.65	2.11	0.62
400	0	291.8±13.5	22	321.0	.407	0.65	2.09	0.60
	1	305.7± 9.8	23	320.1	.457	0.67	2.15	0.62
500	0	282.8±14.1	23	311.1	.435	0.71	2.21	0.68
600	1	275.5±10.7	24	288.4	.410	0.68	1.96	0.66
700	0	245.3± 7.7	22	269.8	.415	0.76	2.04	0.70
800	1	202.3±10.3	24	211.8	.391	0.73	1.54	0.70
900	0	161.9± 4.9	21	178.1	.242	0.72	1.29	0.71

[1] Series C seed (see Table 6).

[2] Number of harvested seedlings after discarding replacements and those whose weights deviated from the mean by more than 3 × std. dev.

[3] Reserve dry weight of series C seed class 2 = 13.77 mg. (see Table 6).

[4] $P_{\%}$ (col. 7) × seedling yield (col. 5) = P_{mg}.

[5] Standard error of mean.

TABLE 14

CALCULATED COMPARED WITH EXPERIMENTALLY DETERMINED YIELDS AND PHOSPHORUS CONTENTS OF WHITE PINE SEEDLINGS FROM NUTRIENT-SAND CULTURES OF VARIED PHOSPHORUS CONCENTRATION [1]

Phosphorus Concentration ppm P	*Dry Wt. of Seedlings in Mg.*[2]		*Phosphorus Content of Seedlings*			
			% Dry Wt. ($P_{\%}$)		*Milligrams* (P_{mg})	
	Experimentally Determined	*Calculated* [3]	*Experimentally Determined*	*Calculated* [4]	*Experimentally Determined*	*Calculated* [5]
(1)	(2)	(3)	(4)	(5)	(6)	(7)
0	170.1	170.1	0.10	0.10	0.18	0.18
50	220.4 224.1	219.6 219.6	0.30 0.27	0.28 0.28	0.65 0.61	0.68 0.68
100	247.3	257.9	0.38	0.40	0.94	1.09
150	....	286.7	....	0.49	....	1.42
200	297.0 316.3	307.1 307.1	0.58 0.57	0.56 0.56	1.73 1.80	1.69 1.69
250	....	320.1	....	0.61	....	1.89
300	328.6 324.6	326.7 326.7	0.62 0.65	0.64 0.64	2.05 2.11	2.05 2.05
350	....	328.3	....	0.67	....	2.15
400	321.0 320.1	325.0 325.0	0.65 0.67	0.69 0.69	2.09 2.15	2.22 2.22
450	....	317.9	....	0.70	....	2.25
500	311.1	307.8	0.71	0.71	2.21	2.25
600	288.4	281.1	0.68	0.72	1.96	*2.15*
700	269.8	248.6	0.76	0.73	2.04	*1.95*
800	211.8	213.8	0.73	0.73	1.54	*1.64*
900	178.1	179.2	0.72	0.73	1.29	*1.26*

---

[1] Basic data from Table 13.

[2] Yields expressed as from series C seed class 2; reserve dry weight = 13.77mg. (see Table 6).

[3] Calculated with the Mitscherlich equation (constants given in Table 12) over the entire range of P concentrations.

[4] Calculated with the Mitscherlich equation (constants given in Table 20) over the entire range of P concentrations.

[5] Calculated with the Mitscherlich equation (constants given in Table 21) up to 500 ppm P; interpolated (see text) from smooth curve (Fig. 13) the remainder of the range.

the same as in the nitrogen series; and greater supplies of phosphorus are toxic to even a greater extent than equivalent nitrogen concentrations. The latter observation is interesting in view of the fact that many nurserymen consider high-analysis nitrogen fertilizers as the only ones apt to ''burn'' coniferous seedlings; undoubtedly phosphorus fixation in the soil is the saving factor. As with nitrogen, the entire phosphorus range may be divided into the following regions on the basis of seedling response: from 0 to 50 ppm, the region of minima; from 50 to 200, the working region; from 200 to 400, the region of tension; and greater supplies the toxic region (see Table 11).

The Mitscherlich equation was used to calculate the curve shown in Fig. 8 B. Numerical values for the various constants, derived from yield data expressed as from seed class 2, are entered in Table 12. In this case the calculated curve fits the observed data over the entire range of phosphorus concentrations used in the experiment. Calculated and experimentally determined yields, which are in close agreement, are compared in Table 14, and the results of statistical analyses are summarized in Table 12.

It will be noted that white pine seedlings grown in a nutrient solution entirely lacking in phosphorus (Fig. 8 B) weigh considerably more than those grown in culture solutions from which nitrogen was absent (Fig. 8 A). This may be due to an inherent difference in the phosphorus and nitrogen requirements of the species. Another explanation is that the 0.18 mg. of phosphorus supplied by the seed—the only source of supply—is greater, in proportion to the needs of the species during the initial season, than the 0.76 mg. of nitrogen supplied by the seed. Whatever the true explanation, the fact is that seedlings grown in solutions lacking in phosphorus are larger than those from cultures in which nitrogen is absent. This no doubt explains why equal increments in the latter element result in relatively greater increases in seedling dry weight, as evidenced by the steeper slope of the nitrogen series yield curve over the range from 0 to 200 ppm.

Total dry weights at concentrations of maximum yield for the nitrogen and phosphorus series are not in perfect agreement. Such lack of correspondence is probably due to a difference in the rates at which the concentration of the basic nutrient solutions were increased; perfect consonance must wait on perfected procedures.

The Relation Between Potassium Supply and Seedling Yield

The dry weights of white pine seedlings grown in nutrient-sand cultures of varying potassium concentration are shown in Fig. 10 A (data from Tables 15 and 16). As with the nitrogen and phosphorus series data, the yields plotted in Fig. 10 A are expressed as from series C seed class 2, reserve dry weight 13.77.

It is apparent from data presented in Fig. 10 A that seedling yield is almost linearly related to potassium concentration up to about 100 ppm; the point of maximum yield is approximately 150, much lower than in the case of either nitrogen or phosphorus; and at greater supplies yield varies inversely as potassium supply. The entire potassium range may be divided into the following regions: from 0 to 25 ppm, the region of minima; from 25 to 100, the working region; from 100 to 200, the region of tension; and supplies greater than 200, where yields tend to be erratic, the region of injury (see Table 11).

Yields corresponding to potassium concentrations up to 320 ppm were smoothed with the aid of the Mitscherlich formula. Values for the various constants, derived from dry weight data expressed as from seed class 2 (13.77 mg.—r.d.w.), are entered in Table 12. The calculated curve of average relationship between the two

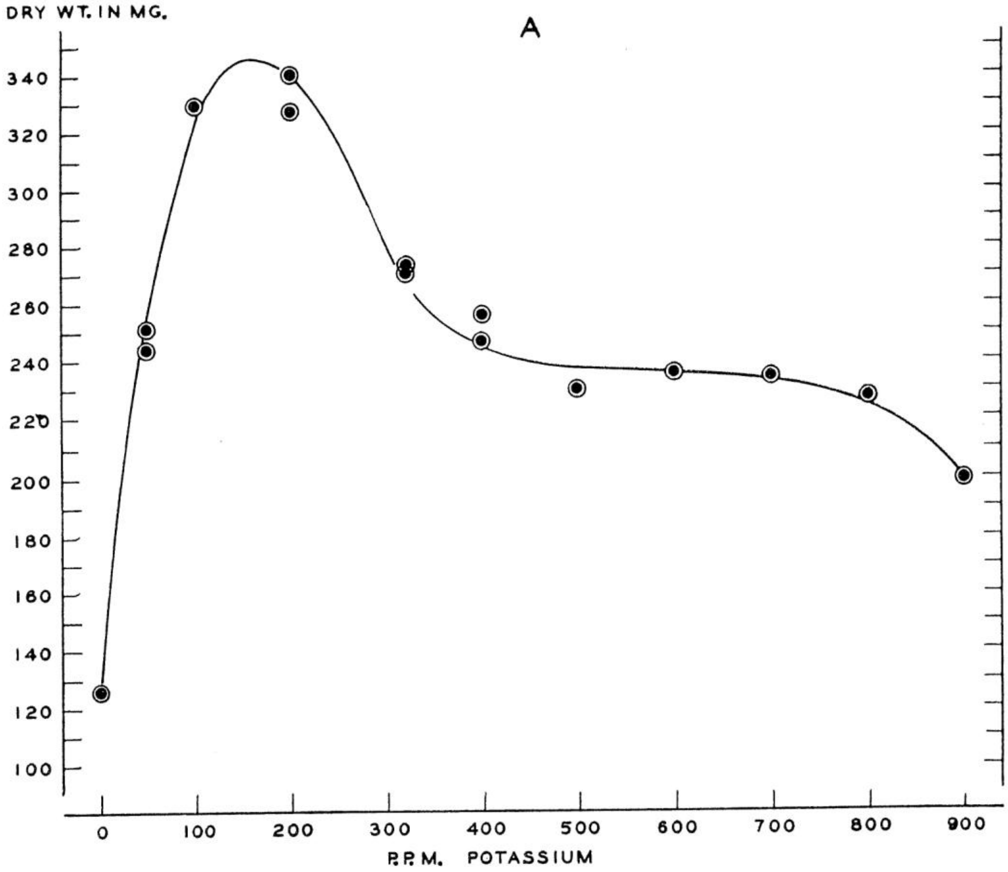

FIG. 10-A.—THE DRY WEIGHTS OF WHITE PINE SEEDLINGS GROWN FOR ONE SEASON IN NUTRIENT-SAND CULTURES OF VARIED POTASSIUM CONCENTRATION.

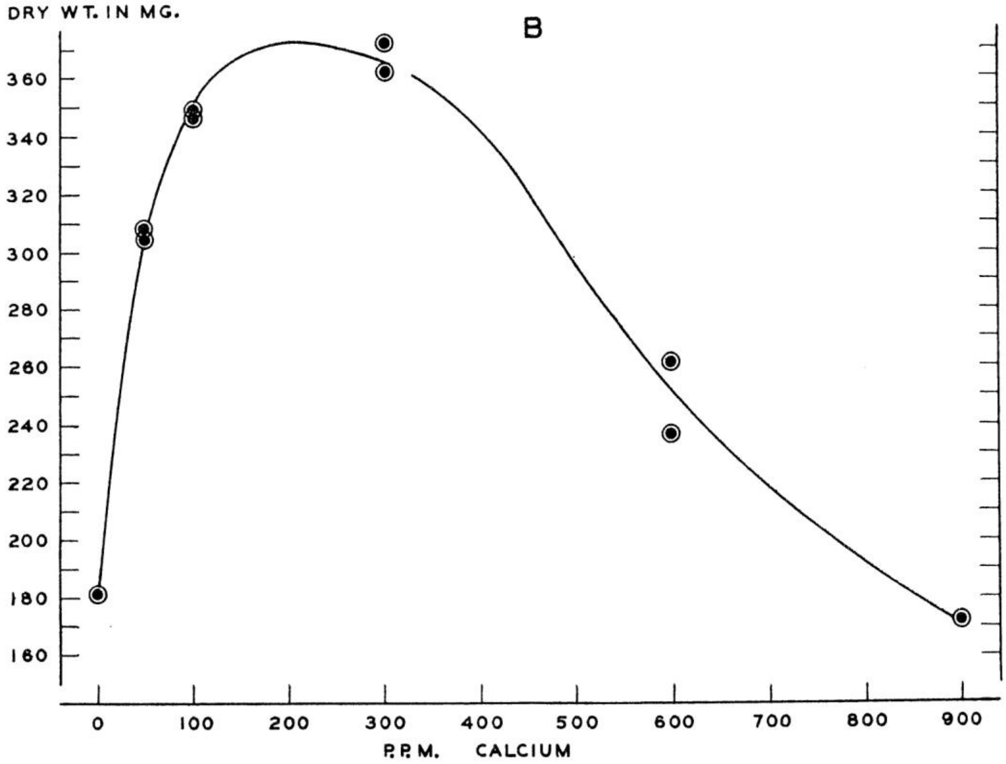

FIG. 10-B.—THE DRY WEIGHTS OF WHITE PINE SEEDLINGS GROWN FOR ONE SEASON IN NUTRIENT-SAND CULTURES OF VARIED CALCIUM CONCENTRATION.

TABLE 15

DRY WEIGHTS, ROOT/SHOOT RATIOS AND POTASSIUM CONTENTS OF WHITE PINE SEEDLINGS FROM NUTRIENT-SAND CULTURES OF VARIED POTASSIUM CONCENTRATION

1933 EXPERIMENT

						Potassium Content		
						Seedlings		*Shoots Only*
Potassium Concentration ppm K	*Seed Class Used* [1]	*Dry Wt. of Seedlings in Mg.*	*No. of Seedlings* [2]	*Dry Wt. Corrected as from Series C Seed Class 2* [3]	*Root/Shoot Ratio*	*% Dry Wt. ($K_{\%}$)*	*Milligrams (K_{mg})* [4]	*% Dry Wt.*
(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
0	1	120.2± 4.3[5]	21	125.8	.316	0.82	1.03	0.63
50	0	240.0±16.0	26	251.3	.415	1.25	3.14	1.15
	1	232.6±13.2	21	243.5	.432	1.30	3.17	1.18
100	1	315.1±14.0	23	330.0	.439	1.50	4.96	1.40
200	1	324.7±13.5	19	340.0	.469	1.85	6.27	1.70
	1	312.3±11.4	23	327.0	.450	1.95	6.38	1.77
319	1	257.9±11.2	20	270.1	.416	2.20	5.95	2.06
	1	261.4± 8.5	21	273.7	.440	2.13	5.83	1.95
400	1	235.5±13.2	24	246.6	.431	2.35	5.80	2.20
	1	244.9±10.1	21	256.4	.416	2.25	5.77	2.00
500	1	219.3±10.5	25	229.6	.355	2.35	5.40	2.21
600	1	225.5± 4.6	19	236.1	.370	2.30	5.44	2.15
700	1	223.6±11.0	23	234.1	.360	2.45	5.74	2.42
800	1	217.2±12.7	24	227.4	.356	2.47	5.62	2.42
900	1	190.5± 6.7	21	199.5	.344	2.37	4.73	2.37

[1] Series C seed (see Table 6).

[2] Number of harvested seedlings after discarding replacements and those whose weights deviated from the mean by more than 3 × std. dev.

[3] Reserve dry weight of series C seed class 2 = 13.77 mg. (see Table 6).

[4] $K_{\%}$ (col. 7) × seedling yield (col. 5) = K_{mg}.

[5] Standard error of mean.

TABLE 16

CALCULATED COMPARED WITH EXPERIMENTALLY DETERMINED YIELDS AND POTASSIUM CONTENTS OF WHITE PINE SEEDLINGS FROM NUTRIENT-SAND CULTURES OF VARIED POTASSIUM CONCENTRATION [1]

Potassium Concentration ppm K	*Dry Wt. of Seedlings in Mg.*[2]		*Potassium Content of Seedlings*			
			% Dry Wt. ($K_{\%}$)		*Milligrams* (K_{mg})	
	Experimentally Determined	*Calculated* [3]	*Experimentally Determined*	*Calculated* [4]	*Experimentally Determined*	*Calculated* [5]
(1)	*(2)*	*(3)*	*(4)*	*(5)*	*(6)*	*(7)*
0	125.8	125.8	0.82	0.82	1.03	1.03
50	251.3	256.6	1.25	1.20	3.14	3.42
	243.5	256.6	1.30	1.20	3.17	3.42
100	330.0	323.2	1.50	1.49	4.96	4.90
150	....	346.0	...	1.72	...	5.75
200	340.0	340.0	1.85	1.89	6.27	6.15
	327.0	340.0	1.95	1.89	6.38	6.15
250	....	315.9	...	2.03	...	6.25
319	270.1	266.7	2.20	2.16	5.95	6.05
	273.7	266.7	2.13	2.16	5.83	6.05
350	....	*256.0*	...	2.21	...	...
400	246.6	*244.0*	2.35	2.27	5.80	...
	256.4	*244.0*	2.25	2.27	5.77	...
450	....	*239.0*	...	2.32	...	...
500	229.6	*237.0*	2.35	2.35	5.40	...
600	236.1	*236.0*	2.30	2.40	5.44	...
700	234.1	*233.0*	2.45	2.43	5.74	...
800	227.4	*224.0*	2.47	2.45	5.62	...
900	199.5	*199.0*	2.37	2.46	4.73	...

---

[1] Basic data from Table 15.

[2] Yields expressed as from series C seed class 2; reserve dry weight = 13.77 mg. (see Table 6).

[3] Calculated with Mitscherlich yield equation (constants given in Table 12) up to 319 ppm K; interpolated from smooth curve (Fig. 10 A) the remainder of the range.

[4] Calculated with the Mitscherlich equation (constants given in Table 20) over the entire range of K concentrations.

[5] Calculated with the Mitscherlich equation (constants given in Table 21) up to 319 ppm K; at greater concentrations the K_{mg} data are too erratic to justify the use of an estimating curve (see Fig. 14).

variables fits the observed data up to 320 ppm. At greater concentrations the calculated values are too low to agree with the experimentally determined yields, which decrease only slightly with increments of potassium above 400 ppm. That portion of the yield curve beyond the break (see Fig. 10 A)—the range which is of least practical importance—was fitted to the plotted points by a simple graphic procedure. Yields calculated with the Mitscherlich formula up to 320 ppm, and estimated from the smooth curve of best fit for the remainder of the potassium range, are compared with experimentally determined yields in Table 16. The results of statistical analyses are summarized in Table 12.

Perhaps the most interesting point regarding the potassium series data is the steepness of slope of the yield curve shown in Fig. 10 A. Seedlings supplied no potassium are only slightly heavier than those grown in solutions from which nitrogen is absent. But since the optimum potassium supply—that is, the potassium concentration which resulted in maximum dry weight increase—is only half as great as for nitrogen or for phosphorus, the response of seedlings to increments of potassium up to the optimum supply is significantly greater than to equal increases in either nitrogen or phosphorus. The relatively small range of potassium supplies in the working region (25 to 100 ppm), the limited region of tension, as indicated by the pointedness of the yield curve, and the toxicity of supplies greater than 200, may not only explain some of the inconsistencies noted in previous nutrient-culture experiments but should be of interest to those concerned with the fertilization of coniferous seedlings.

The Relation Between Calcium Supply and Seedling Yield

The dry weights of seedlings grown in nutrient-sand cultures of varying calcium supply, but with constant concentrations of all other essential elements, are shown in Fig. 10 B (data from Tables 17 and 18). It will be observed that increases in calcium supply up to 100 ppm are accompanied by yield increments somewhat comparable in magnitude to those obtained with equivalent amounts of potassium; over the calcium range of 100 to 350 ppm there is but little change in dry weight increase; and at concentrations above 350 seedling yield decreases as the calcium concentration increases. The entire calcium range may be divided, on the basis of seedling response, into the following regions: from 0 to 25 ppm, the region of minima; from 25 to 100, the working region; from 100 to 350, the region of tension; and supplies greater than 350, the toxic region (see Table 11).

The Mitscherlich equation was used to calculate the yield curve (Fig. 10 B) over the calcium range of from 0 to 300 ppm. Numerical values for the various constants, derived from seedling yields expressed as from series C seed class 2, are entered in Table 12. Above 300 ppm yields calculated with the Mitscherlich formula are somewhat higher than the experimentally determined yields. For this reason, and because the experimental data are so few at calcium concentrations above 300, no accurate predictions for the toxic region are possible. The smooth curve (beyond break) shown in Fig. 10 B is only an estimate, based on available data, of the yield response to the higher calcium concentrations. Yields calculated with the Mitscherlich equation up to 300 ppm, and interpolated from the smooth curve for the remainder of the range, are compared with experimentally determined yields in Table 18. The results of statistical analyses are summarized in Table 12.

TABLE 17

DRY WEIGHTS, ROOT/SHOOT RATIOS AND CALCIUM CONTENTS OF WHITE PINE SEEDLINGS FROM NUTRIENT-SAND CULTURES OF VARIED CALCIUM CONCENTRATION

1933 EXPERIMENT

Calcium Concentration ppm Ca	*Seed Class Used* [1]	*Dry Wt. of Seedlings in Mg.*	*No. of Seedlings* [2]	*Dry Wts. Corrected as from Series C Seed Class 2* [3]	*Root/Shoot Ratio*	*Calcium Content*		
						Seedlings		*Shoots Only*
						% Dry Wt. ($Ca_{\%}$)	*Milligrams (Ca_{mg})* [4]	*% Dry Wt.*
(1)	*(2)*	*(3)*	*(4)*	*(5)*	*(6)*	*(7)*	*(8)*	*(9)*
0	1	173.1 ± 6.4[5]	20	181.2	.424	0.23	0.41	0.22
50	1	290.3 ± 15.6	21	303.9	.440	0.24	0.71	0.23
	1	294.5 ± 16.3	24	308.3	.452	0.25	0.76	0.25
100	1	333.3 ± 10.7	22	349.0	.465	0.29	0.99	0.28
	1	330.6 ± 15.6	24	346.1	.480	0.31	1.07	0.34
300	1	355.4 ± 13.3	23	372.1	.487	0.38	1.41	0.42
	1	345.7 ± 13.8	22	361.9	.466	0.40	1.45	0.41
600	1	249.6 ± 9.3	23	261.3	.398	0.54	1.40	0.53
	1	225.8 ± 9.6	24	236.4	.372	0.65	1.53	0.64
900	1	163.4 ± 8.3	16	171.1	.216	0.70	1.19	0.72

[1] Series C seed (see Table 6).

[2] Number of harvested seedlings after discarding replacements and those whose weights deviated from the mean by more than 3 × std. dev.

[3] Reserve dry weight of series C seed class 2 = 13.77 mg. (see Table 6).

[4] $Ca_{\%}$ (col. 7) × seedling yield (col. 5) = Ca_{mg}.

[5] Standard error of mean.

TABLE 18

CALCULATED COMPARED WITH EXPERIMENTALLY DETERMINED YIELDS AND CALCIUM CONTENTS OF WHITE PINE SEEDLINGS FROM NUTRIENT-SAND CULTURES OF VARIED CALCIUM CONCENTRATION [1]

Calcium Concentration ppm Ca	*Dry Wt. of Seedlings in Mg.*[2]		*Calcium Content of Seedlings*			
			% Dry Wt. ($Ca_{\%}$)		*Milligrams* (Ca_{mg})	
	Experimentally Determined	*Calculated*[3]	*Experimentally Determined*	*Calculated*[4]	*Experimentally Determined*	*Calculated*[5]
(1)	(2)	(3)	(4)	(5)	(6)	(7)
0	181.2	181.2	0.23	0.23	0.41	0.41
50	303.9 308.3	306.9 306.9	0.24 0.25	0.26 0.26	0.71 0.76	0.76 0.76
100	349.0 346.1	352.9 352.9	0.29 0.31	0.28 0.28	0.99 1.07	1.02 1.02
150	....	368.5	...	0.31	...	1.21
200	....	371.8	...	0.33	...	1.34
250	....	369.7	...	0.36	...	1.43
300	372.1 361.9	365.0 365.0	0.38 0.40	0.39 0.39	1.41 1.45	1.48 1.48
350	....	*356.0*	...	0.41	...	1.52
400	....	*341.0*	...	0.44	...	1.53
450	....	*320.0*	...	0.46	...	1.53
500	....	*296.0*	...	0.49	...	1.52
600	261.3 236.4	*252.0* *252.0*	0.54 0.65	0.54 0.54	1.40 1.53	1.46 1.46
700	....	*218.0*	...	0.59	...	1.39
800	....	*192.0*	...	0.65	...	1.30
900	171.1	*170.0*	0.70	0.70	1.19	1.20

---

[1] Basic data from Table 17.

[2] Yields expressed as from series C seed class 2; reserve dry weight = 13.77 mg. (see Table 6).

[3] Calculated with Mitscherlich yield equation (constants given in Table 12) up to 300 ppm Ca; interpolated from smooth curve (Fig. 10 B) the remainder of the range.

[4] Calculated with simple regression equation (constants given in Table 20) over the entire range of Ca concentrations.

[5] Calculated with the Mitscherlich equation (constants given in Table 21) over the entire range of Ca concentrations.

The steepness of slope of the yield curve over the relatively narrow—as compared to N and P—range of calcium concentrations in the minimal and working regions supplies ample proof of the importance to seedling nutrition of this essential element. This is a point which should not be overlooked, even though it is probable that the majority of nursery soils in this country supply calcium in amounts equivalent, in effect, to the higher concentrations of the working range of this experiment.

Another point of interest is the relatively wide range of concentrations—100 to 350 ppm—over which increments of calcium have little or no effect upon seedling yield. As has been shown, somewhat similar results were obtained with equivalent increments of phosphorus in the region of tension (for P), and, to a lesser degree, nitrogen. But, as discussed above, the region of tension for potassium—where changes in external concentration have little effect upon yield—is quite limited. Thus, as regards the nutrition of white pine seedlings, regulation of available calcium supply, as with phosphorus and to a lesser degree nitrogen, need not be so exact, within limits, as in the case of potassium.

Although the calcium series data are too meagre, especially at supplies above 300 ppm, to predict with precision the response of seedlings to the higher calcium concentrations, the experimental evidence is sufficient to prove that increments of calcium above 350 ppm are definitely toxic to white pine seedlings. Here again we have an element which is adsorbed by the soil to a considerable degree, which no doubt explains why nurserymen have not noted this effect of high calcium supplies.

That the low yields obtained at 600 and 900 ppm were due to the toxic effect of high levels of calcium availability and not to unfavorable alkalinity—which frequently results from large calcium supplements—is evidenced by the pH data presented in Table 19. Because of the composition of the basic nutrient solution, which

TABLE 19

HYDROGEN-ION CONCENTRATION VARIATIONS

1933 CALCIUM SERIES[1]

Calcium Concentration of Nutrient-Sand Culture Solutions (ppm Ca)	*Hydrogen-ion Concentration of Solutions (pH)*[2]
0	5.60
50	5.26
100	5.34
300	5.43
600	5.20
900	5.23

[1] Complete details are given in Table 2.
[2] Mean of duplicate pots.

was well buffered, calcium increments had no appreciable effect upon pH. The reaction of every culture solution of the calcium series, regardless of variations in calcium content, was well within the optimum range for the species (see discussion, Mitchell, 1934).

Earlier in the discussion a comparison was made (see Fig. 9) between the efficiency of white pine seedlings in the use of nitrogen—as indicated by this and comparable experiments—and the efficiency of various other coniferous species in the use of this nutrient element, as based upon all available data. But how white pine seedlings compare with other species as to efficiency in the use of phosphorus, potassium or calcium, it is probably impossible to say at present. So far as the writer is aware, very few data are available regarding the phosphorus, potassium and calcium requirements of white pine—or any other tree species. And, unfortunately, such data as have been reported are accompanied by incomplete information regarding seed size and source, solar radiation, water supply, the purity and analysis of the soil, the analysis of the fertilizer used, and other essential information without which it is impossible to make valid comparisons.

Root/Shoot Ratio Variations

The root/shoot ratios of seedlings from the nitrogen, phosphorus, potassium and calcium nutrient-culture series are shown in Fig. 11 (data from Tables 9, 13, 15 and 17). It is apparent that the influence of varying nitrogen concentration upon root/shoot ratio is quite different from that of equal increments of phosphorus, potassium or calcium. Although the heaviest (total dry weight) nitrogen series seedlings are those supplied 300 ppm (see Fig. 8 A), those having the greatest ratio of root weight to shoot weight are from the minimal range of nitrogen supply, and at greater supplies root/shoot ratio varies inversely as the nitrogen concentration. But, in the phosphorus, potassium and calcium series, ratios of root to shoot approach maximum at the same concentrations—approximately 350 ppm P; 150 ppm K; 200 ppm Ca—that result in greatest total yield. Increments of these three elements through their respective regions of tension, and into the toxic ranges of supply, have no appreciable effect upon root/shoot ratio. Only at supplies greater than 800 ppm phosphorus, and 400 to 500 ppm for potassium and calcium, are there significant decreases in root/shoot ratios. Another point of difference is that, in the minimal and working regions, increments of potassium and phosphorus, and to a lesser extent calcium, result in significant increases in root/shoot ratio, whereas the reverse is true of equal increments of nitrogen.

The most probable explanation of the observed differences in root/shoot ratio response, especially in the minimal and working regions of nutrient supply, is that root development is more dependent upon adequate supplies of phosphorus, potassium and calcium than upon nitrogen, increments of which have a relatively greater stimulating effect upon shoot growth. This would account for: (1) the high root/shoot ratios of seedlings

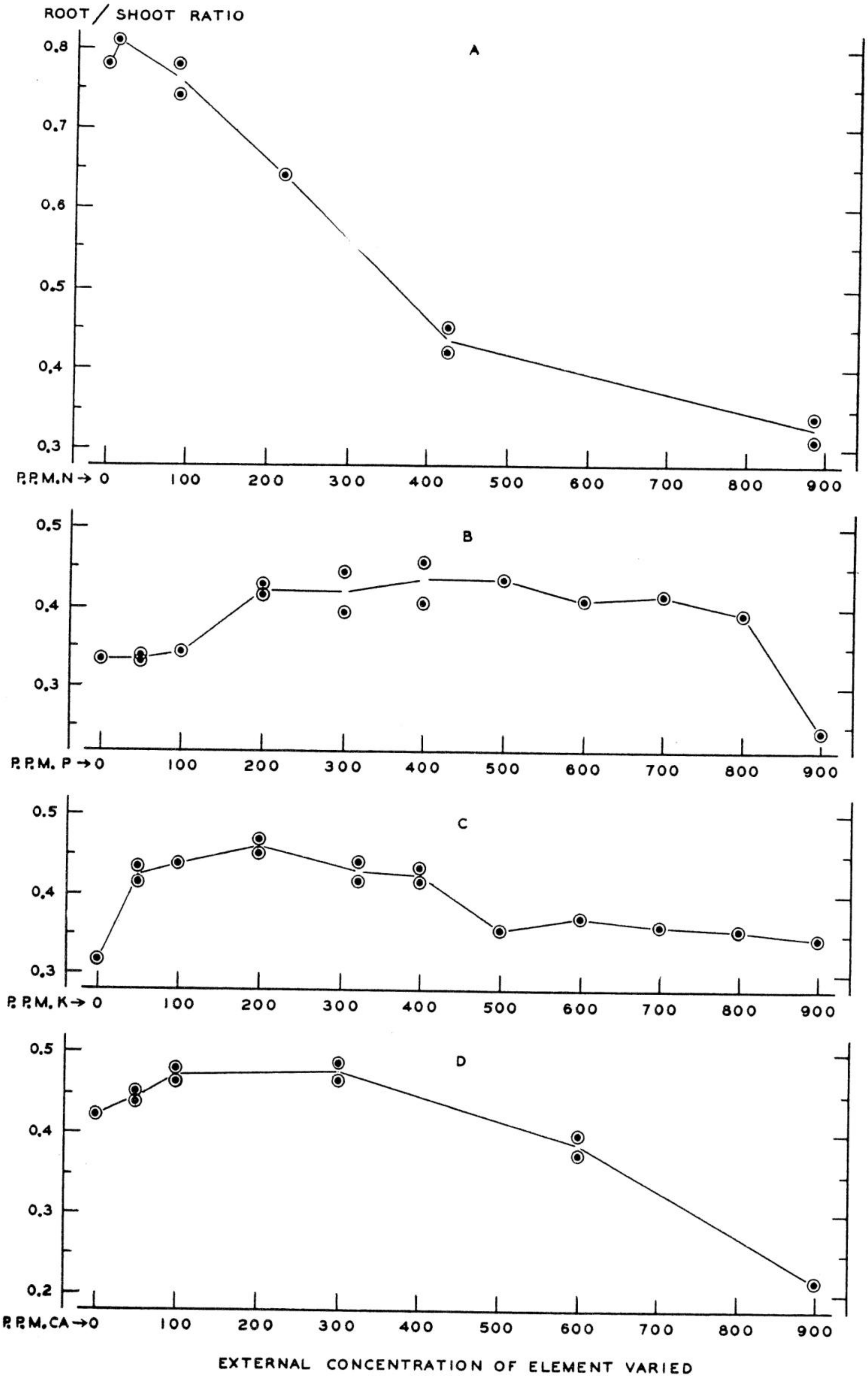

FIG. 11.—THE ROOT/SHOOT RATIOS OF WHITE PINE SEEDLINGS GROWN FOR ONE SEASON IN NUTRIENT-SAND CULTURES OF VARIED: A, NITROGEN CONCENTRATION; B, PHOSPHORUS CONCENTRATION; C, POTASSIUM CONCENTRATION; AND D, CALCIUM CONCENTRATION.

grown in culture solutions deficient in nitrogen, and (2) the significantly lower ratios of those supplied little or no phosphorus, potassium or calcium. In the former case, shoot growth is more limited by the nitrogen deficiency than is root development, which is relatively good owing to adequate supplies of all other essential elements. In the latter, the low ratios of seedlings from cultures deficient in phosphorus, potassium or calcium may be attributed to the fact that the nitrogen was supplied in sufficient amounts to result in fairly well developed shoots, whereas one of the elements more necessary for root development was lacking in each instance.

This differential effect upon relative root and shoot growth of equal increments of the four elements studied would also account for the inverse relationship between root/shoot ratio and nitrogen supply through the working, tensional and toxic ranges, as compared to the relatively small variation, through the latter two regions, of equal increments of phosphorus, potassium and, to a lesser degree, calcium. As regards nitrogen, increments of this element through the working and into the tensional region apparently stimulate the shoots more than the roots and, in the toxic region, retard shoot development less. There is but little difference in the relative effect upon root and shoot growth of increments of phosphorus, potassium and calcium through their respective tensional, and into their toxic ranges of supply.

On the basis of these observations it appears that, in the phosphorus, potassium and calcium series, better-balanced seedlings would have been obtained throughout the series with less nitrogen—175 to 200 ppm instead of 300 ppm—in the basic nutrient solution. Under such conditions the total dry weights of seedlings at the supplies of maximum yield—for each series—should not be appreciably less than those observed, since, in the nitrogen series, there is but little difference in the yield of seedlings through the range of from 175 to 300 ppm (see Fig. 8 A).

Root Extension and Development in Different Nutrient Environments

The character, prevalence and development of the various root structures responsible for nutrient absorption are known to vary greatly with the concentration of available nutrient elements in the culture medium (Hatch, 1937). But since certain root structures in pines, especially the root hairs and short-roots, are so small and succulent that they have but little influence upon dry weight, neither total root weight nor the ratio of root weight to shoot weight is necessarily a good measure of the relative absorbing surface area of seedlings grown in different nutrient environments. Such comparisons, which are difficult at best, are more easily illustrated with photographs than with data based upon the usual quantitative measures.

The silhouettes of representative seedlings from the 1932 nitrogen series, shown in Plate II, indicate that the extensiveness of the root systems varies inversely as the nitrogen concentration. It is apparent that the laterals (mother roots) and secondary laterals decrease in number, branching and length, and that the short-roots decrease in number and development with increases in nitrogen through the greater part of the working region and through the tensional and toxic ranges of supply (root terminology after Hatch and Doak, 1933). Although not shown by the silhouettes, root hairs—which are characteristic of nutrient-culture-grown seedlings but are infrequent in nature—decrease in abundance on both long-roots and short-roots with increases in nitrogen concentration. Seedlings with the most extensive and best-developed root systems are those from solutions in the lower working region of nitrogen supply (about 100

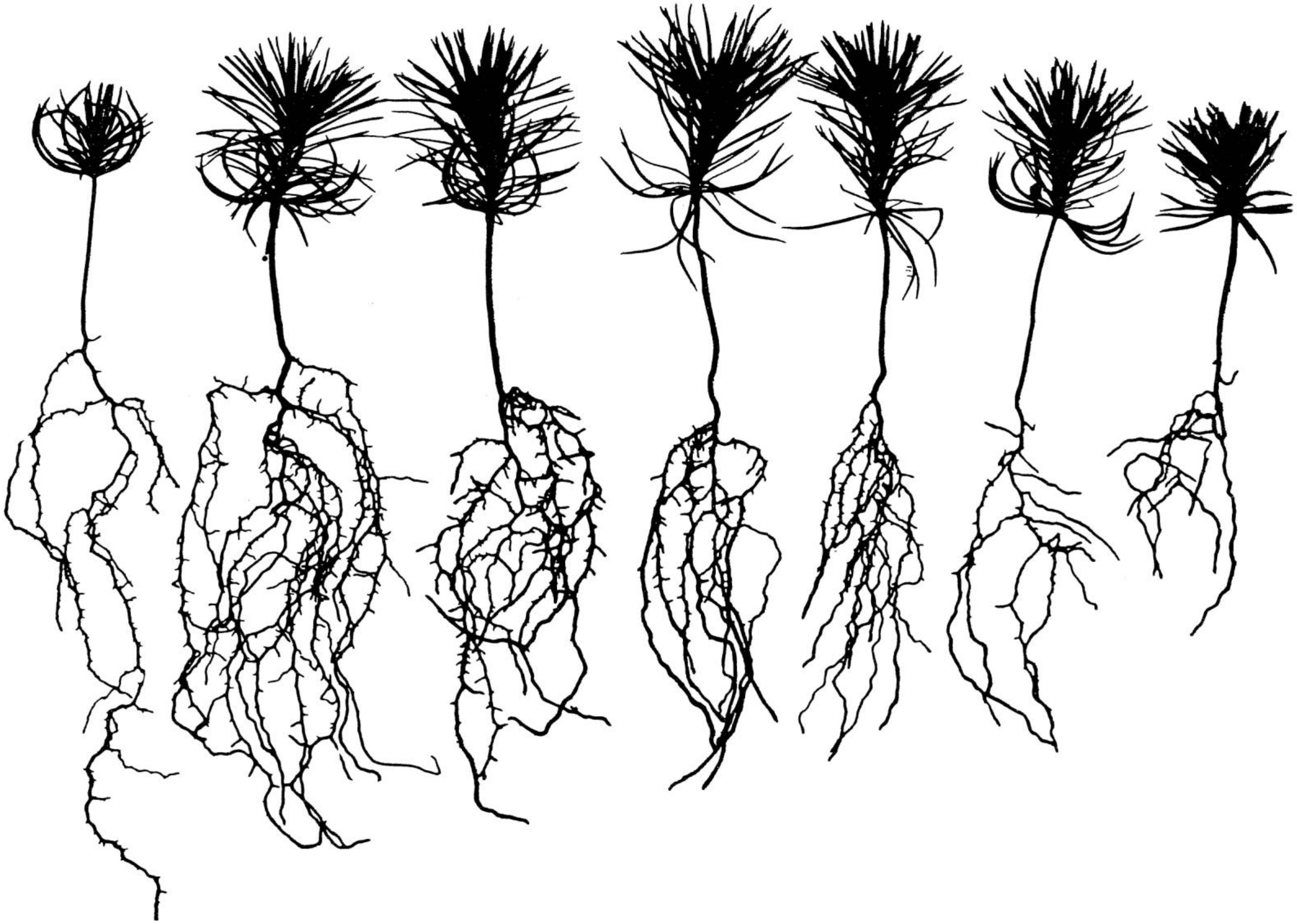

PLATE II.—SILHOUETTES OF WHTE PINE SEEDLINGS GROWN FOR ONE SEASON IN NUTRIENT-SAND CULTURES OF VARIED NITROGEN CONCENTRATION. LEFT TO RIGHT. PPM NITROGEN: 0, 88.3, 425.9, 838.9, 1239.0, 2077.9, 2490.8. FROM THE 1932 EXPERIMENT.

Photo by A. B. Hatch.

ppm). High in the toxic region (concentrations around 2400 ppm) secondary laterals are very infrequent, and short-roots are entirely absent (Plate II, extreme right). The latter observation proves beyond any reasonable doubt that long-roots as well as short-roots may function in nutrient absorption (see discussion, Hatch, 1937).

In general, the root systems of white pine seedlings respond to variations in phosphorus, potassium or calcium supply in much the same way as to equivalent changes in nitrogen concentration. Representative seedlings from the calcium series are shown in Plate III. So far as root response to changing nutrient concentration is concerned, these seedlings are almost identical with those supplied equivalent amounts of either phosphorus or potassium. The only significant difference between the root response of seedlings to any one of these three elements—phosphorus, potassium and calcium—and to equivalent increments in nitrogen supply is that, in the latter case, maximum root extension occurs at relatively lower concentrations. It is evident that increments of nitrogen through the higher working range tend to retard root growth and branching, whereas the effect of comparable supplies of phosphorus, potassium or calcium is stimulating.

It is probable, therefore, that the stimulating effect of small amounts of the latter three elements might have been even more pronounced if less nitrogen had been supplied in the basic nutrient solution. However, under the conditions of the experiment, it is evident that through the regions of tension and injury, root development varies inversely as the concentration of phosphorus, potassium and calcium as well as nitrogen.

The influence of varying nutrient supply upon the incidence and development of short-roots is of greater interest than the response of the other root structures, because, in nature, short-roots are probably the chief absorbing organ of tree species (Hatch, 1937). In the

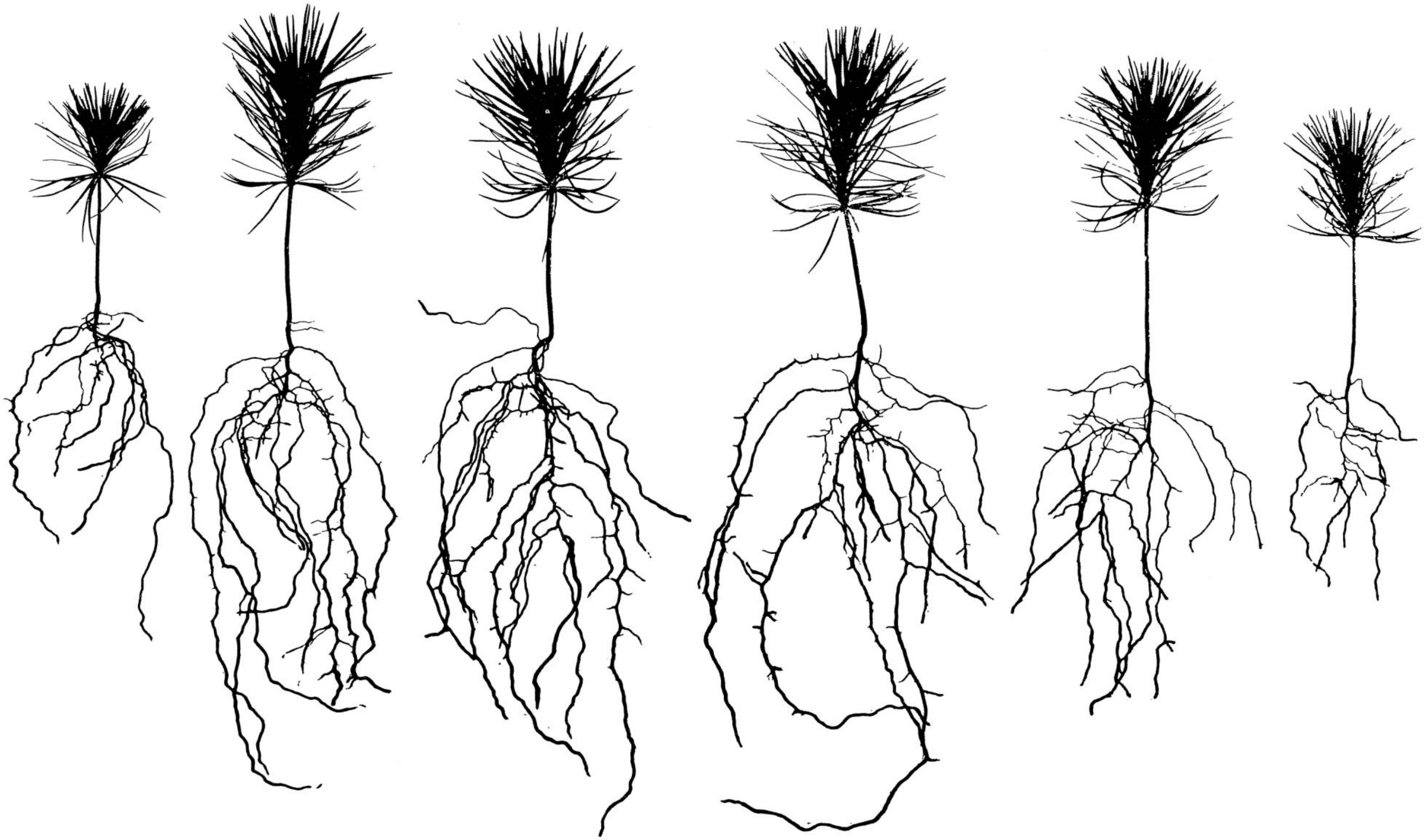

Plate III.—SILHOUETTES OF WHITE PINE SEEDLINGS GROWN FOR ONE SEASON IN NUTRIENT-SAND CULTURES OF VARIED CALCIUM CONCENTRATION. LEFT TO RIGHT, PPM CALCIUM: 0, 50, 100, 300, 600, 900. FROM THE 1933 EXPERIMENT.

Photo by A. B. Hatch.

nitrogen, phosphorus, potassium and calcium nutrient-culture series, the development of short-roots and their number per unit length of long-root tended to decrease with increases in the concentration of each of the elements varied. They were entirely absent on seedlings supplied large amounts of either nitrogen, phosphorus, potassium or calcium. But only one of the three recognized types of short-roots was observed. These were of the type known as ''uninfected,'' as evidenced by the presence of root hairs. Hatch and Doak (1933) have divided the short-roots of *Pinus* into three distinct and clearly defined types: (1) uninfected, which are common in sand and soil cultures of high nutrient concentration, but are infrequent in nature, (2) fungus-infected short-roots in which for some reason the mycorrhizal structure is absent, known as ''pseudomycorrhizae,'' and (3) infected short-roots which have developed the typical mycorrhizal structure (''mycorrhizae''). The three types are shown in Plate IV (see Hatch and Doak, *loc. cit.,* and Hatch, 1937 for a discussion of the anatomical differences on which the classification is based).

It is not the purpose of the present report to discuss the function or relative importance of the three short-root types, but merely to point out how the observed data fit in with current opinion regarding the factors which determine the formation and ultimate destiny of short-roots. The fact that only uninfected short-roots were observed in the nutrient culture series is in agreement with available data on the root systems of seedlings grown in sand and soil cultures of high nutrient concentration (Hatch, 1937). And the complete absence of mycorrhizal short-roots is further evidence of the correctness of the Stahlian-Hatch theory of the distribution of mycorrhizae in nature. According to this theory, when appropriate inoculum is present and other environmental factors are favorable, the incidence of mycorrhizae and the degree of their development vary inversely as the

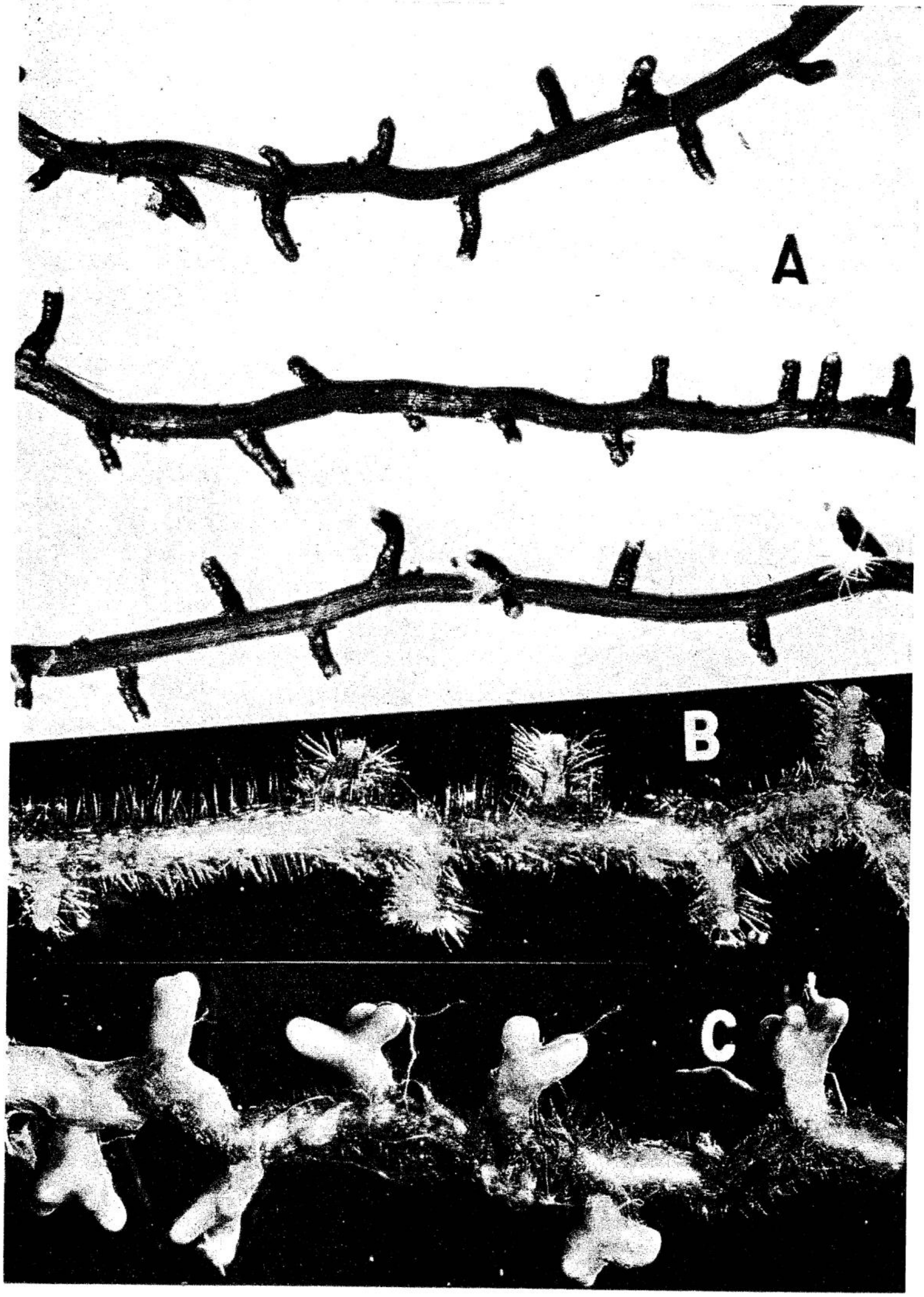

PLATE IV.—THE THREE POSSIBLE DESTINIES OF SHORT-ROOTS IN PINE.

A. Pseudo-mycorrhizal (in the sense of Melin, 1917) in soil where mycorrhiza-formation was inhibited. B. Non-mycorrhizal (uninfected, as evidenced by root hairs) in pure culture. C. Mycorrhizal.

From Hatch and Doak (1933).

availability of mineral nutrients in the substrate. Thus, in nature, mycorrhizae are usually abundant and well developed in infertile soils, but are less frequent, poorly developed or entirely lacking in more fertile substrates. In the present experiment inoculum was probably lacking, since none was introduced into the substrate. And in any event the concentration of mineral elements in the basic nutrient solution was undoubtedly sufficiently high to prevent mycorrhiza formation even in those solutions very deficient in any one of the four essential elements studied. The absence of the other fungus-infected short-root type (pseudomycorrhizae), regarding which there is at present little information, probably can be explained on the same basis.

In view of the above observations it would seem that the root structures chiefly responsible for the absorption of mineral elements by nutrient-culture-grown seedlings —that is, uninfected short-roots, root hairs and, at high concentrations, non-suberized portions of long-roots— decrease in number and development with increases in the concentration of any one of the four elements varied. This response is very similar to that of the absorbing organs—chiefly short-roots—of soil-grown seedlings to variations in soil fertility. For a more complete discussion of modification of roots by nutrition, mycotrophy in *Pinus,* and the physiological rôle of the various root types, the reader is referred to Hatch (1937), who inspected all seedlings from the series of experiments by Professor Gast and the writer in connection with an extensive study of the root systems of coniferous seedlings grown in various nutrient-sand cultures and natural soils of widely different fertility.

Needle Color as an Index to Nutrient Deficiency

The needles of seedlings grown in solutions deficient in nitrogen developed the pale yellow-green color which is universally associated with nitrogen poverty. Seedlings grown for the same length of time in solutions of different nitrogen supply provided a series which showed a gradual transition in needle color from the yellow-green in the region of minima, to the blue-green characteristic of the species in the working region, to an abnormally deep blue-green in the upper limits of the toxic region.

Acute phosphorus deficiency may also be detected on the basis of needle color. The lower needles of seedlings which received no phosphorus, except that supplied by the seed, developed a purple color early in the growing season. This distinctive color became more pronounced as the season advanced. Similar observations have been reported by Deuber (1930) and Němec (1935) for other tree species (see also Mitchell, 1934). Unlike the gradual change in color shown by seedlings supplied varying amounts of nitrogen, the purple lower needles indicative of phosphorus poverty are limited to seedlings grown in nutrient cultures or soils very deficient in this element. Seedlings supplied relatively small amounts of phosphorus (50 ppm or more) showed no trace whatever of the purple color.

Seedlings grown in solutions deficient in potassium were chlorotic, and otherwise unhealthy in appearance. Needles near the terminal bud were very much stunted and of a sickly grey color. Other needles were a pale green. Seedlings supplied no calcium were almost identical in appearance. For this reason, and because deficiencies of several other nutrient elements, notably iron, result in chlorosis and stunted growth, such symptoms cannot be used as specific indicators.

THE RELATIONSHIPS BETWEEN THE EXTERNAL (SOLUTION) CONCENTRATION OF NITROGEN, PHOSPHORUS, POTASSIUM AND CALCIUM AND THE INTERNAL (SEEDLING) CONTENT OF THESE ELEMENTS

Seedlings, and parts thereof, from each of the four nutrient-culture series of the present experiment were analyzed for whatever element was varied in the series. Thus, seedlings supplied varying amounts of nitrogen (nitrogen series) were analyzed for nitrogen, those from the phosphorus series were analyzed for phosphorus, and so on for the potassium and calcium series. The results of these analyses are summarized in Tables 9, 13, 15 and 17. The microanalysis techniques used, and their limits of accuracy, have been discussed in previous papers (Mitchell, 1934, 1936).

The analytical results are expressed in two ways: as the milligrams of N, P, K, or Ca per seedling, and as percentages of dry weight. To facilitate discussion and description of the various illustrations the symbols N_{mg}, P_{mg}, K_{mg} and Ca_{mg} will be used to denote the absolute amounts of these elements, as milligrams per seedling, and $N_{\%}$, $P_{\%}$, $K_{\%}$ and $Ca_{\%}$ to represent percentage (of dry weight) content.

The Relation Between Nitrogen Supply and the Nitrogen Content of Seedlings

The yields and nitrogen content, in milligrams and as percentages, of white pine seedlings grown during the 1932 and 1933 experiments in nutrient-sand cultures of varying nitrogen concentration are compared in Fig. 12 (data from Tables 9 and 10). The duplication, as regards nitrogen content, is almost exact for the two experiments, as was the case with yield.

The Mitscherlich equation, which was used to calculate the various yield curves, may also be used to express the

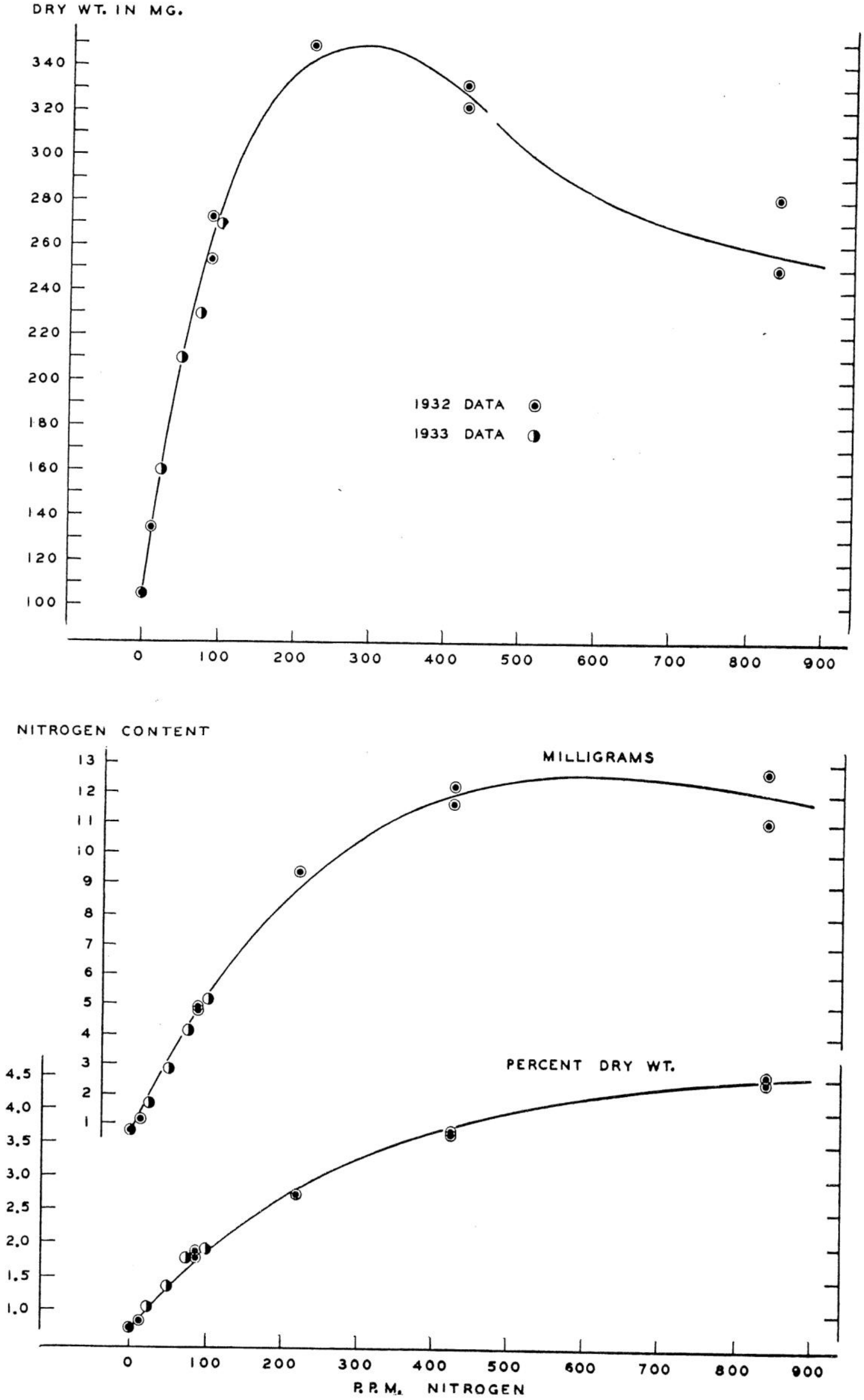

FIG. 12.—THE DRY WEIGHTS AND THE NITROGEN CONTENT, AS MILLIGRAMS AND AS PERCENT, OF WHITE PINE SEEDLINGS GROWN FOR ONE SEASON IN NUTRIENT-SAND CULTURES WITH DIFFERENT NITROGEN SUPPLIES.

relationship between external nitrogen supply and internal (seedling) nitrogen content, expressed either as milligrams per seedling or as percent dry weight. A detailed discussion of the adaptability of the Mitscherlich formula to this purpose was given in a previous report (Mitchell, 1934), and need not be repeated here. The two nitrogen content curves (N_{mg} and $N_{\%}$) shown in Fig. 12 were calculated in this way. Numerical values for the various constants are entered in Tables 20 and 21, calculated and experimentally determined values are compared in Table 10, and the results of statistical analyses are summarized in Tables 20 and 21.

With internal nitrogen content expressed as milligrams per plant (N_{mg}), the relationship is almost linear up to the nitrogen supply (300 ppm) which resulted in greatest yield. Further increments in nitrogen through the region of tension and into the toxic range result in increased nitrogen intake, and an apparent maximum is reached at about 600 ppm. But there is relatively little change over the range of from 300 to 900 ppm. At higher concentrations in the toxic region, which are far greater than those found in nature, the relationship takes the form of a linear decrease. This was discussed in the report on the M-'32 data.

Nitrogen expressed as percent dry weight is a function of seedling yield (y), in milligrams, and the milligram nitrogen content (N_{mg}), and is calculated according to the formula

$$\frac{N_{mg}}{y} \times 100 = N_{\%}.$$

Thus $N_{\%}$ is a measure of internal (seedling) nitrogen concentration in relation to dry matter.

As shown in Fig. 12, internal nitrogen concentration is almost directly proportional to nitrogen supply through the minimal and working regions. At the supply of greatest yield $N_{\%}$ is equal to 3.26. Increases in the nitro-

TABLE 20

STATISTICAL INDEXES AND CONSTANTS FOR EQUATIONS EXPRESSING THE RELATIONSHIPS BETWEEN EXTERNAL (SOLUTION) SUPPLIES OF N, P, K AND CA AND THE INTERNAL (SEEDLING) CONCENTRATIONS OF THESE ELEMENTS[1]

Independent Variable[2]	*Dependent Variable*[3]	*Number of Observations*[4]	*Equation Constants*[5]			*External Concentration Range*[6]	*Correlation Index*[7]	*Standard Error of Estimate*[7]
			A	*b*	*c*			
(1)	*(2)*	*(3)*	*(4)*	*(5)*	*(6)*	*(7)*	*(8)*	*(9)*
Nitrogen Supply (N)	Internal N Conc. ($N_{\%}$)	293	4.704	47.357	0.001477	0 to 900	0.999	0.08
Phosphorus Supply (P)	Internal P Conc. ($P_{\%}$)	341	0.734	23.900	0.002777	0 to 900	0.994	0.02
Potassium Supply (K)	Internal K Conc. ($K_{\%}$)	331	2.475	76.530	0.002270	0 to 900	0.995	0.05
Calcium Supply (Ca)	Internal Ca Conc. ($Ca_{\%}$)	219	$Ca_{\%} = 0.000519\ Ca + 0.229$			0 to 900	0.974	0.04

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[1] Calculated and experimentally determined values of $N_{\%}$, $P_{\%}$, $K_{\%}$ and $Ca_{\%}$ are compared in cols. 4 and 5 of Tables 10, 14, 16 and 18 respectively.

[2] External (solution) concentrations of N, P, K and Ca as parts per million.

[3] Internal (seedling) concentrations of N, P, K and Ca as percent dry weight ($N_{\%}$, $P_{\%}$, $K_{\%}$ and $Ca_{\%}$).

[4] These numbers are sums of harvested seedlings from all pots of each series.

[5] The relationships between external and internal concentrations of N, P and K are expressed by Mitscherlich-type formulæ. The applicability of the normal Mitscherlich yield equation to these relationships is discussed in detail by Mitchell (1934, p. 49). The relation between Ca and $Ca_{\%}$ is a linear increase, and is expressed by a simple regression equation, calculated according to the method of least mean squares (constants given above).

[6] The range of supplies (of N, P, K and Ca, as ppm) over which the calculated $N_{\%}$, $P_{\%}$, $K_{\%}$ and $Ca_{\%}$ values agree with the observed data.

[7] These indexes were computed from observed and calculated values for the entire range of external concentrations used in each series.

TABLE 21

STATISTICAL INDEXES AND CONSTANTS FOR EQUATIONS EXPRESSING THE RELATIONSHIPS BETWEEN EXTERNAL (SOLUTION) SUPPLIES OF N, P, K AND CA AND THE INTERNAL (SEEDLING) CONTENT OF THESE ELEMENTS, COMPUTED AS MILLIGRAMS PER SEEDLING[1]

Independent Variable[2]	*Dependent Variable*[3]	*Number of Observations*[4]	*Equation Constants*[5]				*External Concentration Range*[6]	*Correlation Index*[7]	*Standard Error of Estimate*[7]
			A	*b*	*c*	*k*			
(1)	*(2)*	*(3)*	*(4)*	*(5)*	*(6)*	*(7)*	*(8)*	*(9)*	*(10)*
Nitrogen Supply (N)	Mg. N Content (N_{mg})	293	15.87	12.34	0.00159	0.000000143	0 to 900	0.996	0.42
Phosphorus Supply (P)	Mg. P Content (P_{mg})	341	3.28	16.07	0.00153	0.000000347	0 to 500	0.990	0.09
Potassium Supply (K)	Mg. K Content (K_{mg})	331	7.97	16.31	0.00368	0.000000923	0 to 319	0.995	0.18
Calcium Supply (Ca)	Mg. Ca Content (Ca_{mg})	219	1.78	43.80	0.00260	0.000000208	0 to 900	0.992	0.05

[1] Calculated and experimentally determined values of N_{mg}, P_{mg}, K_{mg} and Ca_{mg} are compared in cols. 6 and 7 of Tables 10, 14, 16 and 18 respectively.

[2] External (solution) concentrations of N, P, K and Ca as parts per million.

[3] Internal (seedling) content of N, P, K and Ca as milligrams per seedling (N_{mg}, P_{mg}, K_{mg} and Ca_{mg}).

[4] These numbers are sums of harvested seedlings from all pots of each series.

[5] The relationships between external supplies of N, P, K and Ca and the internal (seedling) content of these elements, as milligrams per seedling, are expressed by Mitscherlich-type formulæ. The applicability of the Mitscherlich yield equation, with the depression constant, *k*, to these relationships is discussed in detail by Mitchell (1934, p. 53). Values calculated with the above constants are correct only for seedlings from seeds with a reserve dry weight equal to 13.77 mg.

[6] The range of concentrations (of N, P, K and Ca) over which the calculated N_{mg}, P_{mg}, K_{mg} and Ca_{mg} values agree with the observed data. In cases where the estimating formula is not applicable over the entire range, "calculated" values at the higher concentrations are interpolated from smooth curves fitted by statistical procedures to the experimental data.

[7] Except for the K series, where the data obtained at concentrations greater than 320 ppm K were too erratic to justify the use of an estimating curve, the statistical indexes were computed from observed data and curve values calculated (and/or estimated, see foot note 6) over the entire concentration range.

gen concentration of the external solution from 300 ppm, where $N_{\%}$ is equal to 3.26, up to 900 ppm, result in accumulations of nitrogen within the seedlings which become increasingly toxic, as evidenced by the effect upon seedling yield (see Fig. 12). Further increases in nitrogen supply are not reflected in internal nitrogen concentration which, as previously shown (Mitchell, *loc. cit.*), is constant over the range of from 900 to 2500 ppm. This is due to the fact that increments of nitrogen high in the toxic region (above 900 ppm) result in proportionately equal decreases in seedling yield and milligram nitrogen content, of which $N_{\%}$ is a function.

As evidenced by the statistical data summarized in Tables 20 and 21, there is an exceedingly high degree of correlation between the nitrogen concentration of the external solution and the nitrogen content of white pine seedlings, expressed as either $N_{\%}$ or as milligrams per seedling. Similar relationships have been observed for other species of *Pinus* (Aldrich-Blake, 1930; Gast, 1937).

The Relation Between Phosphorus Supply and the Phosphorus Content of Seedlings

The yields and phosphorus content, in milligrams and as percent dry weight, of white pine seedlings grown in nutrient-sand cultures of varying phosphorus concentration are shown in Fig. 13 (data from Tables 13 and 14). The two phosphorus absorption curves ($P_{\%}$ and P_{mg}), like the yield curve previously discussed, were smoothed with the aid of the Mitscherlich formula. Numerical values for the various constants are entered in Tables 20 and 21, calculated and experimentally determined values are compared in Table 14, and the results of statistical analyses are summarized in Tables 20 and 21.

As shown in Fig. 13, the milligram phosphorus content of the seedlings increases in almost direct proportion to phosphorus supply up to about 300 ppm (near the point

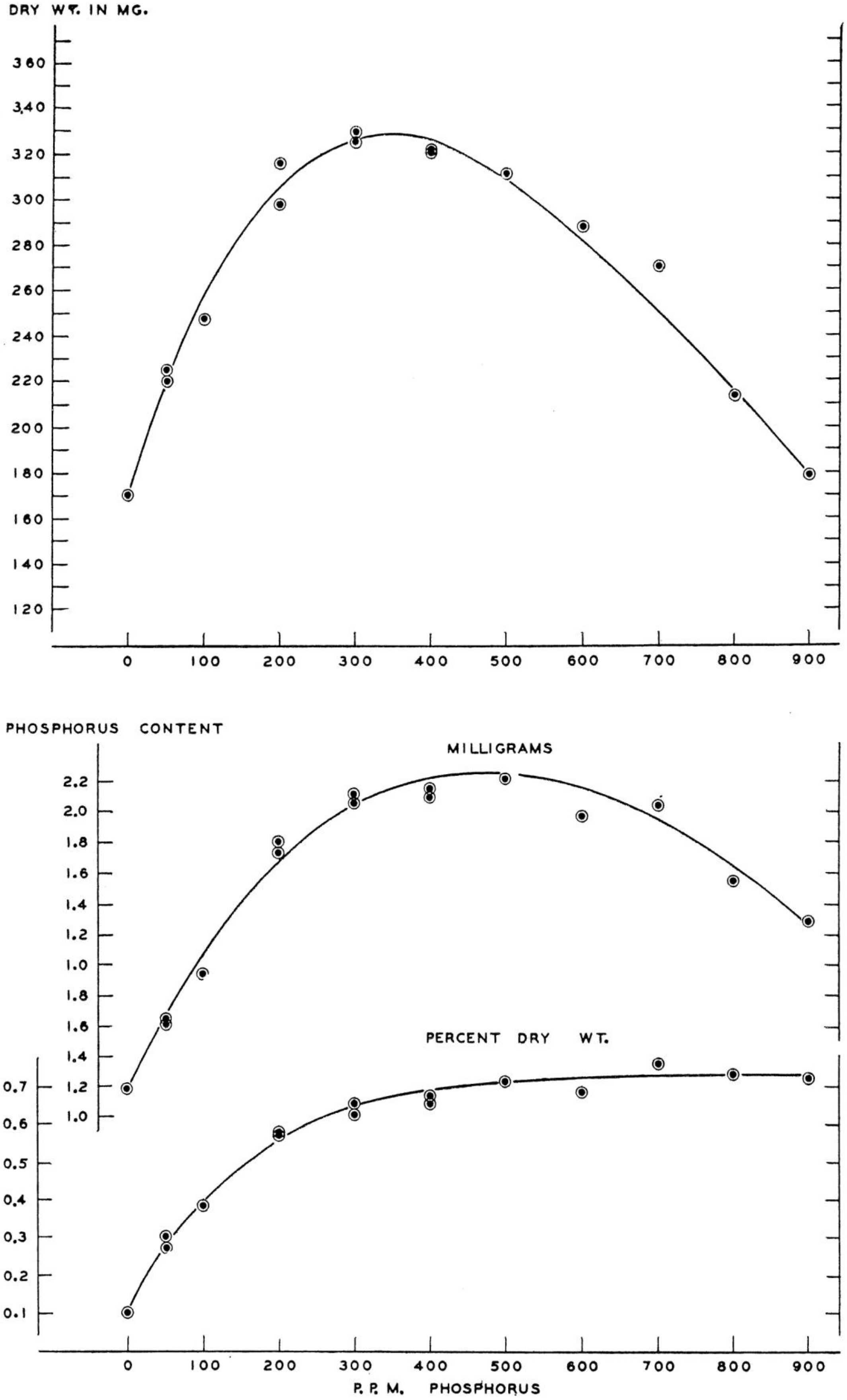

FIG. 13.—THE DRY WEIGHTS AND THE PHOSPHORUS CONTENT, AS MILLIGRAMS AND AS PERCENT, OF WHITE PINE SEEDLINGS GROWN FOR ONE SEASON IN NUTRIENT-SAND CULTURES WITH DIFFERENT PHOSPHORUS SUPPLIES.

of greatest yield), where the curve starts to flatten, a maximum is reached at about 450 ppm, and further increases in the concentration of the external solution result in decreased phosphorus intake.

The relationship between phosphorus supply and internal phosphorus concentration ($P_{\%}$) is very similar to that between nitrogen supply and $N_{\%}$. As regards the former, $P_{\%}$ equals 0.67 at 350 ppm, the supply which produced the heaviest seedlings (approximately the same as for nitrogen), and further increments of P resulted in internal phosphorus concentrations which were toxic, as evidenced by the effect upon seedling yield.

The data shown in Fig. 13 and the statistical indexes presented in Tables 20 and 21 indicate that, as with nitrogen, there is a high degree of correlation between the phosphorus concentration of the external solution and the phosphorus content of white pine seedlings, expressed either as percent dry weight or as milligrams per seedling.

The Relation Between Potassium Supply and the Potassium Content of Seedlings

The potassium content, as $K_{\%}$ and K_{mg}, and also the yields, of white pine seedlings grown in nutrient-sand cultures of varying potassium concentration are shown in Fig. 14 (data from Table 15 and 16). As with yield, the curves expressing the average relationships between potassium supply and the potassium content (as K_{mg} and $K_{\%}$) of the seedlings were calculated according to the Mitscherlich equation. Values for the different constants used in the calculations are entered in Tables 20 and 21, calculated and experimentally determined values are compared in Table 16, and statistical data are presented in Tables 20 and 21.

As with nitrogen and phosphorus, the potassium intake, expressed as milligrams per seedling, is almost

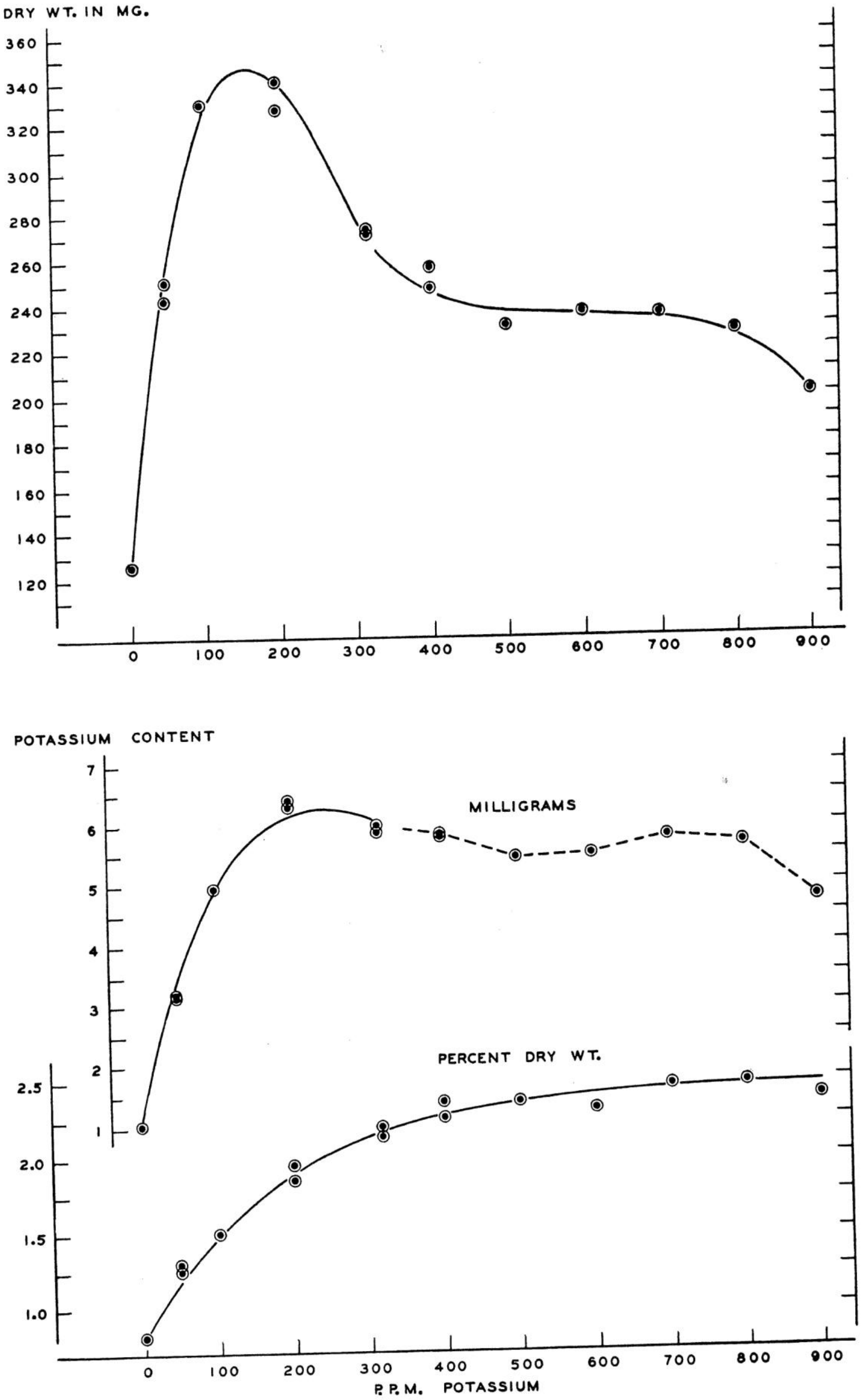

Fig. 14.—The dry weights and the potassium content, as milligrams and as percent, of white pine seedlings grown for one season in nutrient-sand cultures with different potassium supplies.

directly proportional to the potassium concentration of the nutrient solution up to the supply (approximately 150 ppm in the case of K) which produced the heaviest seedlings. With further increments of potassium the absorption curve tends to flatten, and a maximum is reached at about 250 ppm. As shown in Fig. 14, potassium intake appears to decrease with increases in potassium supply over the range of from 300 to 900 ppm. But, for this range, the data are too inconsistent to justify the use of a smooth curve to express the average trend.

According to data presented in Fig. 14, the internal potassium concentration ($K_{\%}$) is equal to about 1.72 at the supply of maximum yield. The curve expressing the average relationship between K supply and $K_{\%}$ is almost identical with those representing similar relationships between N and P supply and the internal concentrations of these elements (see Figs. 12 and 13). In each case the internal concentration of the element varied is almost linearly related to external concentration through the minimal and working ranges of supply, and further increments result in internal concentrations which are definitely toxic, as indicated by decreased yield.

The Relation Between Calcium Supply and the Calcium Content of Seedlings

The yields and chemical analysis data for seedlings grown in the calcium series are shown in Fig. 15 (data from Tables 17 and 18). It is apparent that increments in calcium supply over the range of from 0 to 900 ppm have much the same effect upon the calcium intake (as Ca_{mg}) of white pine seedlings as have similar increases of N, P and K supply upon the absorption of these elements (see Figs. 12, 13 and 14). The curve of average relationship for calcium intake (Fig. 15) was similarly calculated (constants given in Table 20).

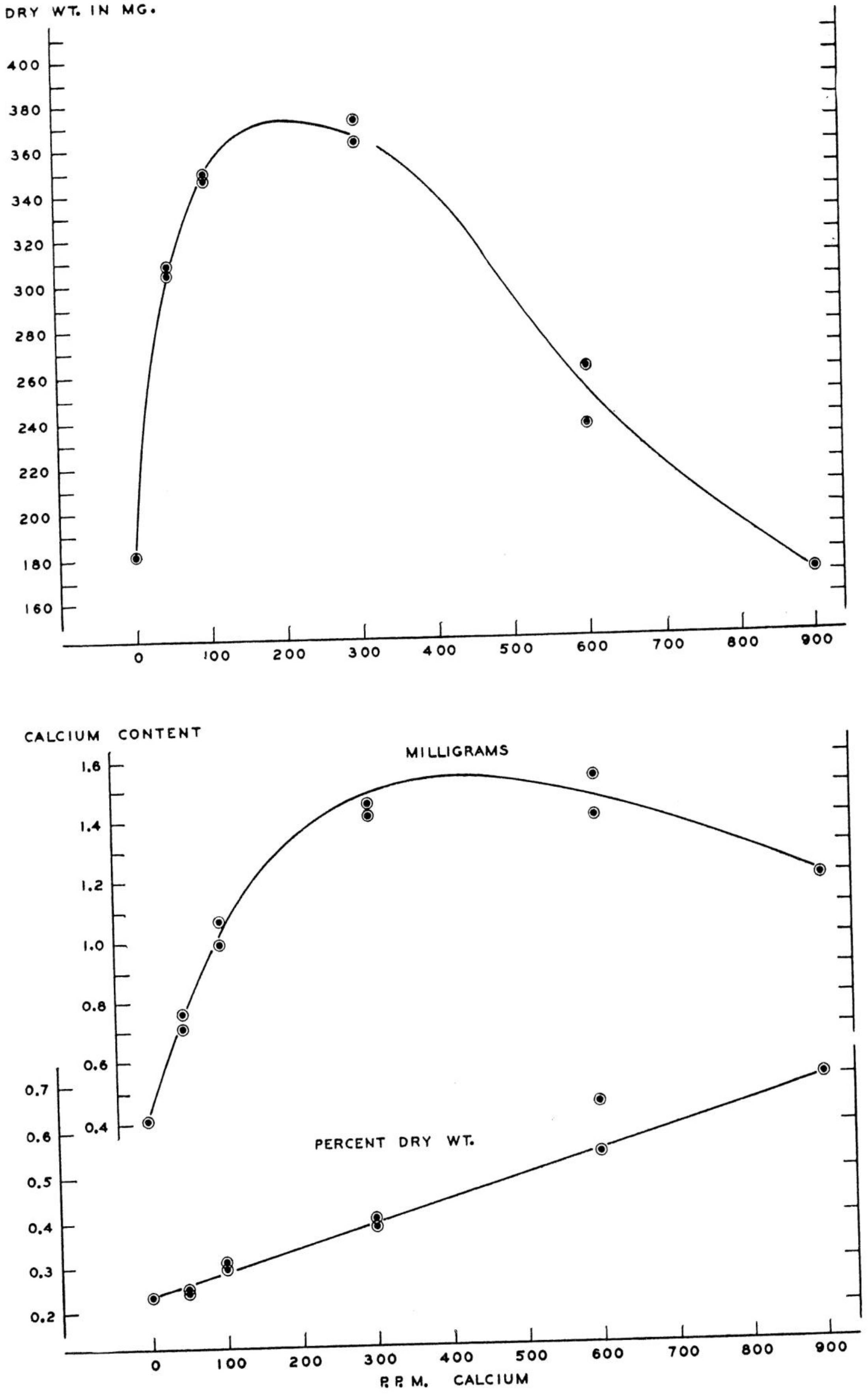

FIG. 15.—THE DRY WEIGHTS AND THE CALCIUM CONTENT, AS MILLIGRAMS AND AS PERCENT, OF WHITE PINE SEEDLINGS GROWN FOR ONE SEASON IN NUTRIENT-SAND CULTURES WITH DIFFERENT CALCIUM SUPPLIES.

As shown in Fig. 15, the effect of increasing calcium supply upon internal calcium concentration ($Ca_{\%}$) is quite different from that of N, P or K supply upon the percentage composition of these elements in white pine seedlings. Whereas the average trend of the former relationship is a linear increase over the entire range of external supplies, with $Ca_{\%}$ equal to about 0.33 at the supply of greatest yield (see Fig. 15), the latter three relationships, as shown in Figs. 12, 13 and 14, take the form of curves which are relatively steep through the minimal and working ranges of supply, but which tend to flatten thereafter. Since percentage composition is a function of yield and the absolute amount of the element absorbed, it appears that calcium supplies through the tensional and toxic ranges tend to retard absorption less and depress growth more than do equal increments of N, P, or K. However this may be, the statistical data summarized in Table 20 indicate that the regression line plotted in Fig. 15 is an entirely satisfactory expression of the average relationship between calcium supply and the calcium concentration of the seedlings.

The Nitrogen, Phosphorus, Potassium and Calcium Content of the Shoots of White Pine Seedlings

Because of the high degree of correlation between mineral nutrient supply and the chemical composition of coniferous seedlings, it has been suggested that the results of plant analysis might provide a more reliable index to the nutrient needs of seedlings growing in soils of unknown fertility than any of the usual methods of soil analysis. In a previous study a consistent difference was observed between the nitrogen content of seedlings supplied various amounts of this element and the N content of the needles (Mitchell, *loc. cit.,* Table 23). In actual practice it would be much simpler to sample only the shoots—that is, the above-ground portion of the seedlings. Plants in nurseries are less disturbed by taking samples from the shoots only; from large trees in plantations a further desirable reduction in material taken may be made by sampling only the foliage. Hence, for the material of the present experiment, separate analyses were made to see if the chemical composition of the shoots was as well correlated with nutrient supply as that of the entire plants. The results of these analyses are compared with data on whole plants from each of the nutrient-culture series in Table 22 and Figs. 16 A, 16 B, 17 A and 17 B (basic data from cols. 7 and 9, Tables 9, 13, 15 and 17).

TABLE 22

COMPARISON OF THE INTERNAL NUTRIENT CONCENTRATION OF WHOLE PLANTS AND THEIR SHOOTS AT THE POINT OF MAXIMUM YIELD [1]

Nutrient Element	*Whole Plant*	*Shoot*
Nitrogen	3.26%	3.51%
Phosphorus	0.67%	0.62%
Potassium	1.72%	1.59%
Calcium	0.33%	0.34%

[1] Curves of average relationship are shown in Figs. 16 A, 16 B, 17 A and 17 B.

The data presented in Fig. 16 A show that there is a definite and relatively consistent relationship between the nitrogen concentration of seedlings and their shoots through the minimal, working and tensional ranges of nitrogen supply. At about 650 ppm N, high in the toxic region, the two curves intersect. But the relationships at the higher supplies, although of interest, are of little moment from the more practical standpoint. It is the range of supplies up to around 200 ppm that are equivalent, in effect, to those found in nature. Through this range $N_{\%}$ of the shoots is significantly and consistently higher than that of the entire plants, and is also highly

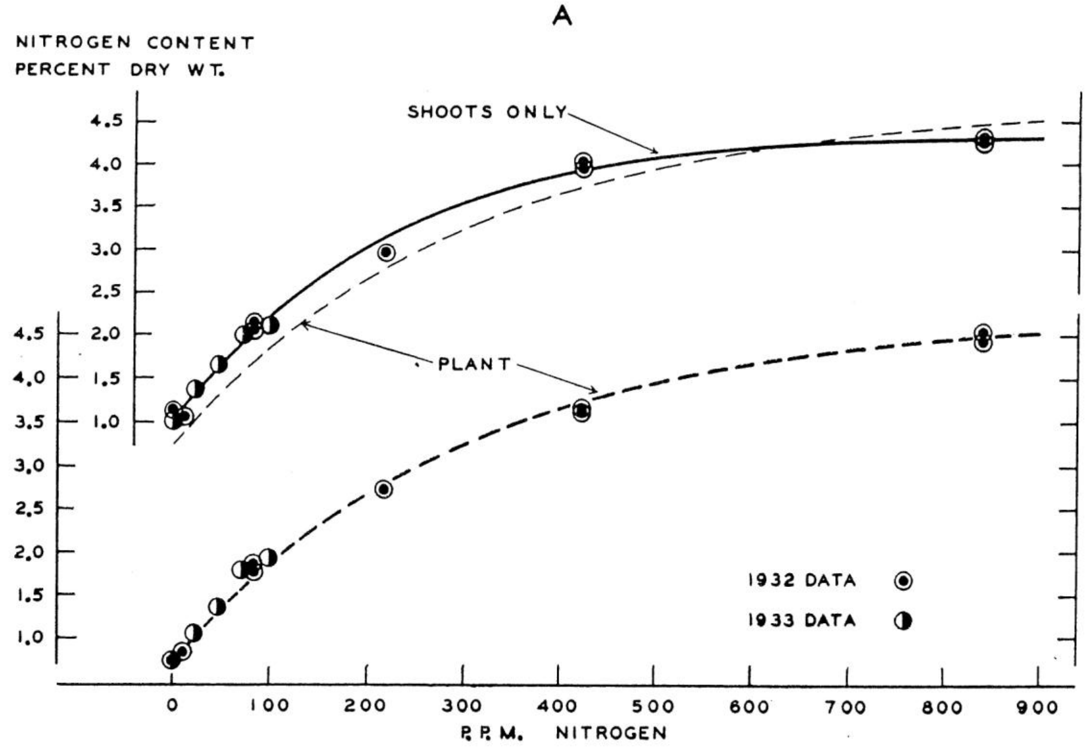

FIG. 16-A.—COMPARISON OF THE PERCENT NITROGEN CONTENT OF WHITE PINE SEEDLINGS (ENTIRE PLANT), AND SHOOTS THEREOF, GROWN FOR ONE SEASON IN NUTRIENT-SAND CULTURES OF VARIED NITROGEN CONCENTRATION.

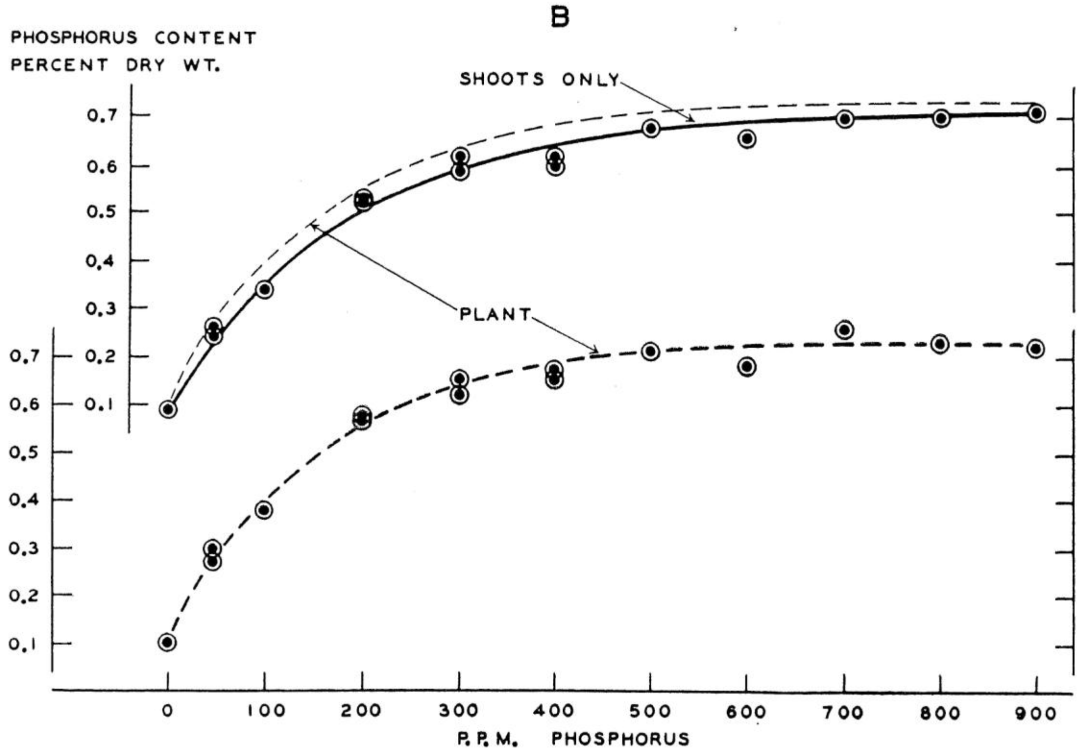

FIG. 16-B.—COMPARISON OF THE PERCENT PHOSPHORUS CONTENT OF WHITE PINE SEEDLINGS (ENTIRE PLANT), AND SHOOTS THEREOF, GROWN FOR ONE SEASON IN NUTRIENT-SAND CULTURES OF VARIED PHOSPHORUS CONCENTRATION.

correlated with nitrogen supply. The correlation indexes and standard errors of estimate for the two relationships are so nearly identical that only those based upon the analysis of entire plants are entered in Table 20.

The fact that the nitrogen concentration of the shoots is significantly higher than that of the entire plants over the greater part of the range of supplies agrees with previous observations regarding pine seedlings (Mitchell, 1934), and is also true of many agricultural crop plants (Miller, 1931). The prevalence of nitrogen in the shoots, and especially the needles, is in keeping with available data regarding the physiological rôle of this element.

As shown in Fig. 16 B, the relationship between the phosphorus content of white pine seedlings, and the shoots thereof, is definite and consistent over the entire range of phosphorus supplies studied. The same is true of potassium (see Fig. 17 A). The correlations between phosphorus and potassium supply and the $P_{\%}$ and $K_{\%}$ of the shoots are equally as good as those between P and K supply and the concentration of these elements in the plants as a whole. Unlike nitrogen, the concentration of P and K in the shoots is lower than in the entire seedlings (Table 22). This suggests that both P and K, which apparently exert a greater influence upon root than shoot development (see Figs. 11 B and 11 C), are present in higher concentrations in the roots than in the shoots. This is especially true since in no case do the roots make up more than 45% of the total seedling weights (see col. 6, Tables 13 and 15).

The comparative calcium analysis data are shown in Fig. 17 B. It is apparent that there is little if any significant difference between the calcium concentration of the seedlings as a whole, and their shoots. And both series of data are equally well correlated with calcium supply. The close agreement between the data presented

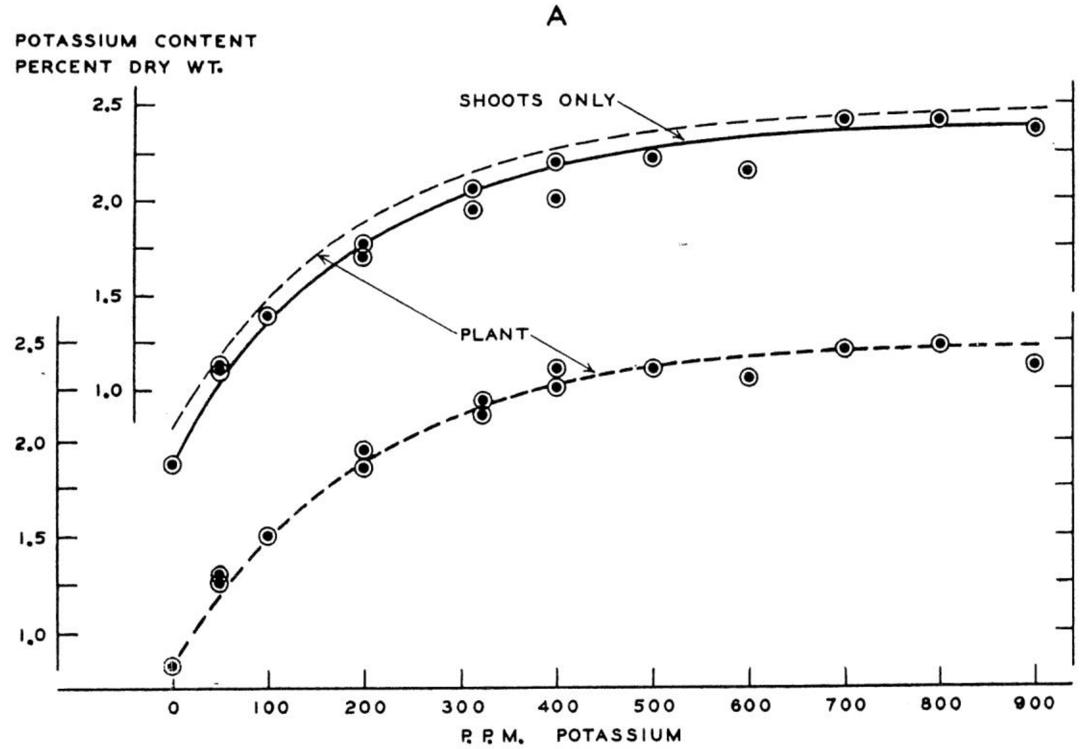

FIG. 17-A.—COMPARISON OF THE PERCENT POTASSIUM CONTENT OF WHITE PINE SEEDLINGS (ENTIRE PLANT), AND SHOOTS THEREOF, GROWN FOR ONE SEASON IN NUTRIENT-SAND CULTURES OF VARIED POTASSIUM CONCENTRATION.

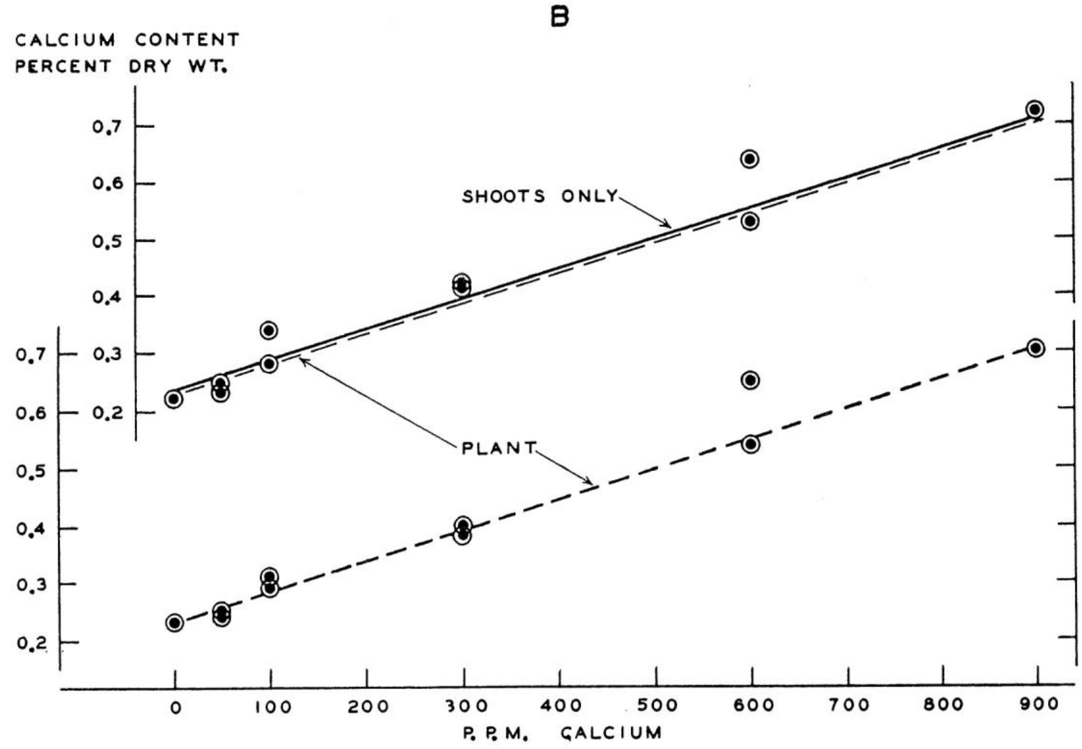

FIG. 17-B.—COMPARISON OF THE PERCENT CALCIUM CONTENT OF WHITE PINE SEEDLINGS (ENTIRE PLANT), AND SHOOTS THEREOF, GROWN FOR ONE SEASON IN NUTRIENT-SAND CULTURES OF VARIED CALCIUM CONCENTRATION.

in Fig. 17 B and the relatively high root/shoot ratios of seedlings grown in calcium supplies up to 600 ppm (see Fig. 11 D) indicate that the roots of these seedlings have a slightly higher calcium concentration than the shoots. At higher supplies the reverse is true, largely because of significantly lower ratios of root to shoot.

The Relationships Between Internal Concentration of Nitrogen, Phosphorus, Potassium and Calcium and Seedling Yield

Thus far in the discussion it has been shown that there is a high degree of correlation between external supplies of nitrogen, phosphorus, potassium and calcium and seedling yield; also that the amounts of these nutrient elements absorbed by the seedlings—expressed either as percentages or as milligrams—are equally well correlated with external supplies. Although seedling yield is proportional to the concentration of these elements in the nutrient medium, the factor which apparently governs nutrient intake, it is the nutrient elements actually absorbed which enter into the physiological processes of the plants. Therefore, assuming that all or at least a relatively constant proportion of the essential elements absorbed by the plants are actually utilized, there should be a correlation between the internal concentration (of N, P, K and Ca) and seedling yield—at least through certain critical ranges.

In a previous experiment (Mitchell, 1934, Fig. 5) such a relationship was found between internal nitrogen concentration (as % dry weight) and the yields of Scots and white pine seedlings. Data from the four nutrient-culture series of the present experiment were examined for similar relationships. In each case seedling yields were reclassified according to the internal rather than the external concentration of the element varied (basic data from Tables 9, 13, 15 and 17). The resultant data

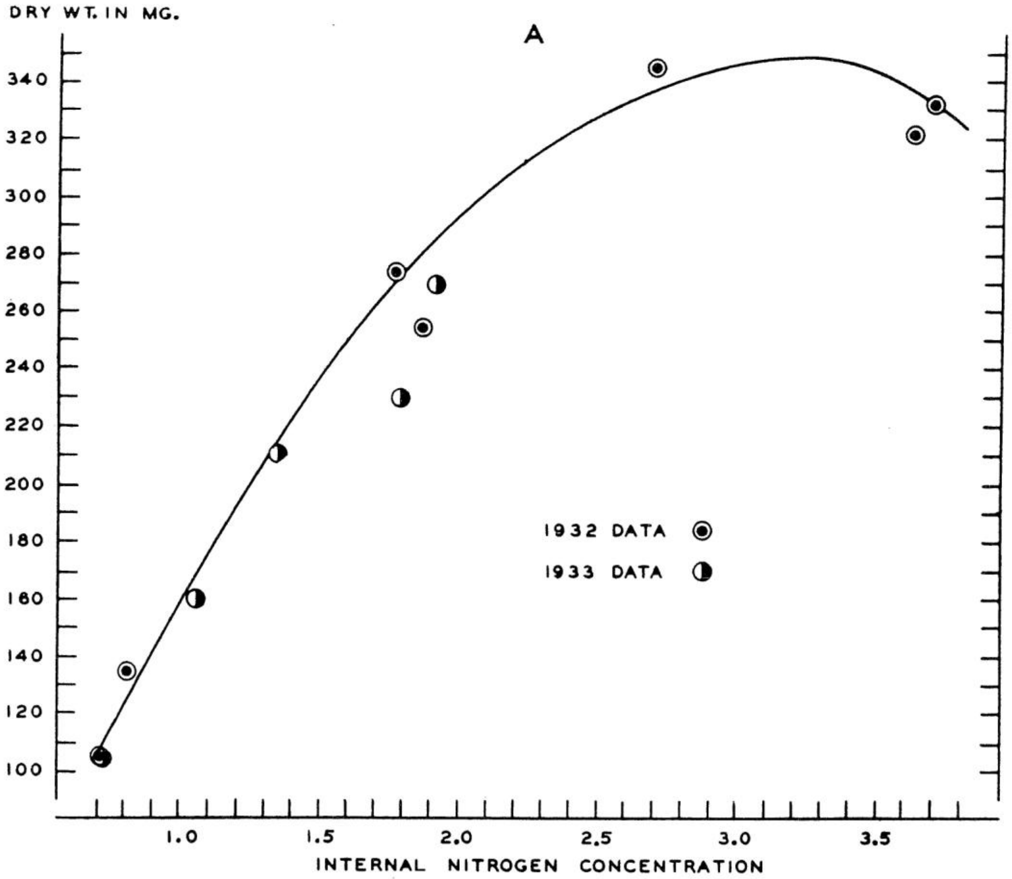

FIG. 18-A.—THE RELATION BETWEEN INTERNAL (SEEDLING) NITROGEN CONCENTRATION (N%) AND THE YIELD OF WHITE PINE SEEDLINGS GROWN FOR ONE SEASON IN NUTRIENT-SAND CULTURES. INTERNAL NITROGEN CONCENTRATION AND YIELD ON ARITHMETIC: ARITHMETIC AXES.

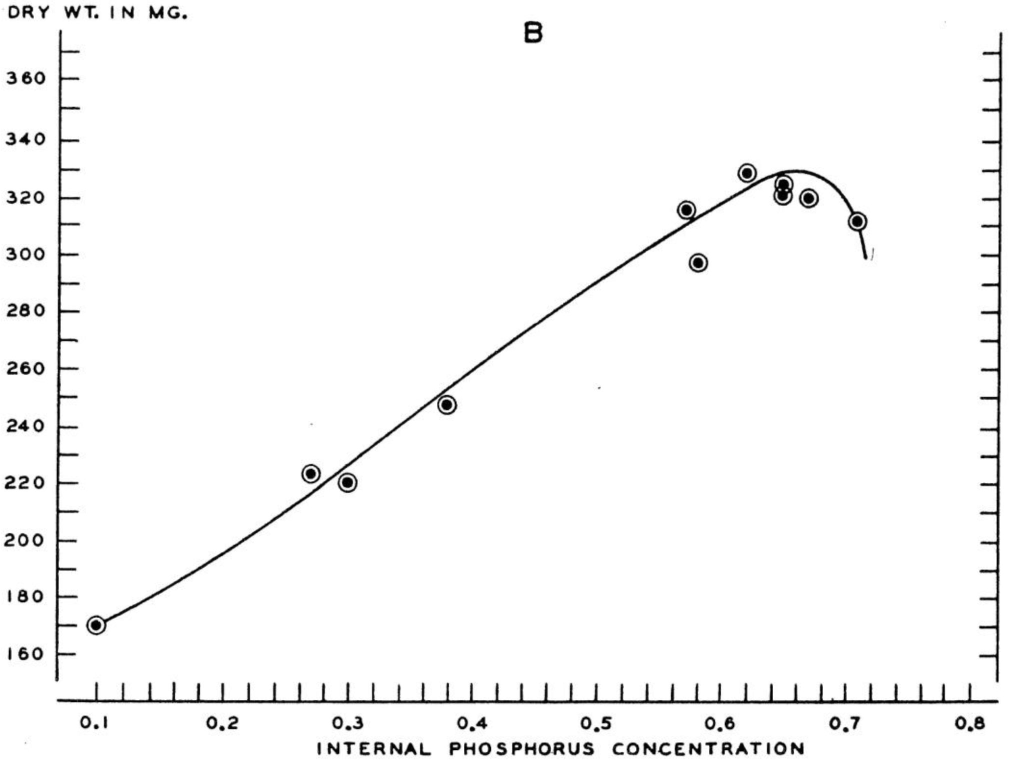

FIG. 18-B.—THE RELATION BETWEEN INTERNAL (SEEDLING) PHOSPHORUS CONCENTRATION (P%) AND THE YIELD OF WHITE PINE SEEDLINGS GROWN FOR ONE SEASON IN NUTRIENT-SAND CULTURES. INTERNAL PHOSPHORUS CONCENTRATION AND YIELD ON ARITHMETIC: ARITHMETIC AXES.

are plotted in Figs. 18 A, 18 B, 19 A, 19 B, 20 A and 20 B. As shown in Figs. 18 A and 18 B, and as evidenced by the statistical data summarized in Table 23, seedling yields are highly correlated with both internal nitrogen and phosphorus concentrations. Similar relationships were observed between internal potassium and calcium concentrations and seedling yield (Figs. 19 A and 19 B). But, as the statistical data presented in Table 23 suggest, in the latter two cases the degree of association between the two variables is not so clear-cut, and predictions based upon the calculated average trends are less satisfactory, than for the nitrogen and phosphorus relationships. This is undoubtedly due to the relative scarcity of data over what might be termed the minimal and working ranges of internal K and Ca concentrations. Since few if any precise data were available regarding the K and Ca requirements of pine seedlings—or any other tree species for that matter—at the time these experiments were planned, the nutrient treatments could not be

TABLE 23

STATISTICAL ANALYSIS OF RELATIONSHIPS BETWEEN INTERNAL (SEEDLING) CONCENTRATIONS OF N, P, K AND CA AND SEEDLING YIELD[1]

Independent Variable	*Dependent Variable*	*Correlation Index*[2]	*Standard Error of Estimate*[2]
(1)	*(2)*	*(3)*	*(4)*
Internal N Concentration ($N_{\%}$)	Seedling Yield (Y) in Mg.	0.978	17.21
Internal P Concentration ($P_{\%}$)	Seedling Yield (Y) in Mg.	0.991	6.89
Internal K Concentration ($K_{\%}$)	Seedling Yield (Y) in Mg.	0.969	18.51
Internal Ca Concentration ($Ca_{\%}$)	Seedling Yield (Y) in Mg.	0.877	29.07

[1] Curves expressing the average relationships are shown in Figs. 18 A, 18 B, 19 A, 19 B, 20 A and 20 B. All were calculated with the Mitscherlich yield equation. Constants were derived from basic data (Tables 10, 14, 16 and 18) reclassified with internal rather than external concentrations (of N, P, K and Ca) as independent variables, and seedling yields as dependent variables.

[2] These indexes were computed from observed and calculated yields over the entire range of internal concentrations (of N, P, K and Ca) shown in Figs. 18 A, 18 B, 19 A, 19 B, 20 A and 20 B.

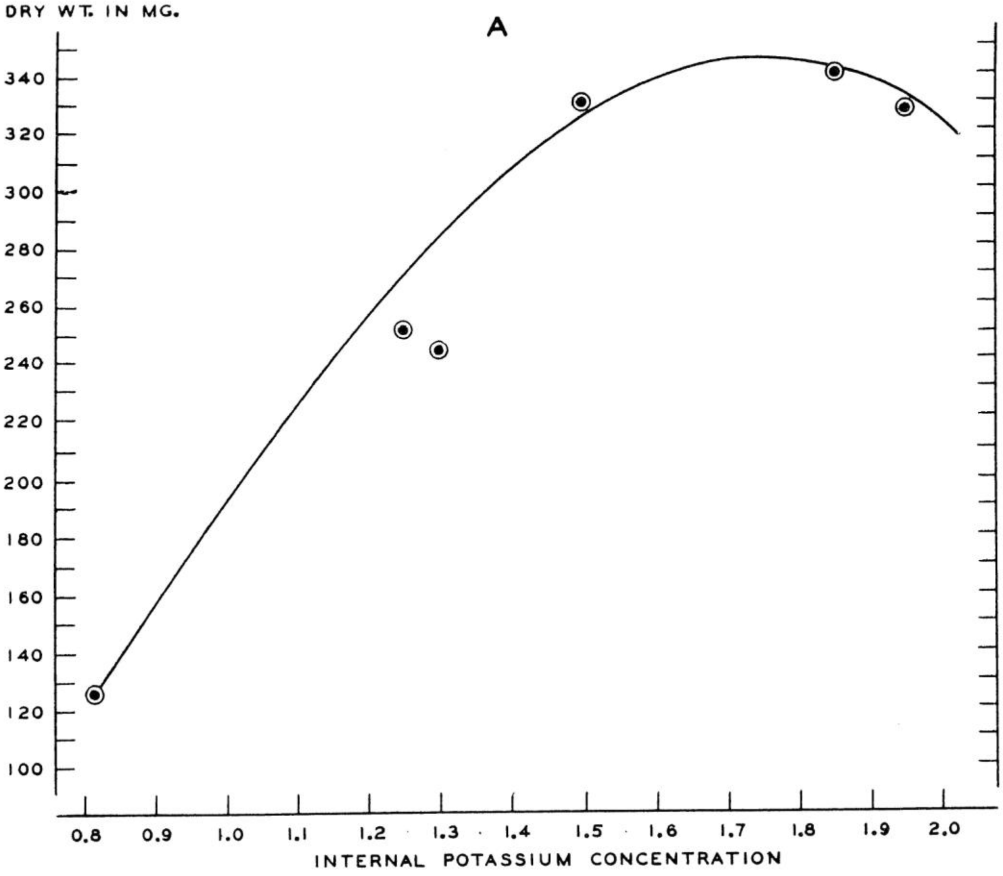

FIG. 19-A.—THE RELATION BETWEEN INTERNAL (SEEDLING) POTASSIUM CONCENTRATION (K%) AND THE YIELD OF WHITE PINE SEEDLINGS GROWN FOR ONE SEASON IN NUTRIENT-SAND CULTURES. INTERNAL POTASSIUM CONCENTRATION AND YIELD ON ARITHMETIC: ARITHMETIC AXES.

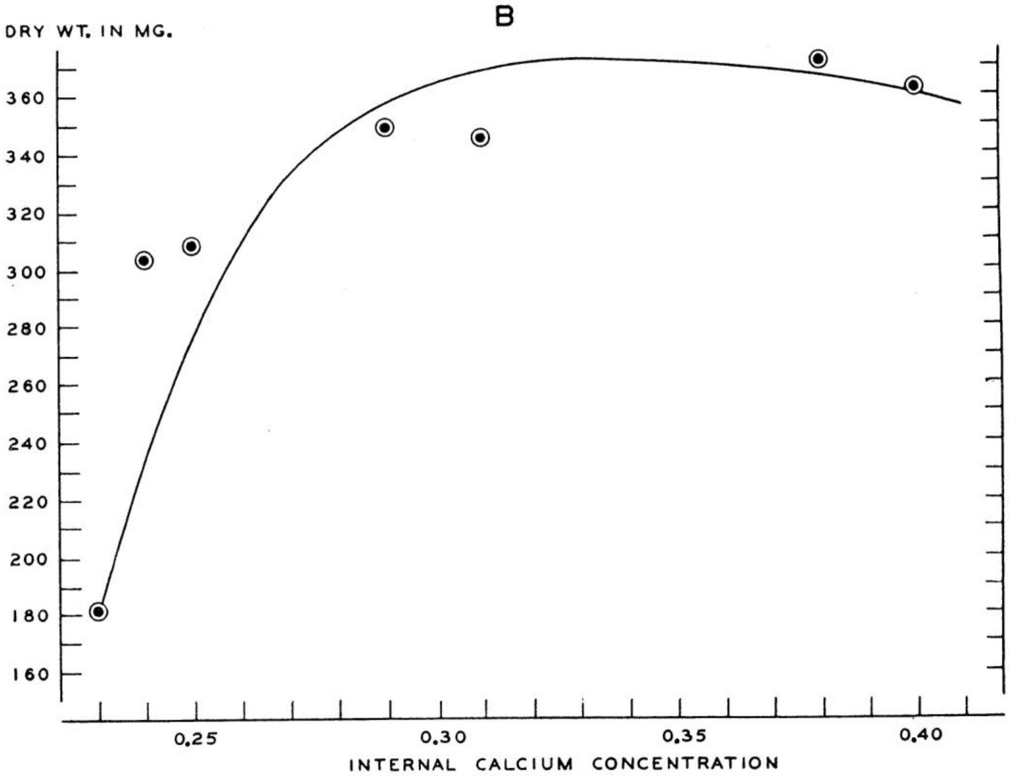

FIG. 19-B.—THE RELATION BETWEEN INTERNAL (SEEDLING) CALCIUM CONCENTRATION (Ca%) AND THE YIELD OF WHITE PINE SEEDLINGS GROWN FOR ONE SEASON IN NUTRIENT-SAND CULTURES. INTERNAL CALCIUM CONCENTRATION AND YIELD ON ARITHMETIC: ARITHMETIC AXES.

grouped with accuracy in the critical ranges of supply as, by reason of preliminary experiments, was possible in the nitrogen series. The more satisfactory spacing of treatments in the phosphorus series was due largely to good fortune since there was little information which could be used in planning the experiment.

When considered alone, the association between seedling yield and the internal concentration of either potassium or calcium, as shown in Fig. 19 A and 19 B, may be of questionable significance because the experimental data are relatively meagre. But since these two relationships are so similar in essential detail to those based on the more numerous nitrogen and phosphorus series data, there can be little doubt regarding their existence.

In his discussion of this subject, Gast (1937) pointed out that for white pine seedlings there is a linear relationship between the arithmetic values of yield plotted over the logarithmic values of internal nitrogen concentration. The 1932 and 1933 nitrogen series data are shown plotted in this way in Fig. 20 A. Some significance may be attached to the fact that this relationship is almost identical with that between seedling yield and the cumulative solar radiation (see Gast, *loc. cit.,* Figs. 14 and 15). The calcium and potassium series data, when plotted in this way—*i.e.,* arithmetic values of yield over logarithmic values of internal concentration—suggest similar (linear) relationships. These regression lines are not reproduced here, since they are based on too few observations in the critical ranges of internal K and Ca concentration. The phosphorus series data, similarly plotted, are shown in Fig. 20 B. It is evident that this relationship does not take the form of a linear proportion, at least not over the entire range of internal phosphorus concentrations. A comparison of the two relationships (Figs. 20 A and 20 B) suggests that increases in internal phosphorus concentration through what might be termed the working region have less ef-

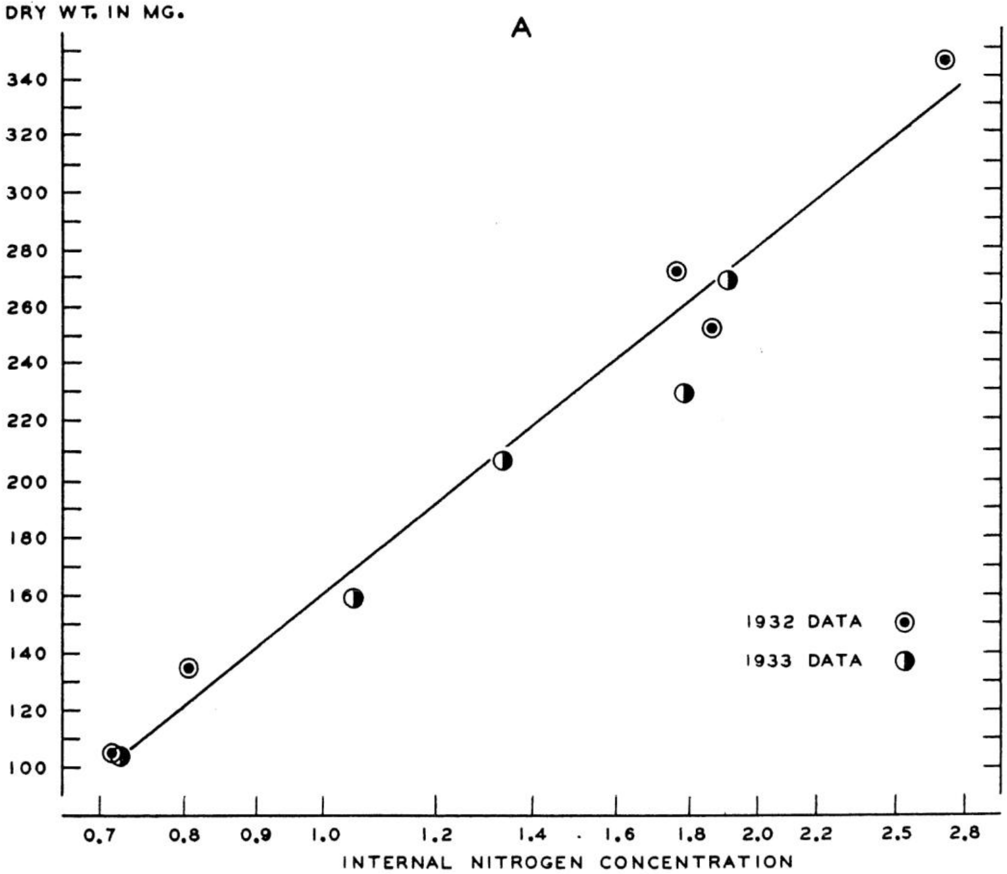

Fig. 20-A.—THE RELATION BETWEEN INTERNAL (SEEDLING) NITROGEN CONCENTRATION (N%) AND THE YIELD OF WHITE PINE SEEDLINGS GROWN FOR ONE SEASON IN NUTRIENT-SAND CULTURES. INTERNAL NITROGEN CONCENTRATION ON LOGARITHMIC AND YIELD ON ARITHMETIC AXES.

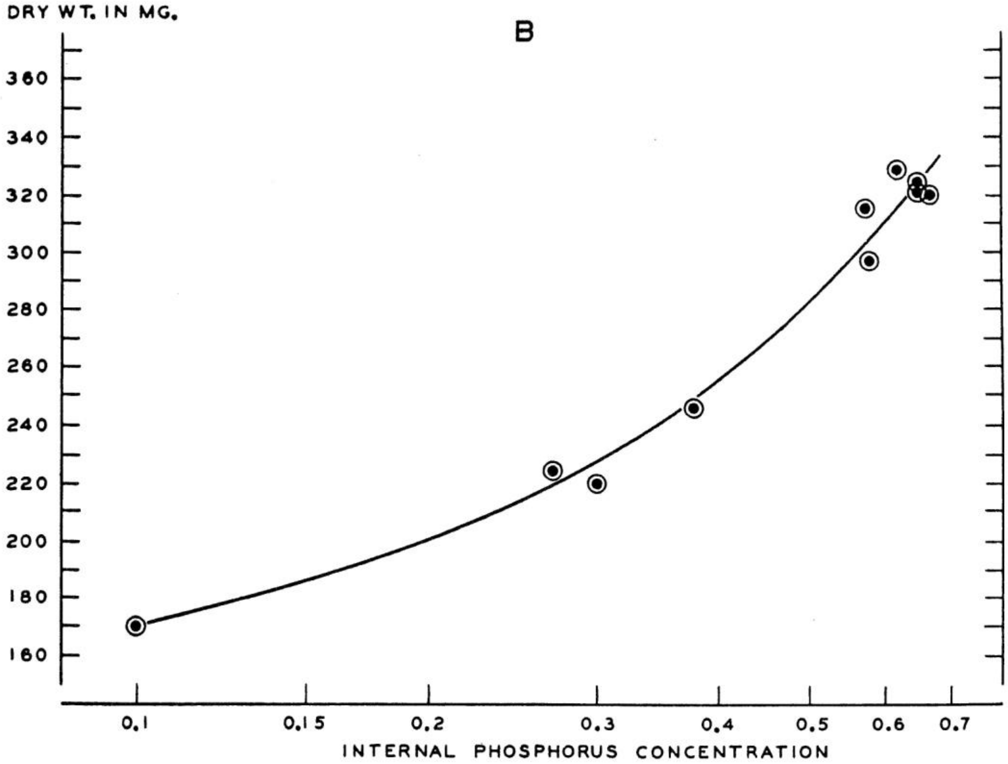

Fig. 20-B.—THE RELATION BETWEEN INTERNAL (SEEDLING) PHOSPHORUS CONCENTRATION (P%) AND THE YIELD OF WHITE PINE SEEDLINGS GROWN FOR ONE SEASON IN NUTRIENT-SAND CULTURES. INTERNAL PHOSPHORUS CONCENTRATION ON LOGARITHMIC AND YIELD ON ARITHMETIC AXES.

fect upon seedling yield than have equal increments in internal nitrogen concentration.

To facilitate further discussion, the internal concentrations will be separated, upon the basis of yield response, into regions corresponding almost exactly to those into which the external supplies (of N, P, K and Ca) were divided. Thus, as regards nitrogen (see Fig. 18 A), the $N_{\%}$ range of from 0.70 to 1.33, where nitrogen is definitely a limiting factor, may be termed the region of minima. Internal concentrations from 1.33 and increasing on up to 2.70, which are equivalent to those of seedlings grown in highly fertile natural soils, can be called the working region. The range from 2.70 to 3.50, through which increments in internal N concentration have little or no effect upon seedling yield, may be termed the region of tension, and greater concentrations, which tend to retard growth, the toxic range. The internal concentration ranges of phosphorus, potassium and calcium may be similarly divided (see Table 24).

TABLE 24

INTERNAL CONCENTRATIONS OF N, P, K AND Ca DIVIDED INTO REGIONS ON THE BASIS OF EFFECT UPON SEEDLING YIELD [1]

Element	*Region of Minima*	*Working Region*	*Optimum Concentration (Calculated)*	*Region of Tension*	*Toxic Region*
Nitrogen	0.70-1.33	1.33-2.70	3.26	2.70-3.50	3.50 +
Phosphorus	0.10-0.28	0.28-0.56	0.67	0.56-0.69	0.69 +
Potassium	0.82-1.02	1.02-1.49	1.72	1.49-1.89	1.89 +
Calcium	0.23-0.24	0.24-0.28	0.33	0.28-0.41	0.41 +

[1] Curves of average relationship between internal concentrations of N, P, K and Ca and seedling yield are shown in Figs. 18 A, 18 B, 19 A and 19 B respectively.

As shown in Figs. 18, 19 and 20, there is, for white pine, and expressed in terms of effect upon yield, an optimum or "critical" internal concentration for each of the nutrient elements studied. For nitrogen the absolute optimum, based upon the calculated average relationship between the two variables (see Fig. 18 A), is 3.26%. However, it will be observed that increases in internal N concentration over the range of from 2.5 to 3.26 have little effect upon yield. Therefore, it is this range rather than any specific point thereof that is important. Greater internal concentrations, which are often referred to as ''luxury consumption,'' become increasingly toxic, as evidenced by their effect upon growth. At smaller internal N concentrations, which have been divided into the region of minima and the working region, there is a definite poverty adjustment. And through the entire range where nitrogen is deficient and a limiting factor, growth is almost directly proportional to the internal nitrogen concentration, which is a function of the external supply. As shown in Figs. 18 B, 19 A and 19 B, similar relationships were observed between the internal concentrations of P, K and Ca and seedling yield. Thus, for phosphorus the optimum internal concentration falls in the range of from 0.56 to 0.67%; that for potassium in the range of from 1.50 to 1.72%; and for calcium in the range of from 0.28 to 0.33%. In each case the latter value is the absolute (calculated) optimum.

The correlation between internal nutrient concentration and the yield of white pine seedlings, as shown in Figs. 18, 19 and 20, is also true of other tree species and of various field and vegetable crop plants (Mitchell, 1934, 1936; Gast, 1937; Chandler, 1936a, 1936b; Chapman, 1933, 1935; Macy, 1936; Thomas, 1937 and literature cited). With crop plants, however, the relationships are frequently not so clear-cut as with trees. This is due to the fact that the growth response of trees, which is largely vegetative, is seldom affected by withdrawals of nutrients, such as are required in the more complicated fruiting metabolism of crop plants (see Mitchell, 1934, p. 44).

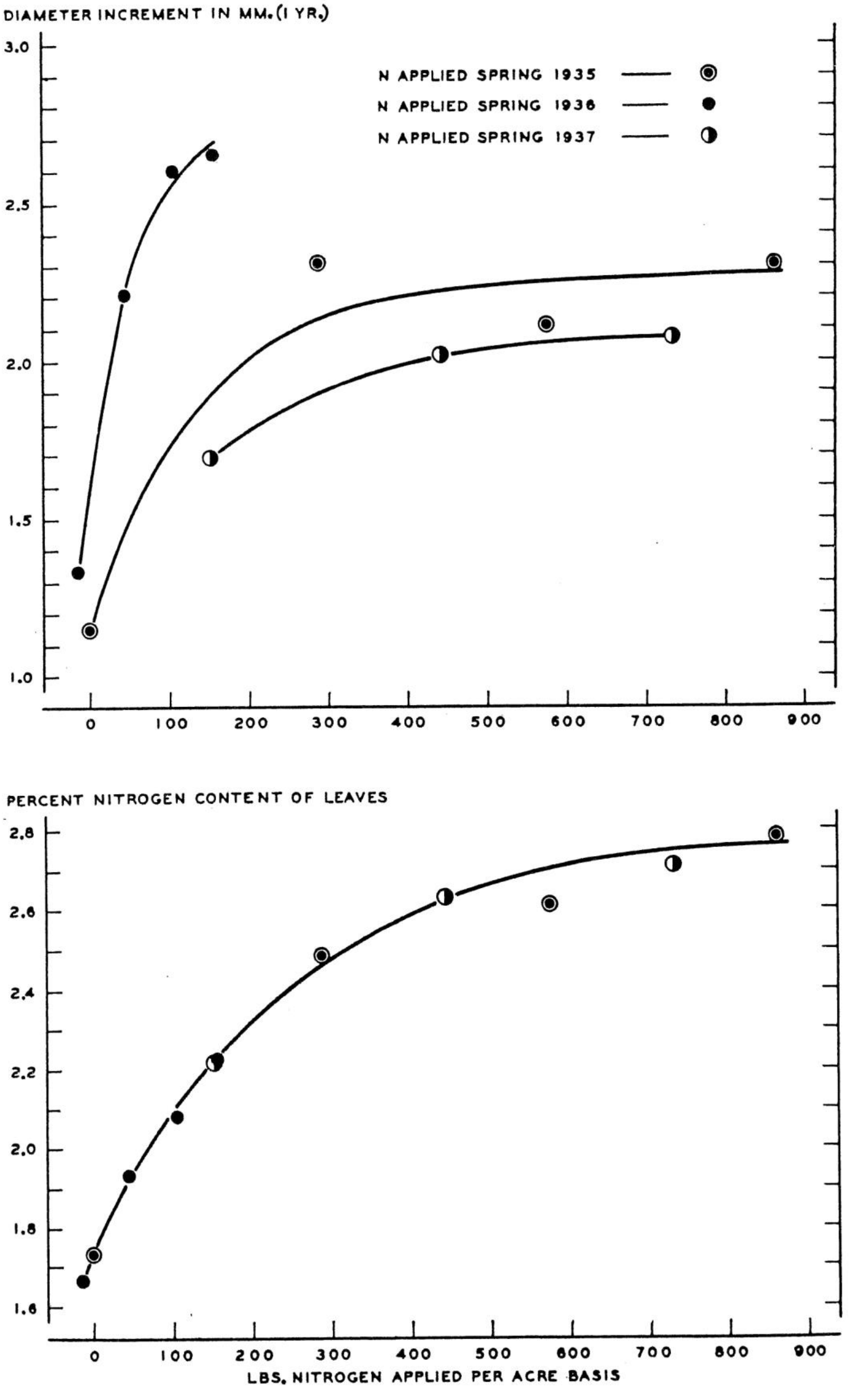

FIG. 21.—THE RELATIONSHIPS BETWEEN THE NITROGEN CONTENT OF THE LEAVES AND THE ANNUAL DIAMETER INCREMENT OF 40- TO 50-YEAR-OLD RED OAKS (*QUERCUS BOREALIS* MICH.) GROWING ON PLOTS SUPPLIED VARYING AMOUNTS OF NITROGEN.

The data plotted in the above figure were obtained from three series of plots, established and fertilized in different years, as indicated in the legend. Growth data are for the growing season following the year fertilizer was applied. The responses of the three series to increasing nitrogen supply are not identical in magnitude, largely because of significant differences in rainfall during the 1936, '37 and '38 growing seasons. But in each case maximum growth (for the series) is approached at essentially the same internal nitrogen concentration. The nitrogen content data are from leaves sampled in the early fall of the year fertilizer was applied. Internal nitrogen concentration apparently is unaffected by variations in rainfall. The mean values shown for the various plots are based upon *individual* measurements and chemical analyses of samples from all red

A survey of the literature reveals a striking similarity in the optimum concentrations (of N, P, K and Ca) of closely related plants. Available data indicate that this is particularly true of forest trees, although the majority of published information on this subject is concerned with crop plants. As regards trees, the optimum internal nutrient concentration appears to be essentially the same for nutrient-sand-culture-grown white pine seedlings—or the needles thereof—as for the leaves of nearly mature deciduous species growing in a natural habitat. Compare, for example, the relationship between the internal nitrogen concentration and the yield of white pine seedlings (Figs. 12 and 18 A) with that discovered in corollary studies between the nitrogen content (concentration) of the leaves and the growth of red oaks, as shown in Fig. 21. The latter data were obtained from 40-to-50-year-old red oaks growing on a group of eleven plots, varying in size from one-fourth to two acres, established on the Black Rock Forest in comparable stands of even-aged mixed hardwoods. One plot, of two acres, served as a control; the others received varying amounts of nitrogen, applied in the early spring as an equal mixture (by weight) of nitrate of soda and sulfate of ammonia. Leaf sampling was standardized according to methods previously discussed (Mitchell, 1936).

It will be observed that the agreement between the white pine and red oak data is almost perfect. Red oaks approximated maximum growth (for each series) on the plots supplied sufficient nitrogen so that the leaves thereof had a nitrogen content of around 2.5%—the same internal concentration at which culture-grown white pine seedlings approach maximum yield (Fig. 18 A). In this connection it is significant that the nitrogen content of the leaves of all other species—chestnut oak, white oak, sugar maple, red maple, pignut hickory, dogwood, yellow poplar and white ash—growing on the nitrogen-fertilized plots where diameter increment approached

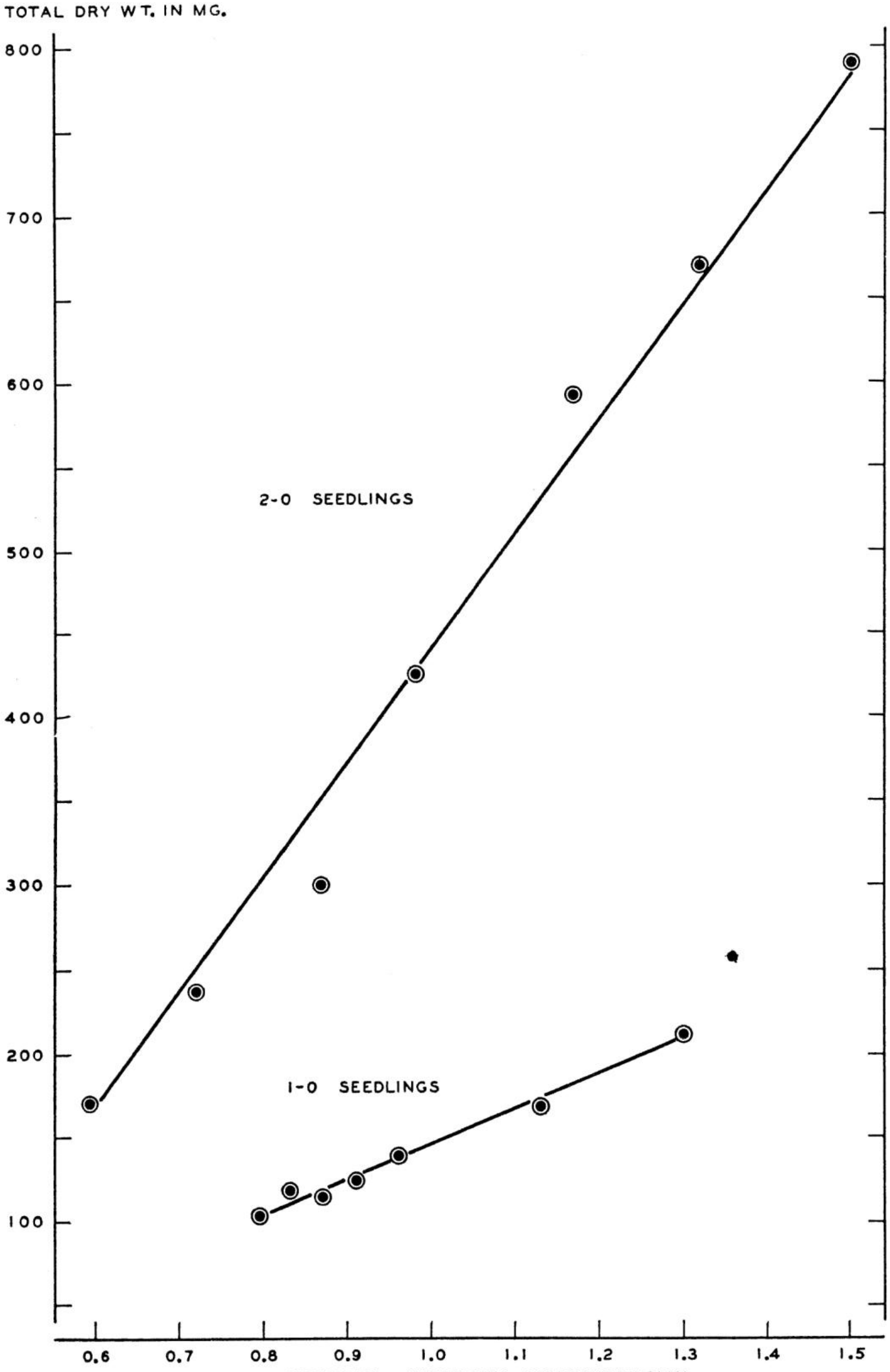

FIG. 22.—THE RELATIONSHIPS BETWEEN THE INTERNAL NITROGEN CONCENTRATION AND THE DRY WEIGHT INCREASE OF NURSERY-GROWN 1- AND 2-YEAR-OLD WHITE PINE SEEDLINGS SUPPLIED VARYING AMOUNTS OF NITROGEN.

Data from an inorganic nitrogen series of the M-'35 and '36 nursery experiments. All seven beds were seeded in the spring of 1935, sampled in the fall of the same year and harvested in the fall of 1936. The control plot (smallest seedlings) received no nitrogen. The others were supplied varying amounts of this element in solution, and in four applications during each growing season. Other essential elements were supplied to all beds in constant and approximately optimal amounts.

maximum, also fell within the range of from 2.5 to 3.0%.[1]

Similar relationships were found between the internal nutrient concentration and the growth of yellow poplar, red oak, red pine, white pine, red spruce, sugar maple, white ash, black walnut and basswood seedlings grown in variously fertilized seed beds of the Black Rock Forest experimental nursery (Mitchell, 1937 and unpublished data). This is illustrated for white pine by the data presented in Fig. 22. These data were obtained from samples taken at the end of the first and second growing seasons from variously fertilized but otherwise similar seed beds. Although it is evident (Fig. 22) that none of the seedlings received nitrogen in amounts sufficient to produce the optimum internal nitrogen concentration, the relationship between this variable and yield over the range actually covered is essentially similar to that true of the culture-grown seedlings (Fig. 18 A). Significantly greater amounts of nitrogen were applied to other series of the nursery experiment, so that more nearly optimal internal nitrogen concentrations were attained during the initial growing season. However, the data in Fig. 22 (*cf.* Table 27) are presented here for comparison because they are complete for two successive years. And it is apparent that the more nearly these seedlings approach, in internal nitrogen concentration, the range found optimum in the cultural studies, the greater the yield.

ADJUSTMENT OF THE EXTERNAL NUTRIENT SUPPLY

The experimental evidence presented in the foregoing discussion indicates that, other factors being favorable, seedling yield is proportional to internal nutrient concentration, which is in turn proportional to the supply

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[1] Scientific equivalents of all common names used in the above discussion and elsewhere in this report are given in Part II of Black Rock Forest Bulletin 7 (Raup, 1938).

of nutrients in the external solution. Also, that for each of the elements studied there is an optimum or "critical" internal concentration. These critical internal concentrations for white pine seedlings fall within the following approximate ranges: 2.50 to 3.26% N, 0.56 to 0.67% P, 1.50 to 1.72% K and 0.28 to 0.33% Ca. Apparently the ideal nutrient medium is one so adjusted that seedlings growing therein will maintain a constant and approximately optimum internal concentration—of each essential element—throughout the growing period (see Gast, 1937, pp. 645-650). Except for increasing seedling size the desired internal concentrations might be maintained simply by keeping the supply of nutrient elements in the external solution at a constant level. But it is well known that external supplies which are optimum for plants of a given size are either too low or too high for larger or smaller plants, as the case may be. This is demonstrated by the data of Mayr (see Rippel, 1931) presented in Gast's Fig. 17.

Although these data were obtained from oat plants supplied various amounts of nitrogen and sampled at different times after planting, the fundamental principles illustrated are believed to be equally true of coniferous seedlings. It is evident from these data (Gast, Fig. 17) that supplies of nitrogen which proved to be optimum for older, larger plants were much too great for younger, smaller plants. In the latter case large supplies resulted in toxic internal concentrations from which the plants never recovered. Similar data regarding pine seedlings, although less complete, were discussed by Gast (*loc. cit.*). In the G M-'31 Scots pine experiment, in the 1932 white pine experiment (Mitchell, 1934), and again in the present (1933) experiment, it was found that recently germinated Scots and white pine seedlings could not be transplanted successfully to nutrient-sand cultures with a nitrogen concentration of from 200 to 300 ppm—the very range of supplies which, for older, larger seedlings, result in optimum internal concentrations. Supplies above 200 ppm invariably result in the absorption, by young seedlings, of amounts of nitrogen much in excess of the optimum internal concentration. Death usually follows within one to two weeks. Proportionately large supplies of P, K or Ca also result in definitely harmful accumulations of these elements in young seedlings.

Because of increasing seedling size it is necessary, as the growing season advances, to make proportionate increments in the nutrient concentration of the external supply. This is the only way in which the internal nutrient concentration can be maintained at the constant and approximately optimum level necessary for continued maximum efficiency in the use of mineral nutrients. In the present experiment such adjustments were made in the rate of nutrient supply. The concentration of all essential elements, including those in the basic solution as well as the one varied in the series, was increased periodically according to the application schedules shown in Table 2 (see also Mitchell, 1934, Tables 1, 3 and 4). The method used—that is, adjustment of the rate of supply—is admittedly crude, but nevertheless fairly satisfactory, as the results obtained indicate. Absolute precision in maintaining a constant internal nutrient concentration can be attained only when complete data are available regarding the relationship between external supply and the internal concentration of seedlings of different age and size.

Another important point to consider is that different plants—even different species of the same genus—often vary greatly as regards nutrient-absorptive capacity and growth rate. For example, the internal nitrogen concentration of Corsican pine seedlings is considerably less than that of either Scots or white pine grown in nutrient-sand cultures of equal nitrogen supply (Aldrich-Blake, 1930; Gast, 1937; Mitchell, 1934). Apparently greater external supplies are necessary to produce the optimum internal concentration of around 2.5 to 3% N in the former species. Similar differences in absorption capacity or "feeding power" have been observed between various tree species growing over a wide range of natural soils. Maples, for example, extract from the soil and transport to the leaves approximately twice as much phosphorus as do oaks growing under identical conditions on the same site (Mitchell, 1935). And the oaks, particularly white, chestnut and scrub oaks, apparently can obtain significantly more nitrogen from relatively infertile soils than can such species as yellow poplar, ash and basswood (Mitchell, unpublished data). This may explain in part the more limited distribution of the latter species, a subject which should be studied further.

It is evident that different trees, even species of the same genus, may vary greatly in nutrient-extractive power. The explanation of such variations is a subject beyond the scope of the present report. However this may be, efficiency demands that differences in feeding power be taken into consideration in the fertilization of tree seedlings—either in culture solutions or seed-bed soils—the manuring of shade and ornamental trees, or in the choice of species to plant or favor on a given forest site. It is very apparent from data cited in the foregoing discussion that a nutrient environment which may be optimum for a given species of a given age may or may not be equally suitable for a widely different species of the same age, or even the same species at a different period of the growing season.

The frequently demonstrated inability of chemical solutions in the laboratory to imitate exactly, or even approximate with consistency, the nutrient-extractive powers of different tree species growing in nursery beds or natural environments limits the usefulness of ordinary methods of soil analysis as a guide to nursery fertilization or tree manuring in general. Such methods make no allowance for characteristic differences in feeding power (Mitchell, 1935, 1936), or for such biological factors as mycorrhizae, which may increase the absorptive capacity of the same species by as much as 300% for certain elements (Hatch, 1936, 1937; Mitchell, Finn and Rosendahl, 1937; McComb, 1938).

Internal nutrient concentration, with which yield is highly correlated, is perhaps the most reliable index to the suitability of any nutrient environment—either culture solution or natural substrate—to a given tree species at any particular time during the growing period. If the internal concentration of any of the essential elements is significantly less than the experimentally determined optimum level, it is certain that an increase is indicated in the rate of supply of that element. Such increases may be expected to result in a growth response proportional to the degree of the deficiency—provided, of course, that environmental factors other than nutrition are not limiting. If, on the other hand, the internal nutrient concentration is significantly higher than the optimum, then it is certain that either: (1) the rate of supply is too great, as often happens in nursery practice when fertilizer is applied *previous* to seeding, or (2) growth, but not absorption, is being inhibited by some other environmental factor, the result being toxic internal accumulations of nutrient elements. In either event the growth rate will be less than that of which the species is capable under more favorable conditions.

DISCUSSION OF DATA IN RELATION TO CURRENT NURSERY PRACTICE

EUROPEAN experience has proven conclusively that the fertility of nursery soils cannot be maintained at a satisfactory level for more than two or three years of intensive cropping without the use of fertilizers (Schwappach, 1916; Leiningen-Westerburg, 1930; Kuhnert, 1930; Toumey and Korstian, 1931 and references cited; Němec, 1932). Ample evidence of the necessity for the fertilization of permanent nurseries may also be found in American forestry literature (Pettis, 1909; Bates and Pierce, 1913; Retan, 1914; Perry, 1924; McIntyre and White, 1930; Buckman, 1932; Wahlenberg, 1929, '30; Wilde, 1936; and Lunt, 1938). Experimental evidence indicates that tree seedlings, especially conifers, remove large quantities of mineral elements from the soil and that they return little or nothing thereto (*cf.* Lunt, *loc. cit.*). Therefore, even the most fertile of nursery soils require some form of nutrient supplements sooner or later if their productivity is to be maintained.

That the need for fertilization is generally recognized is evidenced by the extensive studies which are made from time to time at many of the more important forest nurseries in this country. A review of the literature reveals that the usual procedure is to apply varying amounts of single and mixed fertilizers to a series of uniform experimental beds. Future fertilizer practice is then modified, so far as is practical, according to the treatment which proves most successful. It is clearly recognized, however, that recommendations based upon the results of such experiments are of limited applicability. Soil conditions may not only vary considerably from nursery to nursery but from year to year in the same nursery. Another criticism of this method of approach is that seldom if ever is any attempt made to evaluate the nutrient-supplying powers of the soil in terms of the requirements of tree species. Neither is adequate attention given to the fact that tree species may differ greatly as regards nutrient requirements.

Agronomists, who have a vast background of information concerning the physiology of field and garden crop plants and can therefore predict with a high degree of accuracy the success of a given crop under a given set of conditions, have demonstrated conclusively that there are three prerequisites to efficiency in the use of fertilizers. They are: (1) a knowledge of the nutrient requirements of the plant to be grown, (2) an evaluation of the nutrient-supplying powers of the soil, and (3) data regarding when and in what form it is best to apply fertilizer.

MINERAL NUTRIENT REQUIREMENTS

Precise data regarding the nutrition of native tree species is particularly lacking. It is true that many observations have been made of the response, to various fertilizer applications, of tree seedlings growing in soils of undetermined nutrient-supplying powers. Such observations, since they have local significance, should not be belittled. But it is doubtful if field experiments alone can yield the fundamental and more widely applicable silvical data without which nursery fertilization can never be as efficient as the methods applied to agricultural crops. Field trials may show that white pine seedlings growing in a given nursery soil respond best to dried blood applied at the rate of 2 oz. per five square feet of seed bed. This finding may indicate a nitrogen deficiency in that particular soil, but it tells little or nothing of the absolute nutrient requirements of the species, or the degree of the deficiency in relationship thereto. Data regarding the requirements of the seedlings can be obtained more surely and efficiently from cultural experiments in which nutritional and other factors are subject to more exact control. Fundamental relationships so determined, and subsequently tested and confirmed with field experiments, constitute a widely applicable biological standard of comparison useful in evaluating conditions encountered in the field. Although the nutrient-sand culture technique has certain recognized limitations and disadvantages, the fundamental silvical data obtained from such studies as those reported in this paper and by Aldrich-Blake (1930), Addoms (1937), Pessin (1937), Gast (1937), Mitchell (1934) and others prove the value of this method of approach to the problem of tree nutrition.

Estimating Chemical Fertility

Assuming that the nutrient requirements of a given tree species are known, as a result of cultural experiments confirmed with field studies, the data thus obtained are of little value unless it is also known how nearly a given seed-bed soil meets the requirements of the species to be planted. This brings up the question of soil analysis. It is undoubtedly true that nurserymen make fewer soil tests as a guide to fertilization than do those concerned with the production of agricultural crops. This may be due partly to the fact that so little is known of the requirements of tree species and partly to the questionable reliability, as regards trees, of the usual laboratory methods of soil analysis developed primarily for agricultural use. For example, it is hardly reasonable to believe that trees, which may vary greatly with species, are similar to field and garden crop plants in their nutrient requirements and physiological responses, or that they absorb nutrients from only a single horizon such as the ''plowed layer.'' Also, trees growing in the majority of nurseries and natural habitats are associated with mycorrhizal fungi (Hatch, 1937). Studies at the Black Rock Forest nursery during 1935 and 1936 indicated that yellow poplar seedlings could not survive, because of nitrogen and phosphorus deficiency, in a soil which, according to methods of analysis widely used in agriculture, was sufficiently fertile to produce an excellent crop of corn. It was also shown (Mitchell, Finn and Rosendahl, 1937) that white pine seedlings differing only in mycorrhizal equipment varied significantly in nutrient-absorptive powers and growth, although no differences in soil fertility could be detected by laboratory analysis methods. For these reasons it is doubtful if methods of soil analysis developed for determining the suitability of agricultural soils for various field crops can be used with equal success to evaluate the chemical fertility of nursery soils or forest site in terms of the nutrient requirements of tree species.

In view of the experimental evidence presented and discussed earlier in this report, it is believed that internal (seedling) nutrient concentration—which is proportional to nutrient supply, and with which yield is highly correlated—is the most reliable index to the fertilizer needs of seedlings growing in nursery soils of unknown fertility. Soil evaluations based upon leaf or plant analyses are not confined to any particular soil zone or horizon, and they are selective only in so far as the roots of a given tree species are selective in their absorption of mineral elements from any artificial substrate or natural soil. This solves the otherwise perplexing problem of nutrient "availability," and the question of differential absorption by species does not arise. Thus the applicability to nursery practice of the principle of proportional nutrient absorption is by no means limited to one particular soil or nursery. Once the approximate optimum internal nutrient concentration is established by experiment, as with white pine seedling, the resultant data serve as a standard of comparison. If the internal nutrient concentration of seedlings growing in nursery soils of unknown nutrient-supplying powers is found to be unbalanced or significantly greater or smaller than the experimentally determined optimum, fertilization should be modified so as to correct the indicated deficiency, oversupply or lack of balance as the case may be.

It is true that the value of fertility estimates based upon standards derived according to methods discussed in this paper may be suspect because of the artificiality of the nutrient-sand culture technique. In nutrient cultures, where all ions are free in solution, the rate of nutrient intake by plants is no doubt greater than in natural soils. In the latter, even soils of high fertility, a large portion of the mineral elements are adsorbed in organic and inorganic base-exchange compounds from which they are liberated slowly. However, controlled field studies made from 1935 through 1937 in the Black Rock Forest experimental nursery, and in which all of the various nutrient-culture series were duplicated under more nearly natural conditions (*cf.* data presented in Fig. 22), confirmed the basic relationships between external and internal nutrient concentration and seedling yield, as indicated by the cultural experiments. As might be expected, values equivalent to those representing the optimum ranges of internal nutrient concentration (of N, P, K and Ca) reported for the nutrient-culture studies (see Table 24) were not attained in the field experiments. The nearest approach was to the working ranges of internal nutrient concentration. The optimum ranges true of the cultural studies probably represent an ideal of efficiency in the absorption and use of nutrients which can never be exactly duplicated under field conditions. But this should not detract from their value as a standard of comparison. Experience in the nursery has shown that success with fertilizer applications varies almost directly with the degree to which these standards are approximated (see Fig. 22).

Timing of Application and Fertilizer Source

The data presented and discussed under the heading "Adjustment of the External Nutrient Supply" suggest that efficiency in the use of mineral elements is maximum when the rate of nutrient supply is adjusted so as to maintain the internal (seedling) nutrient concentration at or near the experimentally determined optimum during the entire growing season. Thus the supply of available nutrients must be relatively low at the beginning of the growing season in order to avoid toxic internal accumulations and should be increased gradually thereafter in proportion to increasing seedling weight. It is relatively simple to make such adjustments in the external concentration of nutrient-sand culture solutions. And in highly fertile natural soils there is a potentially available (reserve) supply of mineral elements, adsorbed in organic and inorganic base-exchange compounds, upon which the plants may draw. Thus, in nature, there may be increases in the rate of nutrient intake—resulting from the activity of normal microflora and microfauna, weathering, chemical exchange reactions and the gradually increasing absorbing surface area of the growing roots—which approximate, in effect upon internal nutrient concentration, the artificially increased rate of supply found optimum for nutrient-culture-grown seedlings. But the importance of the fundamental relationships between the rate of nutrient supply, internal nutrient concentration and seedling growth are often overlooked or disregarded in the restoration, by artificial means, of exhausted seed-bed soils. According to current nursery practice *all* fertilizers, regardless of analysis or source, are mixed with the soil previous to seeding, as is customary in agriculture. In view of available data regarding tree nutrition, it is obvious that this practice, which is often justified as the most "practical," may not always be the most efficient. The fertilizer is applied at a time when the resulting high mineral nutrient concentration of the soil solution is most apt to be harmful to the germinating seedlings and when they need nutrient supplements the least. This is especially true if readily soluble fertilizers are applied to soils of low nutrient-absorptive capacity.

Although this discussion is primarily concerned with the application to nursery practice of certain fundamental principles regarding seedling nutrition, the physical properties as well as the nutrient-supplying powers of soils must be considered in deciding what fertilizer to use and when and how it should be applied. No amount or type of nutrient supplements will stimulate seedling growth in soils which are unfavorable as regards drainage, aëration, or nutrient-absorptive and exchange capacity. Thus, if improvement of physical properties is of primary importance, it is often good practice to use as a fertilizer some organic compound which will improve soil texture and at the same time supply some of the essential nutrient elements. However, the current trend toward the almost exclusive use of organic fertilizers under any and all conditions may be seriously questioned, expecially on the basis of cost.

A review of the literature reveals that nurserymen are prone to favor green manures, stable manure and other organic sources over the more concentrated inorganic fertilizers. This is due in part to the importance of organic materials in improving the physical structure of soils. Another reason is that few nurserymen have experimented with delayed fertilizer applications, and the results obtained from applying high-analyses fertilizers in the usual way—before seeding—have frequently been unsatisfactory if not disastrous. If applied to the soil previous to planting, it is true that high-analysis fertilizers such as nitrate of soda, sulfate of ammonia, superphosphate and muriate of potash, since they are very soluble, must be used with greater care than such low-analysis inorganic sources as rock phosphate, or organic sources such as stable manure, dried blood or bone meal. It should be emphasized, however, that in many cases chemical fertilizers are more economic to use; also that, when applied with the proper timing, they are just as safe and even more effective in stimulating seedling growth than the highly favored organic fertilizers. The latter, because they contain such small quantities of mineral elements (stable manure, for example, averages only 0.5% N, 0.25% P_2O_5 and 0.5% K_2O), usually cost, per unit of active ingredient, two or three times as much as chemical fertilizers. Thus, if physical structure of soil is not the only or the most important consideration, it is often more economic to use high-analysis chemical sources to build up mineral nutrient supply. But such fertilizers cannot be added to the average soil in amounts sufficient to produce anything approaching maximum growth response if applied in the usual way—*i.e.,* previous to seeding. Some of the data obtained during the 1935 and 1936 experiments at the Black Rock Forest nursery are of interest in this connection.

In these studies various species were grown in chemically infertile sand-sawdust-clay ('35) and sand-humus-clay ('36) mixtures contained in specially constructed seed-bed frames (Mitchell, Finn and Rosendahl, 1937). Although the soil mixtures used were poor as regards mineral nutrient availability, as required for the experiment, their physical properties were as good or slightly better than average. Several nutrient elements were varied in individual series similar to those used in the nutrient-sand culture studies. In the 1935 experiment, in which inorganic sources were used almost exclusively, the fertilizer was applied to the majority of the beds in several light applications starting two weeks *after* the germinating seedlings had shed their seed coats. In several beds, however, the fertilizer was applied previous to the seeding of white pine, so as to study the effect of this practice on germination, survival and growth.

The fertilizers applied to the test beds, and the data on survival one month after germination, are summarized in Table 25. The prepared soil mixture in these beds was the same as that used throughout the experiment. Seeds in all the test beds started to germinate simultaneously, and no differences were apparent at that time. But two weeks later the seedlings in beds 2 and 3 (see Table 25), which received different amounts of the inorganic fertilizers, started to die, apparently from damping off. Damping off continued in these two beds, particularly No. 3, even though the soil was acid in reaction, the seeds had been sterilized with bichloride of mercury before planting, and all beds were treated previous to seeding with acetic acid as recommended by Doran (1932). Germination and survival were average for the species in the

TABLE 25

SURVIVAL, ONE MONTH AFTER GERMINATION, OF WHITE PINE SEEDLINGS GROWN IN VARIOUSLY FERTILIZED SEED BEDS

1935 NURSERY EXPERIMENT

Bed Number	*Fertilizer Treatment*[1]	*Survival*[2] *(as per cent of bed number 1)*
1	None	100%
2	3.52 grams ammonium nitrate 0.82 grams muriate of potash 9.08 grams 16% superphosphate	48%
3	14.01 grams ammonium nitrate 3.28 grams muriate of potash 36.32 grams 16% superphosphate	19%
4	31.72 grams dried blood 37.88 grams bone meal	98%

[1] The amounts given in this column are for 5 sq. ft. of seed bed. All fertilizers were thoroughly mixed with the soil *previous* to seeding.

[2] The same number of seeds were planted in each bed. The percentage germination in the control bed, which received no fertilizer, was 88%, about the average for after-ripened white pine seed.

unfertilized (control) bed and in the bed (No. 4) supplied the mixture of dried blood and bone meal. No damping off was observed in either of these beds, although they were located side by side with beds 2 and 3. In the latter two beds initial germination was satisfactory, but survival varied inversely as the amount of fertilizer applied previous to seeding. The readily soluble inorganic fertilizers increased the availability of nutrients in the soil solution to such an extent that the seedlings absorbed sufficient to produce toxic internal concentrations. This was proven by chemical tests. Probably because of their weakened condition, the seedlings were more susceptible to fungus attack. Even those which survived damping off never fully recovered from the effects of toxic internal nutrient concentration. But inorganic fertilizers in even greater amounts than those applied to beds 2 and 3 can be used successfully *if applied in two or three light applications starting after germination is complete.* In the main part of the experiment seedlings fertilized in this way made excellent response to significantly greater amounts of inorganic fertilizers, and no damping off was observed.

In that part of the 1936 experiment pertinent to the present discussion there were four 7-bed nitrogen series and four 7-bed phosphorus series, seeded to red pine, white pine, red spruce and hemlock, as indicated in Table 26. Nitrogen was varied as dried blood and was applied, previous to seeding, in amounts up to twice the maximum which had proven safe for white pine the previous year. The N-4, N-5 and N-6 beds were to receive increasing amounts of dried blood later in the growing season. Phosphorus was varied as rock phosphate, which is relatively insoluble, applied previous to seeding. All seeds were sterilized with bichloride of mercury, and all seed beds were treated with acetic acid. Germination of the four species was satisfactory in all beds of each series. But within two weeks red pine, and especially red spruce

TABLE 26

SURVIVAL, ONE MONTH AFTER GERMINATION, OF RED PINE, WHITE PINE, RED SPRUCE AND EASTERN HEMLOCK SEEDLINGS GROWN IN VARIOUSLY FERTILIZED SEED BEDS

1936 NURSERY EXPERIMENT

Bed Number	*Grams of Dried Blood per 5 sq. ft. of Seed Bed*[1]	*Survival*[2] *(as per cent of bed N-O)*	*Bed Number*	*Grams of Rock Phosphate per 5 sq. ft. of Seed Bed*[3]	*Survival*[2] *(as per cent of bed P-O)*
Red Pine (*Pinus resinosa*)					
N-0	none	100%	P-0	none	100%
N-1	10.57	98%	P-1	50	97%
N-2	31.73	81%	P-2	100	96%
N-3	63.45	24%	P-3	250	98%
N-4	63.45	22%	P-4	500	70%
N-5	63.45	21%	P-5	1000	32%
N-6	63.45	23%	P-6	3000	20%
White Pine (*Pinus strobus*)					
N-0	none	100%	P-0	none	100%
N-1	10.57	96%	P-1	50	99%
N-2	31.73	105%	P-2	100	95%
N-3	63.45	99%	P-3	250	101%
N-4	63.45	103%	P-4	500	92%
N-5	63.45	94%	P-5	1000	89%
N-6	63.45	97%	P-6	3000	72%
Red Spruce (*Picea rubra*)					
N-0	none	100%	P-0	none	100%
N-1	10.57	97%	P-1	50	92%
N-2	31.73	26%	P-2	100	95%
N-3	63.45	none	P-3	250	20%
N-4	63.45	none	P-4	500	none
N-5	63.45	none	P-5	1000	none
N-6	63.45	none	P-6	3000	none
Eastern Hemlock (*Tsuga canadensis*)					
N-0	none	100%	P-0	none	100%
N-1	10.57	94%	P-1	50	96%
N-2	31.73	21%	P-2	100	32%
N-3	63.45	none	P-3	250	11%
N-4	63.45	none	P-4	500	none
N-5	63.45	none	P-5	1000	none
N-6	63.45	none	P-6	3000	none

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[1] The amounts of dried blood indicated in this column were thoroughly mixed with the soil *previous* to seeding. In addition, all nitrogen series beds received the *same* basic nutrient treatment including small amounts of P, K, Mg, Ca, S and Fe, applied two weeks *after* germination was complete.

[2] The same number of seeds were planted in each bed. Germination in the control beds (N-O and P-O) averaged: 82% for red pine; 89% for white pine (after-ripened); 77% for red spruce (treated according to Baldwin, 1932); and 72% for hemlock.

[3] The amounts of rock phosphate (finely ground) indicated in this column were thoroughly mixed with the soil *previous* to seeding. In addition, all phosphorus series beds received the *same* basic nutrient treatment including small amounts of N, K, Mg, Ca, S and Fe, applied two weeks *after* germination was complete.

and hemlock, started to damp off in beds supplied the greater amounts of dried blood and rock phosphate. A month after initial germination there were few red pine in certain of the beds (see Table 26). Hemlock and red spruce were even more susceptible. Survival of these three species varied inversely as the amount of either dried blood or rock phosphate applied previous to seeding. White pine, however, responded quite differently. There was practically no damping off in any of the white pine beds except the one (P-6) supplied rock phosphate far in excess of the requirements of the species. In a parallel series of experiments, nearly identical except that no fertilizer was applied until after germination was complete, red pine, hemlock and red spruce responded satisfactorily to mineral nutrient supplements according to their requirements, and no damping off was observed.

Data from these experiments indicate that fertilization should be modified according to species. It is obvious that small-seeded, slow-growing species such as spruce and hemlock cannot be fertilized as heavily, especially early in the growing season, as the larger-seeded more rapidly growing white pine. Neither, for some less apparent reason, can red pine. It is also evident that if the usual fertilizers are to be added to average soils in amounts sufficient to produce maximum growth response, they must be applied so as not to produce toxic internal concentrations, especially early in the growing season. This is particularly true of high-analysis inorganic fertilizers, but also applies in a lesser degree to certain organic sources such as dried blood. Even though the nutrient-absorptive capacity of the substrates used in these studies was average or better, the growth of seedlings supplied fertilizers in amounts it was safe to apply previous to seeding in no case approached that of seedlings grown in seed beds where the rate of nutrient supply was increased gradually with subsequent fertilizer applications. The marked superiority of seedlings thus fertilized suggests the desirability of modifying the usual technique of application to correspond more closely with available data regarding the requirements of coniferous seedlings. As a *supplement* to materials which it is safe to mix with the average nutrient-deficient nursery soil previous to seeding, some form of delayed fertilizer applications are believed to be practical as well as highly effective. Experience has shown that readily soluble chemical fertilizers may be applied to seed beds in solution, with various sprinkling devices, at any required time during the growing season, and without injury to seedlings if the latter are watered directly thereafter to remove all traces of fertilizer from the needles. Commercial forms of organic materials and slowly soluble inorganic fertilizers may also be applied at any time during the growing period, either by hand or with the aid of a mechanical fertilizer spreader. Because of constant weathering and leaching, materials thus applied are quite effective even though not worked into the soil.

Neither the indiscriminate nor the exclusive use of delayed fertilizer applications is being suggested. In general, the potential advantages of this procedure tend to vary inversely as the absorption capacity of the soil, the factor which determines the reserve (adsorbed) supply of mineral elements which can be built up previous to seeding. Therefore, delayed fertilization should be considered more as a valuable supplement to, rather than a substitute for, the usual technique of application. According to available data, delayed nutrient supplements, if regulated so as to maintain constant and approximately optimal internal nutrient concentrations, result in a greater stimulation to coniferous seedlings—especially slow-growing species such as spruce—than can be obtained with the limited amounts of fertilizer, either organic or inorganic, which it is safe to apply to the average nutrient-deficient soil previous to seeding. They also permit greater use of the more economic chemical fertilizers than is otherwise possible. Even in soils unfavorable as regards absorption capacity as well as nutrient supply, it is frequently more efficient to improve the former with inexpensive organic wastes such as composted sawdust than with such ''double purpose'' but relatively expensive organic sources as tankage, dried blood, bone-meal, stable manure, commercial humus or even green manures. Mineral nutrient supply can be built up at the desired rate with the relatively large amounts of concentrated inorganic fertilizers which delayed application permits.

The solubility of the fertilizer, the nutrient requirements of the species and the nutrient-absorptive capacity of the soil are the factors which determine the amount of fertilizer it is safe to apply to exhausted seed-bed soils at the beginning of the growing season. The absorption capacity of such soils can be improved by the addition of various organic and inorganic base-exchange materials, thus permitting heavier initial fertilization—that is, up to the point of saturation—without danger to germinating seedlings. However, an equally important consideration is the rate at which the initial reserves of mineral elements are liberated—through chemical exchange reactions, weathering, microbiological activity and increasing ''feeding power'' of the roots—from a substrate so improved. In this respect as well as total absorption capacity and economy, the usual organic materials do not appear to be completely satisfactory under all conditions. In the nursery experiments previously referred to it was found that seedlings growing in a nutrient-saturated substrate of very high humus content responded significantly to subsequent nutrient supplements, thus suggesting deficiencies in the rate at which mineral elements were liberated from the initial ''reserve'' supply. As a substitute for humus and other organic compounds, inorganic materials such as bentonite (a clay-like decomposition product of volcanic ash) and various base-exchange clays offer promising possibilities which should be thoroughly investigated in connection with nursery fertilization as well as cultural studies (Madhok, 1937).

PRACTICAL CONSIDERATIONS

Seedlings grown in nutrient-sand cultures in which the external supply of essential elements is adjusted so as to maintain the internal concentration at or near optimum during the growing period are significantly larger than those which can be produced in the same length of time in nursery beds by methods commonly used, or in a natural forest habitat, for that matter. This is true of white pine and other species which have been studied to date. Natural fertility in the forest is by no means perfect, and nursery fertility is usually far from desirable. Thus the growth rate which is usually considered ''average'' or ''normal'' for a species may be much less than that of which the species is capable. And the growth rate is far less than ''average'' in exhausted nursery soils or those in which differential absorption by successive crops of planting stock has resulted in an unfavorable balance between the essential nutrient elements. It is not being suggested that it would be practical to grow planting stock on a large scale in trays or some similar device flooded with nutrient solutions. It is believed, however, that because of the marked superiority of seedlings grown in carefully controlled nutrient cultures, the data obtained from such studies can be used to advantage in improving fertilizer practice in forest nurseries. Field trials have shown that success in the use of fertilizers varies with the degree to which nutrient conditions in seed-bed soils approximate, in *effect upon internal nutrient concentration,* the nutrient environment which cultural studies indicate as most nearly optimum for the species.

Just how far it is economic to go in modifying the chemical properties of seed-bed soils in large nurseries to conform more closely to the nutrient requirements—if known—of various tree species is a question beyond the scope of this report. In view of available data it is believed, however, that the increase in efficiency which would result from more accurate control of nutritional factors might justify a greater expenditure for research along these lines than is now being made. Fertilizer applications at the Black Rock Forest nursery, based upon the results of periodic chemical analyses of seedlings, have proven entirely satisfactory. In seed beds where nutrient environment was adjusted with periodic tests and corrections so as to maintain constant and approximately optimum internal concentrations it was possible to grow, in two years and without transplanting, white pine seedlings which are comparable in every measurable respect with the 3-0 or even the 2-1 stock produced in the average nursery.[1] The data summarized in Table 27, for example, show the very marked superiority of 2-0 stock thus produced, over the average and perceptibly better than average (in relation to other nurseries) 2-0 and 3-0 stock grown at the Windsor (Connecticut) nursery in seed beds fertilized in the usual way—that is, without regard to internal nutrient concentration. Even better results have been obtained with small-seeded slow-growing seedlings such as spruce and hemlock. Any procedure which reduces by even a year the usual time required to grow planting stock of a given size is worthy of consideration.

The belief that coniferous species cannot be greatly stimulated with nutrient supplements during the initial growing season is absolutely without foundation, as the data presented in Figs. 8 and 10 prove (see also Aldrich-

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[1] The symbols 3-0, 2-1, etc. are those usually used to identify nursery stock; the first numeral refers to the time (in years) in the seed bed, and the second to the time in the transplant bed.

TABLE 27

SEEDLINGS GROWN IN THE BLACK ROCK FOREST NURSERY COMPARED WITH THOSE FROM THE VARIOUSLY FERTILIZED SEED BEDS OF THE WINDSOR NURSERY[1]

Source of Data	*Plot No.*	*Treatment*	*Species*	*Class of Stock*	*Reserve Dry Wt. of Seed*	$\frac{Shoot}{Root}$ *Ratio*[2]	*Total Dry Wt. of Av. Seedling*	*Standard Error of Mean*
From M-'35, '36 nursery experiments at the Black Rock Forest	N-6	Highest treatment of nitrogen series.[3] Nitrogen, P, K, Ca, S, Fe and Mg supplied in solution in four applications during each season. No N and only small amounts of other elements applied previous to seeding	White Pine	2-0	13.77[4] mg.	1.04	789.4 mg.	± 38.4 mg.
From Lunt (1938, Tables 2 and 3).[5] Seed-bed fertilization studies at the Windsor (Conn.) nursery	Av. 1, 5, 9, 11 & 14	Unfertilized (control) beds. Poorest of series at the end of second season	Red Pine	2-0	Not reported	Not reported	134.0 mg.	Not reported
	12	Peat moss + 20-8-8 fertilizer applied in one application at beginning of second season. Most successful treatment of series	Red Pine	2-0	Not reported	Not reported	226.0 mg.	Not reported
	Av. 2 & 15	Milorganite applied beginning of second and third seasons. Poorer than control beds at end of third year	Red Pine	3-0	Not reported	3.58	308.0 mg.	Not reported
	12	Peat moss + 20-8-8 fertilizer applied at beginning of second and third seasons. Most successful treatment of series	Red Pine	3-0	Not reported	5.31	654.0 mg.	Not reported

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[1] Ordinarily it is not fair to compare the effectiveness of fertilizer treatments on the basis of the response of two different species, as is done in this table. However, studies at the Black Rock Forest and other nurseries have shown that, at the end of the second and especially the third growing seasons, red pine are, if anything, larger than white pine grown under identical conditions. In view of this, the above comparisons are all the more significant.

[2] Elsewhere in this report the balance between root and shoot is expressed as root/shoot ratio. Shoot/root ratio, an equally useful index, is used in the above table because Lunt's data are expressed in this way. It is apparent (see above) that the "forced" seedlings grown at the B. R. F. nursery are very much superior as regards balance between shoot and root. The roots are approximately as heavy as the shoots. The very unfavorable shoot/root ratios of seedlings grown in the various beds of the Windsor nursery suggest exceedingly high internal N concentrations in relation to the internal concentrations of P, K and Ca.

[3] Data for the entire series at the end of the first and second growing seasons are plotted in Fig. 22. The series was composed of seven identical beds which received constant and approximately optimal amounts of P, K, Ca, S, Mg and Fe. Only N was varied, as indicated in Fig. 22. Data for seedlings from the highest nitrogen treatment (Bed N-6) are given in the above table.

[4] All white pine data reported in this paper are expressed as from seeds with a reserve dry weight of 13.77 mg.

[5] In the series of seed-bed studies at the Windsor nursery, Lunt (*cf.* Tables 2 and 3) used a total of 15 plots to study the response of red pine seedlings to eight different fertilizer treatments. Only data from the poorest and the most successful treatments, as based upon results at the end of the second and third seasons, are used in the above table. The results of Lunt's nursery studies were selected for comparison largely because his published data are more complete than in reports on the majority of similar investigations, many of which do not even include total dry weights and root/shoot ratios (that is, in absolute rather than relative values, *cf.* Wahlenberg, 1930, tables 4 and 5) to say nothing of data on solar radiation and seed weight, both of which are necessary for precise comparisons.

Blake, 1930; Mitchell, 1934; Gast, 1937). And, contrary to the opinion of certain investigators, seedlings thus stimulated need not be unsatisfactory as regards the ratio of root to shoot—provided they receive sufficient solar radiation and are grown in a properly balanced nutrient environment. It is clearly recognized that shading retards root growth (Mitchell, 1936; Gast, 1937) and that nitrogen supplies excessively high in proportion to phosphorus, potassium and calcium result in abnormal shoot development (see Fig. 11 and discussion). Futhermore, seedlings grown in well-balanced nutrient-sand cultures and subsequently imbedded (in pots) in seed beds, and those grown in heavily fertilized beds of the nursery studies referred to in the above discussion, formed normal buds at the usual time in the fall and proved their hardiness during an unusually severe winter. Although they were not mulched or otherwise protected, these seedlings showed less evidence of frost injury during a winter marked by alternate freezing and thawing than did seedlings grown in less favorable nutrient environments. And the survival of these "forced" seedlings, many of which were transplanted to a not too favorable site in the forest in the spring of 1934, was significantly better than average. The idea of producing stunted stock to plant on unfavorable sites is too absurd to warrant discussion.

SUMMARY AND CONCLUSIONS

The experiments reported in this paper were devised to study the nitrogen, phosphorus, potassium and calcium nutrition of white pine (*Pinus strobus* L.) seedlings. In brief, the experimental procedure was as follows: Recently germinated plants from individually weighed seed of a single tree were transplanted to nutrient-sand (pot) cultures and grown therein for 108 days. Except for partial shading during the two weeks following transplanting and protection during rains, the seedlings were exposed to the weather continuously and received full sunlight during the entire period. Each of the four nutrient elements studied was varied individually in a series of cultures to which all other essential elements were supplied in constant and approximately optimal amounts. The nutrient solutions were made by dissolving pure chemicals in distilled water. Nutrition was the only variable.

At the end of the growing period the seedlings were harvested, washed, inspected under a microscope, measured, cut into two portions—root and shoot for ratio determinations—each part placed in a labeled glassine envelope, dried at + 70° C., weighed to ± 0.1 mg., ground to pass through a 0.55 mm. mesh screen and analyzed for nitrogen, phosphorus, potassium or calcium, depending upon the nutrient series in which they grew.

The precision of the quantitative relationships discovered in this and previous experiments indicates that nutrient-sand cultures may be used to advantage to study the nutrition of pine seedlings if other factors affecting seedling growth—*i.e.*, seed size and source, temperature, moisture supply, aëration and solar radiation—are controlled, measured or otherwise taken into account.

Seed weight, which exerts an important control on the early cumulative dry weight of pine seedlings, is a very important factor that must be taken into consideration if accurate comparisons are to be made of the results of different experiments with seeds of varied size and source. For certain comparisons seed-size correction factors may be derived from the relationship between fresh weight of seed and seedling yield, which are linearly but not directly correlated. Because of variations in the ratio of mass to volume, oxidation of food reserves during storage, differences in seed-coat thickness and changes in moisture content, fresh weight is not necessarily an accurate measure of the food reserves—the seed-size factor which influences yield—in seed of different lots. Thus correction ratios based upon the relationship between fresh weight of seed and seedling size are applicable only to seedlings grown the same year from seed of a single lot. Reserve dry weight, which is the dry weight of the seed less the dry weight of the seed coat and with which seedling yield is directly and highly correlated, is a more precise measure of the material available for the development of the embryo. Correction factors derived from this relationship may be used to convert to a common basis the yields of seedlings grown in the same or different years from seed of varied size and source.

Under conditions of the experiment seedling dry weights were found to be proportional to individual variations in the external supplies of nitrogen, phosphorus, potassium and calcium. In each case a maximum was reached, and further increases in the external concentration of the element varied resulted in decreased yields. To facilitate comparisons and discussion, the range of supplies of each of the elements studied was divided, on the basis of yield response, into the following regions: the ''region of minima,'' which includes definitely limiting supplies; the ''working region,'' over which the supplies are equivalent in effect to those found in nature; the "region of tension," through which increases have little or no effect upon yield; and the "toxic region," over which yields are inversely related to external nutrient concentration. Curves of average relationship between seedling yields and each of the elements varied were calculated with the Mitscherlich equation, which is an entirely satisfactory estimating formula through the more important ranges of external concentration and into the toxic regions. For white pine the absolute (calculated) optimum supplies of each of the elements studied were as follows: 300 ppm N, 350 ppm P, 150 ppm K and 200 ppm Ca.

The results of previous nutrient-sand culture and nursery studies have shown that the dry weight increase of coniferous seedlings is proportional to the cumulative solar radiation. The close agreement between data from these experiments and those herein described demonstrates that accurate comparisons are possible if solar radiation as well as seed weight and other factors affecting seedling growth are taken into consideration.

As evidenced by the relative steepness of slope of the yield curves for each nutrient series, the response of seedlings is greater to individual increases in the supply of N and particularly K and Ca, than to equal increments of P. The range of supplies through which yield approaches maximum is much more limited for K than for P, Ca and, to a lesser extent, N. This may explain certain inconsistencies noted in previous nutrient-culture studies and is of particular interest in connection with nursery fertilization. External supplies greater than 300 ppm of P, Ca and, to a lesser degree, K, are much more toxic in effect than equal increments of N.

The root/shoot ratios of seedlings grown in the nitrogen series tended to vary inversely as the nitrogen supply over the greater part of the range studied. Individual increases in the supplies of P, K and Ca through the minimal and working ranges resulted in increases in the ratio of root weight to shoot weight. Increments of these three elements through their respective regions of tension and into the toxic ranges of supply had no appreciable effect upon root/shoot ratio. Only at concentrations greater than 800 ppm P, and 400 to 500 ppm for K and Ca, were there significant decreases in root/shoot ratios.

In general, the root structures chiefly responsible for the absorption of mineral elements by nutrient-culture-grown seedlings—that is, uninfected short-roots, root hairs and, at the higher concentrations, non-suberized portions of long-roots—tended to decrease in number and development with increases in the concentration of any one of the elements varied. These root structures are so small and succulent that they have but little influence upon root weight (dry) or, therefore, root/shoot ratio.

Seedlings grown in *properly balanced* nutrient-sand cultures are far superior, as regards total weight, balance between root and shoot and, to a lesser degree, root development, than the average nursery-grown seedling of the same age.

The needles of seedlings grown in solutions deficient in nitrogen developed the pale yellow-green color characteristic of nitrogen poverty. The lower needles of seedling which received no phosphorus, except that supplied by the seed, turned purple early in the growing season. Those supplied no calcium or potassium were chloritic and otherwise unhealthy in appearance.

The results of chemical analyses revealed an exceedingly high degree of correlation between the internal (seedling) content of N, P, K and Ca, expressed either as milligrams (N_{mg}, P_{mg}, K_{mg}, Ca_{mg}) or percent of dry weight ($N_{\%}$, $P_{\%}$ etc.), and the external (solution) concentration of these elements. With but one exception the curves of average relationship were calculated with the Mitscherlich formula. A simple regression equation was used to express the relationship between Ca supply and the internal Ca concentration, which is a linear increase over the entire range studied.

Separate analyses showed consistent relationships between the internal nutrient concentration of the plants and the shoots thereof, the latter being equally well correlated with the external nutrient supply. At the nitrogen supply of maximum yield, $N_{\%}$ of the shoots was somewhat higher than for the seedlings as a whole. As regards the other nutrient series, the seedlings supplied different amounts of either P or K had higher internal concentrations of these elements than did the shoots. There was little difference in the $Ca_{\%}$ of shoots and plants at any of the Ca supplies studied.

Yield data from the various nutrient series, when reclassified and plotted over internal rather than external nutrient concentration, show that seedling yields are highly correlated with the internal content of each of the elements varied. This follows since it is the nutrient elements actually absorbed by the plants that enter into the physiological processes which control growth. The internal concentration range of each of the elements may be separated, on the basis of yield response, into regions corresponding almost exactly to those into which the external supplies were divided, *i.e.*, the region of minima, the working region, the region of tension and the toxic range. The curves of average relationship were calculated with the Mitscherlich yield equation.

For each of the elements studied there appears to be an optimum or "critical" internal concentration range, through which the seedlings approach or attain maximum growth. At lower internal supplies there is a definite poverty adjustment; at higher concentrations the effect upon yield is toxic. Under conditions of the nutrient-sand culture experiments the optimum internal concentration for nitrogen falls within the range of from 2.50 to 3.26%; that for phosphorus in the range of from 0.56 to 0.67%; that for potassium in the range of from 1.50 to

1.72%; and for calcium in the range of from 0.28 to 0.33%. In each case the latter value is the absolute (calculated) optimum for white pine seedlings.

Data are presented to show that the optimum internal nutrient concentrations of various nursery-grown coniferous and deciduous seedlings, and the leaves of nearly mature hardwoods growing in a natural forest habitat, are essentially the same as those found true of white pine seedlings produced in the carefully controlled environment of the nutrient-sand cultures.

There is reason to believe that the ideal nutrient environment is one so adjusted that seedlings growing therein will maintain a constant and approximately optimal internal concentration—of each essential element—throughout the entire growing period. Because of the influence of increasing seedling size upon the rate of nutrient uptake and, therefore, internal concentration, an external supply which is optimum for a given species of a given age may be either too low or too high for larger or smaller seedlings, as the case may be. Therefore it is desirable as the growing season advances to make proportional increases in the rate of nutrient supply. Experience with nutrient cultures and in the nursery has shown that this is the only way in which internal nutrient concentration can be maintained at the constant and approximately optimal level necessary for continued maximum efficiency in the use of mineral elements.

The importance of the fundamental relationships between the rate of nutrient supply and internal nutrient concentration, with which seedling growth is highly correlated, should not be overlooked or disregarded in the restoration, by artificial means, of exhausted seed-bed soils. Comparative data on results obtained in the nursery with various fertilization techniques clearly demonstrate the superior efficiency of fertilizer applications regulated so as to avoid high or toxic internal nutrient accumulations, especially early in the growing season.

More often than not the failure of seedlings to respond significantly to manuring during the initial growing season can be traced to improper timing of fertilizer applications. This is particularly true of small-seeded, slow-growing coniferous species such as spruce and hemlock.

Available data indicate that different plants—even species of the same genus—may vary greatly as regards nutrient-absorptive capacity. Thus a nutrient environment which is optimum for a plant of a given age may or may not be equally suitable for another species or even the same species of a different age. Efficiency demands that these differences, for which the usual methods of soil analysis make no allowance, be taken into consideration in the fertilization of tree seedlings—either in culture solutions or seed-bed soils—the manuring of shade and ornamental trees, or in the choice of species to plant or favor on a given forest site. It is believed that internal nutrient concentration, which is proportional to the external supply and with which yield is highly correlated, is the most reliable index to the suitability of any nutrient environment—either culture solution or natural substrate—to a given tree species at any particular time during the period of growth. If the internal concentration of any of the essential elements in seedlings or the leaves of trees growing in soils of unknown fertility is found to be significantly less than the experimentally determined optimum, it is certain that an increase is indicated in the rate of supply of that element. If other environmental factors are favorable, such an increase may be expected to result in a growth response proportional to the degree of the deficiency. Internal concentrations higher than the optimum indicate that either the rate of nutrient supply is too great, or growth, but not absorption, is being inhibited by some other environmental factor. In either event the growth rate will be less than that of which the species is capable under more favorable conditions.

These fundamental relationships discovered in nutrient-sand culture studies and subsequently tested in the field, appear to be equally true of nursery-grown seedlings or mature trees growing in a natural habitat. They are especially valuable in their application to nursery practice. Fertilizer applications at the Black Rock Forest nursery, based upon the results of periodic chemical analyses of the seedlings, are apparently more effective than nutrient supplements made in the usual way—that is, without regard to internal nutrient concentration. Comparative data are presented to show that in seed beds where nutrient environment was adjusted with periodic tests and corrections so as to maintain constant and approximately optimum internal concentrations, it is possible to grow, in two years and without transplanting, white pine seedlings which are significantly larger and much better balanced (root/shoot ratio) than the 3-0 or even the 2-1 stock produced in the average nursery by methods commonly employed.

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