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III. THE GROWTH OF SCOTS PINE (PINUS SILVESTRIS L.) SEEDLINGS IN POT CULTURES OF DIFFERENT SOILS UNDER VARIED RADIATION INTENSITIES

STUDIER ÖVER BARRTRÄDSPLANTANS UTVECKLING I RÅHUMUS

III. TALLPLANTANS (PINUS SILVESTRIS L.) UTVECKLING I KRUKKULTURER I OLIKA JORDAR OCH UNDER OLIKA BESTRÅLNINGSINTENSITETER

BY

P. R. GAST

Redogörelse för verksamheten vid Statens skogsförsöksanstalt under år 1935

Redogörelse för verksamheten vid Statens skogsförsöksanstalt under år 1936

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INNEHÅLL:

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STUDIES ON THE DEVELOPMENT OF CONIFERS IN RAW HUMUS.[1]

III. THE GROWTH OF SCOTS PINE *(PINUS SILVESTRIS* L.*)* SEEDLINGS IN POT CULTURES OF DIFFERENT SOILS UNDER VARIED RADIATION INTENSITIES.

Foreword.

The experiments described in this report were done partly at the Swedish Institute for Experimental Forestry at Experimentalfältet near Stockholm, and partly at the Harvard Forest in Petersham, Massachusetts. The experiments in 1929—30 in Sweden were made during the tenure of a National Research Council Fellowship. The calculations and laboratory analyses were completed in the laboratory of the Harvard Forest. This additional study and the later experiments were supported in part by the Forest Production Research Fund of the Harvard Forest and by grants from the Milton Fund of Harvard University. The writer is happy to acknowledge the assistance received from these sources.

The work in Sweden was sponsored by Professor HENRIK HESSELMAN, Director of the Institute. For his advice on the technical problems, for the facilities of the Institute which he generously made available, for aid in the preparation of this report, and for innumerable courtesies the writer wishes to express his deep appreciation.

The studies at the Harvard Forest were made possible through the support and encouragement of the late Professor RICHARD THORNTON FISHER. As Director of the Harvard Forest he contributed wise counsel and allocated the funds necessary for the continuance of the work. No less important was his steady belief in the value of more information about the physiology of trees. To this knowledge he looked for the background essential to more skillful silviculture.

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[1] Angående införande av denna av en amerikansk forskare författade avhandling hänvisas till den svenska sammanfattningen. Undersökningen utgör en fortsättning på de två studier över barrträdsplantans utveckling i råhumus, som publicerades i Meddelanden Häft. 23, 1927, därav titeln och nr III på avhandlingen.

The writer is indebted for many kindnesses to every member of the staff of the Institute, and of the Chemistry Department of the Central Agricultural Experiment Station. The late Professor SVEN ODÉN was exceedingly helpful. Particular mention should be made of the help of Dr. CARL MALMSTRÖM, Dr. OLOF TAMM, Dr. HANS EGNÉR, Dr. GÖSTA KÖHLER, Miss GURLI LAURENTZ and Mrs. KARIN KNUTSON.

For critical review of the mathematical discussion the writer is indebted to Mr. LARS TIRÉN of the Institute.

The numerous counts of needles and roots and the length measurements on the 1930 seedlings were made by Mrs. CHARLOTTE M. GAST and Mrs. WALBORG FELLENIUS.

The 1931 experiments at the Harvard Forest were under the care of Mr. H. L. MITCHELL as Student Assistant. The results obtained by him in cooperative experiments at the Black Rock Forest have also been drawn upon. The information thus generously shared is explicitly acknowledged in the text.

The 1932 and 1934 experiments and the chemical analyses were in the care of Mr. ELMER SNOW, Research Assistant. The aid of Mr. ROBERT HODSDON and Mr. CLAYTON KNOWLTON should also be mentioned.

All the seedlings have been available to Dr. ALDEN B. HATCH for study in connection with his work on mycorrhizae. Some of the results have already been printed and more details will be available in forthcoming publications. Such phases of the influence of fungal infection as are discussed in this paper are the writer's interpretation of the results of our several common studies.

Experimentalfältet, November, 1935.

P. R. GAST
The Harvard Forest
Petersham, Massachusetts, U. S. A.

Contents.

Introduction.

The experiments which this report describes were devised to study the effects of simultaneously varied mineral nutrition and radiation on the growth of Scots pine (*Pinus silvestris* L.) and white pine (*Pinus strobus* L.). The mineral nutrition was varied by using as substrates sand, and sand mixed with humus — the so-called humus-sand cultures. In addition, pots of sand flowed with the nutrients dissolved in distilled water — the nutrient-sand cultures — have been used. The radiation was altered by lath and by wire-cloth screens, and by filtering out the infra-red energy.

Experimental plant physiology has made marked advance by the method of varying by known amounts separate factors in the environment. In this way much has been discovered about the extent to which the factors of radiation, nutrition, and temperature alter the growth and yield of many plant species in the somewhat artificial environment of the »controlled experiment». Enough has been learned to suggest that further progress now requires the variation of two or more factors simultaneously. But if the individual effects

Table A. **List of experiments cited.**
Förteckning över anförda experiment.

Reference abbreviation[1] Försöket utfört av[1]	Species of pine Tallart	Factors varied Varierande faktorer		Place Plats
		Radiation Strålning	Mineral Nutrition Mineralnäring	
G-'30	Scots *P. Silvestris* L	Yes	Natural soil, raw humus and sand, (five)	Skogsförsöksanstalt Experimentalfältet Sweden
GM-'31	Scots	Yes	Raw humus Raw humus plus nutrients: P, Ca, Mg, S, Fe, (no N) Nutrient-sand cultures with varied nitrogen	Harvard Forest, Petersham, Massschusetts
G-'32	Scots and White	Yes Yes	Nutrient-sand cultures with varied nitrogen	Harvard Forest
M-'32	White *P. strobus* L	No	Forest soils (four) plus P, Ca, Mg, S, Fe, and varied N Nutrient-sand cultures with varied nitrogen	Black Rock Forest, Cornwall-on-Hudson, New York
M-'33	White	No	Forest soils (two of M-'32 repeated) Nutrient-sand cultures with N, P, and K varied in individually	Black Rock Forest
G-'34	White	Yes	Nutrient-sand cultures with N and K varied in combination	Harvard Forest
M-'34	White	Yes	Seed spots in nursery soil	Black Rock Forest
A-B-'29	Corsican *P. larico* Poir., *var. corsicana* Loud.	No	Nutrient-sand cultures with varied N	Kennington, England

are to be separated, increased precision is necessary in the measures both of growth and of the factors conducive to growth.

During the progress of these studies, the methods of measuring radiation have been continuously improved. It has been found that the yield formula of MITSCHERLICH and the compound interest formula can be used with surprising precision to relate to each other the nutrition and the cumulative dry

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[1] G for Gast, M for Mitchell, A-B for Aldrich-Blake; '29, '30 etc. are the years of the experiments.

weights of the seedlings. On the basis of these results it can be expected that further careful work will demonstrate rigorously quantitative associations, in pot trials, of growth factors and growth rates. With this data in hand, even though suspect because of its artificiality (BALLS, 1929; GREGORY, 1929), attention may be directed with more confidence to the controlled field experiment, and finally to the uncontrolled field experiment.

A list of the experiments to which reference will be made is provided (Table A). The experiment listed as A-B—'29 is the work of ALDRICH-BLAKE (1930, pp. 51—57). Not a part of the series started under the direction of the writer, it is included because the nutritional data are complete and so stated that they can be compared with the information on Scots and white pine seedlings; frequent use will be made of the results. Of the other experiments, only a part of the GM-'31 and the M-'32 have been published (MITCHELL, 1934).

The first experiment, using sand and humus-sand mixtures, conducted at the Skogsförsöksanstalt, was highly successful. But it also raised certain questions the answers to which appeared to be necessary if its full significance was to be understood. The tests with Scots pine in nutrient-sand cultures and humus-sand cultures conducted at the Harvard Forest were planned with these questions in mind. The opportune publication of the studies on Corsican pine by ALDRICH-BLAKE (1930) proved very helpful, and they were freely used in planning the later work. Afterward, experiments with white pine were started at the Harvard Forest to gain further silvical information and to substantiate the tentative conclusions drawn from the earlier trials with Scots pine. Improvement of the technique was an additional, though secondary, purpose. Later, co-operative experiments at the Black Rock Forest were started. In these, study of the pot culture as a method for testing forest soil fertility was the primary purpose; new silvical information was secondary.

SECTION I. The Försöksanstalt Experiment — 1930.

In the autumn of 1929 an experiment was started on the effect of varied radiation and nutrition on the growth of Scots pine in the basement of the building of the Chemistry Department of the Swedish Central Agricultural Station. Through the courtesy of the late Professor SVEN ODÉN the pine seedlings were grown in the photoperiod chambers used in the tests being conducted there at that time (ODÉN, 1929, pp. 67—69, 80—125). One chamber received continuous illumination; others were furnished with high wattage electric lamps connected through an ingenious time clock so regulated as to give respectively 6, 9.3, and 13.3 hours of illumination per day. By proper choice of the bulbs, it was possible to obtain intensities such that the products of intensity and time were the same for all chambers. By arranging the pots in two places in each chamber, two values of total radiation were obtained, about 20 and 40 gram calories per square centimeter per day. For the soil substrates, samples of slowly decomposing raw humus, a highly nitrifying raw humus and two samples of spruce raw humus from the south of Sweden were used. The experiment did not yield highly satisfactory results. The indications were that of the four photoperiods, the 13.3 hour illumination time was the optimum for the strain of Scots pine used. If the experiment were to be repeated, the writer would use in addition photoperiods between 15 and 21 hours. The work was most valuable in demonstrating the refinements desirable in later experiments if greater precision was to be obtained. No more details concerning it will be reported.

With the aid of the experience gained in the winter, a new experiment was started in the spring of 1930. This will be referred to herein as the Försöksanstalt experiment of GAST, 1930, abbreviated to G-'30. Individually weighed Scots pine seed were grown in humus-sand and sand pot cultures in varying radiation intensities as classified in Table 1. The physical arrangements at the Försöksanstalt were the same as those previously employed by HESSELMAN (1927).

For the protection of the seedlings the same glass shelter was used (See Fig. 1, HESSELMAN, 1927, p. 344). The seedlings were grown in the same 20 cm (8 inch) pots imbedded in coarse sand to within about 2 cm (¾ inch) of the top. A force pump delivering a fine spray was used for watering, sufficient distilled water being added to keep the moisture content at the optimum dictated by experience.

Radiation Screens.

Three spaces under the glasshouse were fitted with lath screens (Fig. 1) to vary the radiation intensity; in part of a fourth space not fitted with a lath screen, a water screen was used to vary the quality, and this necessarily changed the intensity also.

In the construction of the lath screens, the lath, 1 cm wide, were so spaced as to pass $^1/_2$, $^1/_4$ and $^1/_{16}$ of the radiation. The long dimension of the lath ran parallel to the long dimension of the glass shelter; both were true north and south. By beveling the edge of the lath at an angle of about 60° and placing the narrow edge on top, the aperture between them was open for the passage of direct sunlight the greater part of the day.

The water screen was devised to reduce the infra-red radiation received by the seedlings. Theoretically it absorbed 97 % of the radiation longer than λ 1.0 μ. On pp. 620—621 are described the tray as used in Experimentalfältet and the modification of it used in Petersham. Reduced by absorption and reflection of both infra-red,

Table 1. **Distribution of pot numbers and seed sizes among the radiation intensities and the various humus-sand mixtures, with their differing nitrogen mobilization coefficients. 1930.**

Kruknummer och fröstorlek vid försök med olika strålningsintensiteter och i olika jordslag, speciellt med hänsyn till kvävemobiliseringen.

Humustype Humusslag		Radiation Strålning														
	N mobilization Kvävemobilisering	Screen density 15/16			3/4			1/2			10 cm water screen Vattenskärm			0		
		Screen openings 1/16			1/4			1/2			Radiation λ 0.3 to 1.0 μ only			1/1		
	Total $N_{NH_4+NO_3}$ mg/kg	Radiation relative to open by measurement *4* %			*11* %			*22* %			*27* %			*50* %		
	Total	Pot Kruka	Seed weight Frövikt		Pot Kruka	Seed weight Frövikt		Pot Kruka	Seed weight Frövikt		Pot Kruka	Seed weight Frövikt		Pot Kruka	Seed weight Frövikt	
			Class No.	mg		Class No.	mg		Class No.	mg		Class No.	mg		Class No.	mg
II. Good raw humus God råhumus	75·4	5 6	4 3	4·75 4·25	15 16	4 3	4·75 4·25	25 26	4 5	4·75 5·25	 46	 5	 5·25	35 36	4 5	4·75 5·25
III. Severely burnt raw humus Hårt bränd råhumus	46.2	7 8	4 3	4·75 4·25	17 18	4 3	4·75 4·25	27 28	4 5	4·75 5·25	 48	 5	 5·25	37 38	4 5	4·75 5·25
I. Bad raw humus Dålig råhumus	1.3	3 4	4 3	4·75 4·25	13 14	4 3	4·75 4·25	23 24	4 3	4·75 4·25	43 44	4 5	4·75 5·25	 34	 5	 5·25
IV. Inoc. humus Inf. humus	49.6	10	3	4·25	20	3	4·25	30	5	5·25	50	3	4·25	40	5	5·25
XIII. Mixture[1] Blandprov[1]	46.3	9	4	4·75	19	3	4·25	29	4	4·75	49	5	5·25	39	3	4·25
X. XI. Sand XII.	0.5 0.7 0.2	1 2	4 3	4·75 4·25	11	4	4·75	S1 S2 (21) S4 (22) S5 S6 S7 S8 S9	1 2 4 5 6 7 8 9	3·25 3·75 4·75 5·25 5·75 6·25 6·75 8·00				31 32	4 5	4·75 5·25

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[1] Mixture of 5/6 inoculum humus and 1/6 bad raw humus.
Blandprov av 5/6 infectionshumus och 1/6 dålig råhumus.

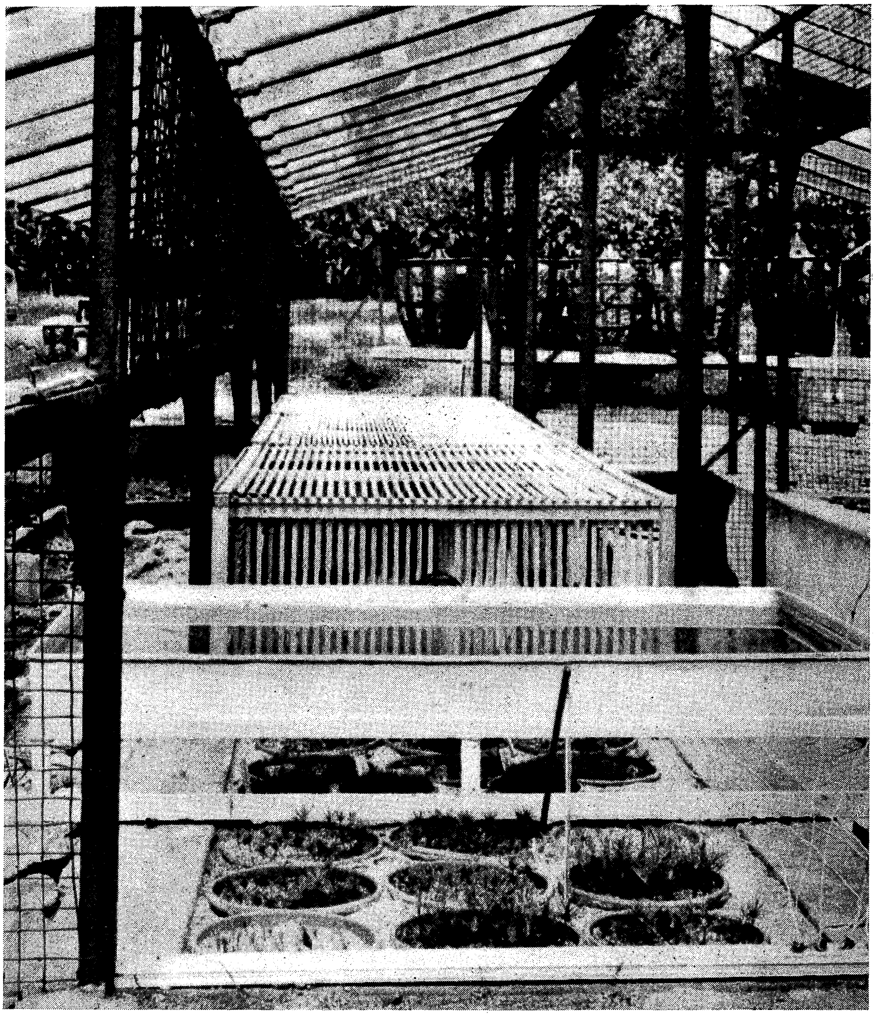


Photo by A. B. Hatch.

Fig. 1. Interior view of the glass shelter, looking north. In front are the plants without lath shade, next is the water screen, then the 1/2 lath shade, the 1/4, and the 1/16. Skogsförsöksanstalt, 1930.

Interiör från växthuset från söder. I förgrunden plantor utan spjälburar, sedan en vattenskärm och där bakom spjälburar med olika beskuggningsgrad, 1/2, 1/4, och 1/16. Skogsförsöksanstalten, 1930.

and visible energy, the intensity of the radiation transmitted by the water screen was measured and found to be 54 %.

Measures of the transmission of the screens were obtained from a limited number of simultaneous records of the radiation intensities underneath them. Pyrheliometers connected to a recording galvanometer were placed in the open, under the various lath screens and in a space in the glasshouse not screened. Critical discussion of the characteristics of various devices for determining the intensity of solar radiation for correlation with plant growth will be postponed until pp. 621—623.

Table 2. **Radiation intensities in the glasshouse and under the screens.**
Strålningsintensiteter i växthuset och i spjälburarna.

Measurements by the Skogsförsöksanstalt: June 1—September 3, 1935 (14 days' observations missing)
Mätningar utförda vid Skogsförsöksanstalten: 1 juni—3 september 1935 (14 dagars observationer saknas).

	Lath screens Spjälburarna			Water screen Vattenskärm	Glasshouse Växthuset
	1/16	1/4	1/2		
Number of observation days Antal observationsdagar	19	22	21		81
A. Total kg cal./cm^2. Registered in glasshouse or under lath screens during the observation days Registrerat i växthuset eller i spjälburarna under observationsdagarna	0.392	1.072	2.067		16.435
B. Total kg cal./cm^2. Registered in the open during the same days as for A Registrerat i det fria under samma observationsdagar som föreg.	6.760	8.964	8.249		30.277
A/B, per cent transmission for season	*5.8* %	*12.0* %	*25.1* %		*54.6* %
Average of per cent transmissions on individual days Medeltal av dagliga intensiteter uttryckt i procent	6.0 %	12.2 %	24.8 %		55.0 %
σ	1.33 %	1.99 %	3.35 %		2.94 %
ε	0.30 %	0.42 %	0.73 %		0.32 %

Measurements by Gast: September 4—September 28, 1930
Mätningar utförda av Gast: 4 september—28 september 1930

Number of observation days Antal observationsdagar	14	6	10	5	12
Average of per cent transmissions on individual days Medeltal av dagliga intensiteter uttryckt i procent	4.4 %	11.3 %	22.5 %	27.3 %	50.6 %
σ	1.45 %	2.04 %	3.51 %	3.46 %	3.01 %
ε	0.38 %	0.83 %	1.11 %	1.55 %	0.87 %

In the summer of 1935 three of the pyrheliometers of the type devised by Dr. T. Aurén, the description of which has not been published, were used to measure again the radiation intensities in the same places. Through the courtesy of Professor Hesselman the following resume of the results obtained by him in 1935 is available. One pyrheliometer was kept in the open, a second recorded the intensity of the radiation in the glasshouse and a third was placed alternately under the various lath screens. Records from June 1 through September 3 are available, with the exception of fourteen days the records for which were imperfect and therefore discarded. The available data are summarized in two different ways in Table 2. The first values were obtained from A) the radiation in kilogram calories received for all the days in which the radiation was being measured in a given place, and B) the radiation received in the open on the same days. The ratios A/B in per cent are the expressions of the relative intensities in the different chambers. The second values were obtained by calculating for each day the per cent intensities in the chambers compared with the radiation in the open. This second method was used by the writer in the calculation of intensities from the observations in September, 1930. In Table 2 are given the means of the daily transmissions, with the standard deviations (σ) and standard errors (ε) of the means, as obtained by the two sets of observations.

The more adequate measurements made in 1935 show good agreement with the earlier measurements made in 1930. The differences between the values for the transmissions in the so-called 11 % and 22 % radiation chambers are not statistically significant. Apparently the transmissions in the so-called 4 % and 50 % chambers were closer to 6 % and 55 % respectively. For the purposes of the study the differences are of no importance, since they do not influence the conclusions.

Not only the average transmission of energy by the screens is important in studying the physiology of the seedlings, but also the amplitude of the fluctuations of the intensity. In the opinion of Professor Hesselman the type of screens to be preferred should be such as to permit high intensities to fall upon the needles for short periods. Plants growing under the canopy of other vegetation are exposed alternately to high and low intensities of radiation. For the greater part of the time they are receiving sky radiation through the larger openings and some of the high-intensity direct radiation sifting between the small openings in the high canopy. But periodically, in the passage of the sun, larger openings permit high-intensity radiation to fall upon the plants for longer periods of time. The lath screens used in these experiments more or less reproduce these natural alternations in intensity. The reduction of intensity by the glasshouse used as a shelter satisfied the same requirement. By comparison with a metal cage with much less iron work (cf. Fig. 1), in which measurements of the radiation were also taken, and under which a loss of 25 % was attributable to metal parts without glass, it may be estimated that at least 30 % of the loss due to the glasshouse was the result of interference by the metal frame work. The rest of the loss of 15 % is probably to be accounted for by reflection, by absorption in the glass, and by absorption in the dust deposited on the glass which in spite of occasional cleaning must have resulted in some interference. This may be checked in yet another way. Estimates of the highest intensities found in the various chambers, taken from the records at favorable cloudless moments, indicate that intensities as high as 85 % of that in the open were periodically reached in the glasshouse — the so-called »50 %» chamber. Similar measurements under the lath screens gave occasional values as high as 60 % in the »22 %» chamber, 50 % in the »11 %» chamber, and 30 % in the »4 %» chamber. These measurements are influenced by the size of the thermopile surface exposed. A large surface will average a greater area which may be receiving varying intensities, and in such a case a small area of high intensity will merely be averaged with the rest of the low intensity area. Small thermopile surfaces, on the contrary, will be wholly irradiated by a comparatively small high-intensity area and will therefore show momentarily high per cent transmissions. The Aurén Pyrheliometer has an aperture of 4 mm, and will therefore show higher momentary per cent transmissions than a thermopile with larger receiving surface.

Statement of the radiation intensities in terms of values relative to full sunlight, the method used above, is common practice. But to bring together the results of different experiments there is required in addition the measure of the full sunlight in terms of absolute units. From this measure and the relative intensities can be determined the absolute amounts of energy available to the plants under the different screens.

The record for the total radiation in the open was not obtained at Experimentalfältet in the summer of 1930. From the records published for Stocksund, an adjacent suburb, can be obtained approximate values for the total direct + diffuse radiation on a horizontal surface in the open during the summer — the so-called vertical component of sun and sky radiation. By use of the 1935 transmissions the approximate absolute intensities received by the plants in the 1930 experiments can be estimated; they are given in Table 3.

The importance of stating the absolute intensities received by the plants may be shown by comparing the records for different years. The records from Stocksund may be used. For the three months — June, July and August — the published values for 1930—35 show the following excess values over the normal value of 34.86 kg.cal./cm^2:

	1930	1931	1932	1933	1934	1935
Excess in kg.cal./cm^2	+ 0.65	+ 0.31	+ 1.33	+ 3.42	+ 0.52	+ 2.96

The radiation received in 1933 was 22 % greater than would have been received with a deficit of 3.42 kg.cal./cm^2 from the normal instead of an excess over it. In precise work this would have a significant effect on the yields of the plants.

Table 3. **Approximate total radiation received by the plants in 1930.**
Plantornas approximativa bestrålning år 1930.

Chambers Burarna	1/16 »4%»	1/4 «11%«	1/2 «22%«	Water screen Vattenskärm »27 %›	Glasshouse Växthuset ›50 %»
Radiation.[1] Kg cal./cm^2 ...... Strålning July 1—September 15	1.5	3.0	6.2	6.8	13,8

[1] Calculated from the transmissions determined in 1935 (Table 2) and the records in the open for Stocksund, published by Statens Meteorologisk-Hydrografiska Anstalt (Årsbok, 1930).

Beräknad på grundval av 1935 års genomlysningsbestämningar (tab. 2) och resultaten av strålningsbestämningar i det fria från Stocksund, publicerade av Statens Meteorologisk-Hydrografiska Anstalt (Årsbok 1930).

Temperatures.

It is to be expected that with unequal shading the temperatures underneath the screens would be different and the growth of the seedlings would thereby be affected. To minimize the temperature differences three fans were installed. Their speed was so regulated by series rheostats as to create a forced air current just sufficient to stir a small piece of paper, but not enough to keep the seedlings in motion. On alternate days near noon, readings were taken of air and soil temperatures with thermometers calibrated against a standard thermometer and found to check within 0.1° C. In Table 4 are given the values of the ranges (A) and the means (B) of these readings. More significant comparisons of the temperature differences between the chambers were obtained when the observations of air and soil temperatures were summarized separately by days, since the variation between days was greater than the variation between situations. The first step was to obtain the mean of all the air temperatures recorded at a given time. The difference between this mean and the individual readings was then calculated. These differences were then averaged and the standard deviation of the differences calculated. They are the values (*C*) recorded in Table 4. Similar summaries, also recorded

Table 4. **Air and soil temperatures in 1930.**

A. The range of the daily noon temperatures.
B. The mean of the daily noon temperatures.
C. The noon temperatures of air and soil in each chamber given as the average of the differences from the daily averages of the noon temperatures for air and for soil in all chambers.

Luft- och marktemperaturen i 1930 års försök.

A. Middagens temperaturextremer.
B. Middagens temperaturmedeltal.
C. Middagens luft- och marktemperatur i varje enskild bur angives såsom medeltal av dess avvikelser under varje enskild dag från medeltalet av middagens luft- och marktemperatur i samtliga burar samma dag.

	Lath chambers Spjälburarna						Water screen Vattenskärm	Glasshouse Växthuset	Range of daily averages Medeltalens extremer
	1/16 »4%»		1/4 »11%»		1/2 »22%»		»27%»	»50 %»	
Air temperature °C Lufttemperatur A	14.0—27.0		14.8—27.3		14.5—27.7			15.7—29.6	
B	21.65		22.23		22.34			23.61	
C	— 0.81		— 0.23		— 0.12			+ 1.16	15—27
σ	0.61		0.30		0.30			0.82	
Soil temperature °C Marktemperatur A	12.5—22.0	12.2—21.6	13 0—22.1	13.6—24.1	14.0—25.5	14.1—25.4	14.6—25.5	16.0—27.5	
B	19.46	18.83	18.87	20.34	20.23	21.09	21.23	23.18	
C	— 1.48	— 1.50	— 1.46	+0.02	— 0.10	+ 0.76	+ 0.88	+ 2.86	15—23
σ	0.70	0.80	0.65	0.83	0.60	0.70	0.48	1.71	

in Table 4, were made for the soil temperature records, of which there was one series for the »full radiation» (50 %), one for the water screen (27 %), and two for each of the lath screens.

The summaries indicate a maximum difference between the air temperatures of the two extremes — the 4 % and the 50 % chambers — of approximately 2° C. The corresponding soil temperature extremes were found to be 4.3° C. The air temperature differences are probably of little importance to the relative growth rates of the plants, but an average difference of more than 4° C in the soil temperature might be expected to have an effect on the nitrogen mobilization and the activity of the roots. But experiments of Professor HESSELMAN subsequent to 1930, to be published shortly, show that the nitrogen mobilization rates of samples of humus in glass beakers placed beside the pots in the various chambers were not significantly different. From the work of ADAMS (1934) may be obtained data on the effect of soil temperature on plant development. The description of his methods indicates the possibility of refinement especially in the control of the soil temperature and the correction for seed size. The results are highly instructive, however. They indicate that for the race of white pine used, the increase in the weight of the whole plant is about 5 % for each degree Centigrade increase in soil temperature within the range of 15° to 31° C. The difference between the soil temperatures in the 4 % and 50 % radiation chambers cited above is 4.3° C. This temperature effect alone would account for an increase in dry weight of about 23 % for the seedlings raised in the 50 % radiation over the seedlings raised in the 4 % radiation. This estimate depends on the assumption that the temperature coefficient of the Scots pine is identical with that of white pine. As will be shown, the largest plants raised in the most fertile soil in the 50 % radiation are about 1300 % of the weight of those raised in the same soil in the 4 % radiation. An increase of 23 % is therefore not important. Nevertheless, the necessity is indicated of confining the soil temperature to an exceedingly narrow range in any precise experiments involving radiation differences.

Humus Samples.

The use of various types of forest humus samples in an experiment of the sort described in this paper requires an extensive knowledge of their fertility. A question as to the relative importance of the factors of radiation and nitrogen supply had been raised previously in a field study of the effect of radiation on the growth of seedling white pines (GAST, 1930, pp. 57—59). This question could be answered only by study of the effect of simultaneously varied nitrogen supplies and radiation intensities. The earlier cultural experiments of HESSELMAN (1927) suggested a method of attacking the problem. In a series of studies (HESSELMAN, 1917 a, b, c, 1926, 1927) an extensive range of widely varying humus types had been investigated. This experience was fundamental to the use of forest humus as a source of mineral nutrition.

The humus samples listed in Table 1 were taken from sources similar to those previously studied by HESSELMAN. A mixture of the same proportions, one part by volume of humus and two parts by volume of sand, was employed. As a relative measure of nitrogen availability the nitrogen mobilization coefficients for the total of ammoniacal and nitrate nitrogen are given in Table 1, p. 593. The humus types from which the samples were obtained may be characterized briefly as follows.

I. **Bad Raw Humus** from the hill Storliden in the Kulbäcksliden Research Forest, northern Sweden (province of Västerbotten, station 24 on map, Fig. 3, HESSELMAN, 1926, p. 209). It was taken from a stand of spruce with a small admixture of pine about 250 years old, showing slow growth. Characterized as a *Hylocomium*-rich wood of the *Vaccinium myrtillus* type (MALMSTRÖM in TAMM and MALMSTRÖM 1926, pp. 38—41) the humus is rather deep, containing approximately equal parts of *F* and *H* layers with a total thickness of 5.1 cm. The nitrogen mobilization of this type is usually very small; inoculation with nitrifying organisms and the addition of lime are usually without effect.

For references to previous studies see HESSELMAN (1926) p. 466, area No. 3: vegetation description, Table 83, number 3; humus analysis, Table 84, number 3; discussion in text, pp. 347—356 area No. 3, (p. 348). Note especially Figs. 66 and 67; Fig. 44, p. 351. In addition, see HESSELMAN (1927) pp. 370—395, the samples of Series D, group I, tests a.—d. (pp. 370—371) comprising growth tests with pines on the same material.

II. **Good Raw Humus** from Brända Holmen in the bog Degerö stormyr near the hill Kåtaåsen, Kulbäcksliden Research Forest. (The stand was about 2 kilometers — 1.2 miles — from the stand in which sample I was obtained.) The stand was spruce with some pine and birch originating after a fire (Brända Holmen means Burned Island) and making good growth. The sample contained about equal proportions of *F* and *H* layer material, being taken from a total *F* plus *H* layer about 6.0 cm deep. Although a vigorous nitrogen mobilization occurs naturally, the addition of inoculum containing nitrifying organisms and lime increases it markedly.

For references to previous studies see HESSELMAN (1926) pp. 347—356, area No. 5 (p. 348), nitrogen mobilization tests detailed in Table 39, No. 5 (p. 356), analyses for nitrogen, lime and loss on ignition in Table 40, No. 5 (p. 356). Note particularly Fig. 46 (p. 353). See also HESSELMAN (1927) pp. 370—395, the samples of Series D, group III, a.—d. (p. 371) comprising growth tests with pines on the same material.

III. **Burnt (Bad) Raw Humus** from a clear-cutting north of the hill Storliden in the Kulbäcksliden Research Forest. (The area was about 0.8 kilometer — 0.5 mile — from the stand in which sample I was obtained.) The area had previously borne a slowly growing spruce stand similar to the one under which the bad raw humus was obtained. After the clear-cutting the humus was subjected to deliberate controlled burning in May, 1927 (Fig. 2). In the

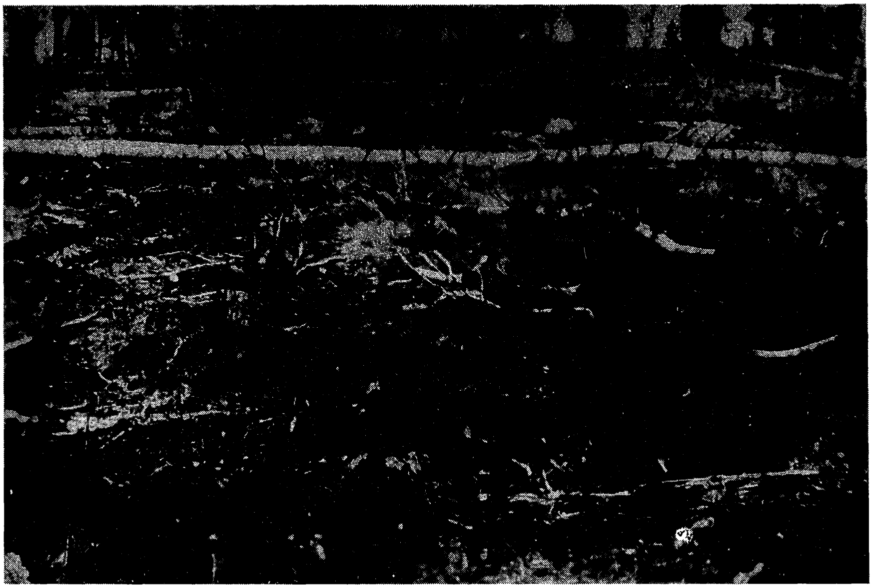


Photo by A. B. HATCH.

Fig. 2. Area from which the severely burnt (bad) raw humus samples were collected. Near Storliden, Kulbäcksliden Research Forest, 1930.

Plats varifrån prov av hårt bränd (dålig) råhumus insamlats. Nära Storliden, Kulbäckslidens försökspark, 1930.

places from which the samples were taken the fire had burned the *F* layer, but had scarcely affected the *H* layer. Compared with sample I, the development of small-crumb structure in the *H* layer was noteworthy. A moderately high nitrogen mobilization and nitrification were found. Necessarily the sample was taken from the *H* layer.

IV. »**Inoculum**» **Humus** from an esker near Glindran in Södermanland in central Sweden (station 5 on map, Fig. 3, HESSELMAN, 1926, p. 209). It is called »inoculum» humus because it was used to infect samples with nitrifying organisms in the previous experiments of HESSELMAN (1926, p. 203). The sample collected in 1930 was taken from an area from which Scots pine had been clearcut about five years previously. The herbaceous flora which was present at the time of collection was similiar to that given for the clear-cutting of 1911—1912 (HESSELMAN, 1917 b, p. 1034). The evidence of this nitrophilous flora is substantiated by tests indicating a moderately high nitrogen mobilization and a very high nitrification. The *F* layer was very thin or often lacking. The humus material had been carried into the mineral soil which was dark, with a loose structure, and worked by worms — well on the way to becoming a mull. Not a superficial organic horizon, it was comparatively low in organic matter; the loss on ignition before mixing with sand was 57 %.

For references to previous studies see HESSELMAN, 1917 b, and 1926. The descriptions on p. 1032 (1917 b) apply to vegetational succession generally following on clear-cuttings in the region. The later study (1926) demonstrates under what conditions nitrification takes place in forest humus. To obtain humus of this type the localities from which the samples are taken necessarily must be changed from time to time.

X, XI, XII. **Sand.** Various lots of commercial cement sand of fluvioglacial origin were used as the base for the mixtures. It was sieved to pass a 10 mesh and to be retained on a 28 mesh Standard Tyler Screen — the diameters of the particles were from 0.59 to 1.65 mm (0.013 to 0.035 inches). The organic and nitrogen contents were negligible.

XIII. **Mixture.** By the combination of one part of the bad raw humus-sand mixture with five parts of the inoculum humus-sand mixture a material high in nitrates but containing some resistant organic nitrogen was obtained. Of this mixture one pot was placed in each of the radiation chambers.

By the use of raw humus as a substrate in these experiments it was hoped that advantage might be taken of several desirable features. It was anticipated that progressive nitrogen mobilization would supply increasing quantities of nitrogen as the plants increased in size. Secondly, the naturalness of the substrate was considered an advantage. Thirdly, the results of such experiments might be of more value and interest to the practicing forester than experiments with sand cultures.

The choice of the good and the bad raw humus was well made, and the use of the sand control was advantageous. The choice of the severely burnt (bad) raw humus was not so fortunate, since the area from which it was taken has since failed to develop the usual nitrophilous flora, and it seems probable that the same untoward condition was the reason that the seedlings grown on this substrate did not develop as well as had been anticipated. The inoculum humus contained a fungus, *Mycelium Radicis atrovirens*-type Melin, which attacked the plants. The mixture of five parts inoculum humus and one part of bad raw humus gave a highly artificial substrate.

Seed.

The seed used in the 1930 Försöksanstalt experiment were Scots pine (*Pinus silvestris* L.) from Eriksberg near Katrineholm, Södermanland, 115 km west and slightly south of Stockholm. At the request of Mr. SVEN PETRINI, they were kindly collected by Mr. C. CEDERGREN in the autumn of 1929 from well-formed, mature, dominant trees. The average seed weight was 4.47 mg; they germinated well, and seed from the same lot were used in the GM-'31 and the G-'32 experiments. The moisture content was 7.2 %, the average dry weight of seed coats of 4.75 mg seed was 1.48 mg. The provenance of this seed is characterized by LANGLET (private communication) as a region of 165 days with an average temperature of 6° C or higher, the average temperature of the warmest month (July) being 16.3° C.

The winter experiment of 1929-30 indicated the desirability of correcting the weight of seedlings for the amount of food reserves in the seed available at the time of germination. The seeds were therefore individually weighed and separated into classes differing by 0.5 mg. These classes were kept separate in the subsequent treatments.

Planting and Care of Seedlings during Growth.

The seeds were soaked, sterilized in 0.1 % $HgCl_2$ solution for one minute, thoroughly washed in sterile water, and germinated in sterile Petri dishes. On June 22, when the radicles were about 4 mm — $^3/_{16}$ inch — long, 30 seeds of a single weight class, as shown in Table 1, p. 593, were planted in each pot.

The seedlings were under the care of Miss GURLI LAURENTZ, Mrs. KARIN KNUTSON and Miss MARGARETA JOHANSSON during the prolonged absences of the writer from Experimentalfältet. It was owing to their alert interest that the experiment was carried through successfully.

The only untoward incident was a heavy infestation of aphids on the plants in the 4 % radiation chamber.

Harvesting.

Terminal buds had set on all plants early in September. Harvesting was started September 14th and completed on September 23rd. The unshaded pots were removed first, those in the 4 % intensity last. Duplicate pots were harvested on different days; it is believed that any differences in weight accruing from additional time for growth were of no moment.

The entire contents of the pot were dumped onto a coarse mesh screen. The roots were next washed free from sand and humus by a stream of water. They were then cleaned with a soft brush and further inspected under the microscope; such scrutiny revealed no breakage. The plants were separated into large numbered test tubes and kept wet during subsequent measurements.

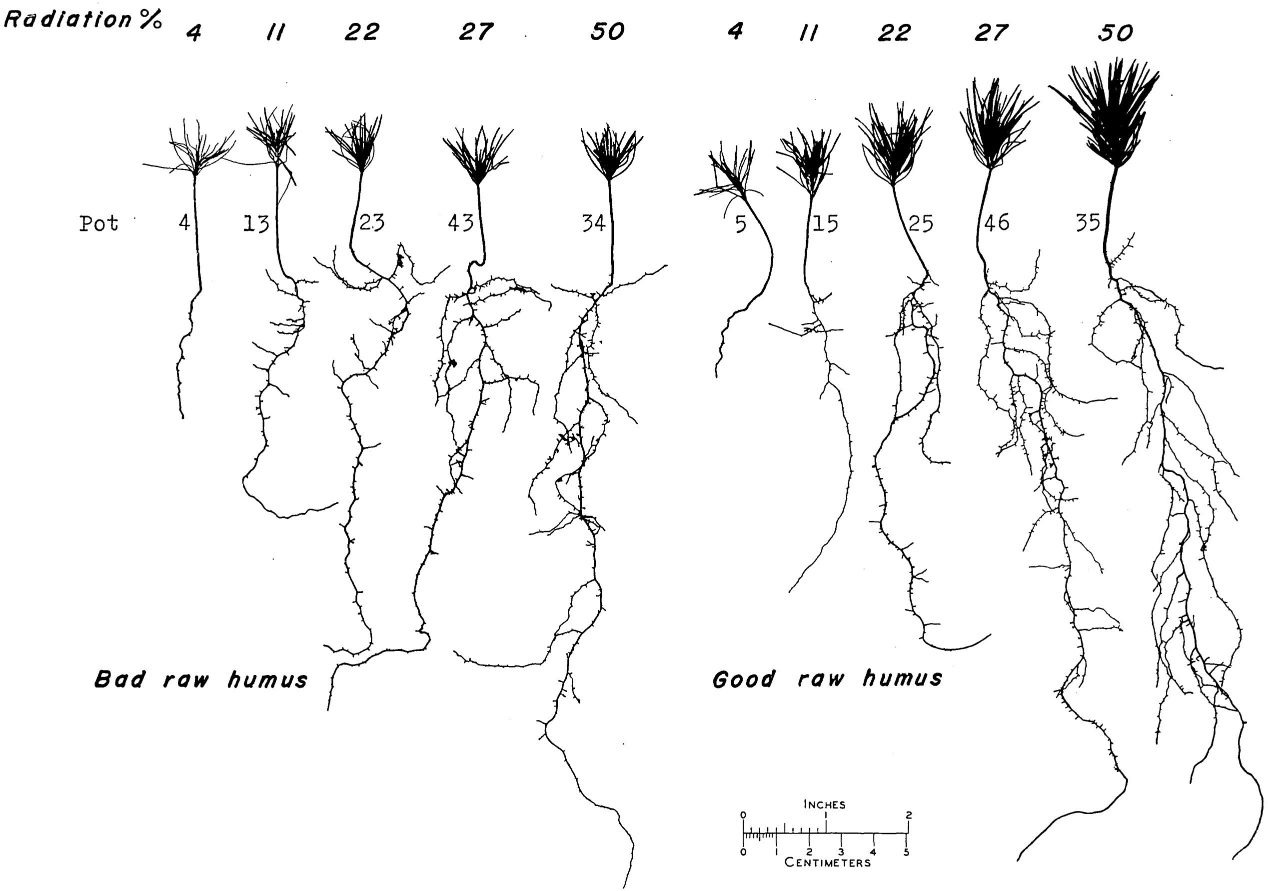
Lengths of primary leaves, stems, and roots were taken, and a count was made of the numbers of primary leaves. Notes on the character of the short roots were made by Dr. A. B. HATCH and are to be discussed by him in another paper.

Fresh weights were taken for the tops and roots separately for approximately half of the plants. The others were cut apart and dried immediately. The electric oven was maintained at about 80° C during the drying.

The material was then transported to the laboratory of the Harvard Forest for further analysis.

SECTION II. Experimental Results of the Försöksanstalt Work — 1930.

The silhouette photographs in Fig. 3 show the marked differences in the appearance of the average seedlings grown from seed of the same size in the good raw humus and the bad raw humus under the different radiation



Silhouettes by A. B. HATCH.

Fig. 3. Seedlings grown in the good raw humus- and the bad raw humus-sand mixtures. Skogsförsöksanstalt experiment, 1930.

Plantor uppdragna i god råhumus-sand och i dålig råhumus-sand. Från försök å Skogsförsöksanstalten, 1930.

intensities. It is evident that with low radiation the greater availability of nitrogen is without influence, and that the greater the radiation intensity the greater the benefit from an increased supply of nitrogen. This variation in the size of the seedlings was to be expected from the earlier work of HESSELMAN, CIESLAR, and others. But the purpose of this experiment was to obtain, if possible, more precise quantitative descriptions of seedling growth under different environmental conditions. To this end numerous measurements were collected on seedling weights, root weights, lengths, and development, needle numbers and shoot lengths. When refined by statistical methods, these quantitative data furnish a description of the reaction of the Scots pine seedlings to changes in radiation and nitrogen supply.

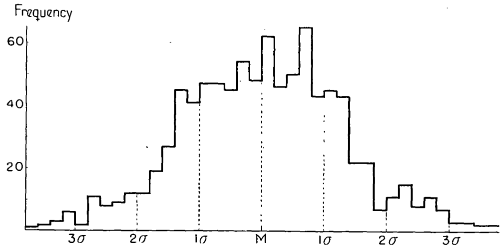


Fig. 4. Frequency distribution by 0.2 σ classes of seedling weights from all pots. Skogsförsöksanstalt, 1930. M = mean.
Viktsfördelningen på 0,2 σ klasser av plantorna från alla krukor, Skogsförsöksanstalten, 1930. M = medeltal.

Seedling Dry Weights.

Some of the plants harvested were at once discarded: plants with evident malformations were rejected on the basis of appearance alone. Thus the plants in the 4 % radiation chamber attacked by insects were readily detected and their weights not included. From a total of 1203 seedlings, 107 were rejected by inspection. Of these, 49 were in the ten pots in the 4 % chamber and had been injured by aphid attack. The remaining 58 were discarded from the other 42 pots, an average of slightly more than one plant per pot being thus discarded.

The »first average» was further refined by discarding those plants whose weights differed from the mean by an amount greater than $l \cdot \sigma$[1]; thus 142 plants were eliminated. The value of l, which varies between 1.92 and 2.35, is determined by the size of the sample. This criterion for rejection is due to CHAUVENET (PALMER, 1912, pp. 127-130, 226). It is derived from study of the normal curve of distribution, and may be used only with normally distributed samples. That the distribution of the plants was approximately normal around the means of the individual

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[1] The usual formula for the calculation of the standard deviation, σ, is

$$\sigma = \sqrt{\frac{\Sigma (x - M_x)^2}{n}}$$

where x is the variate, M_x the arithmetic mean, N the total number of items, and $n = N - 1$. This formula is not convenient in calculating the values of the mean and σ as they are refined by discarding the plants whose weights show excessive deviations. These operations are facilitated by the use of the formula used extensively by WALLACE and SNEDECOR (1931):

$$\sigma = \sqrt{\frac{\Sigma x^2 - M_x \cdot \Sigma x}{n}}$$

pots is shown in Fig. 4. This distribution curve was obtained by summing the occurrence of seedling weights in classes determined by the pot means and standard deviations of the 1096 seedlings remaining after the first discard.

By this rejection both superior and inferior genotypes were eliminated. Only those plants which fell within the range of the normal distribution curve of very small samples were retained.

The mean dry weights of the »second average» series did not differ from the weights obtained for the »first average». An improvement was observed in the value for the standard deviation, σ. The standard deviation expressed as a per cent of the mean — herein designated as $\sigma_{\%}$ and sometimes called the coefficient of variation — was calculated for each pot. They indicated that after discarding lighter and heavier plants by the use of the CHAUVENET criterion, the weights of 68 % of the plants lay within about thirteen per cent — actual average, 12.3 % — of the mean weight of the plants in the pot, although in some pots the figure is rather larger. The significance of the mean weight of the plants in the pot can be further defined by a statistic called the standard error of the mean, σ_M, or ε. If as above the coefficient of variation is symbolized by $\sigma_{\%}$, then the standard error of the mean expressed as a per cent of the mean may be symbolized by $\varepsilon_{\%}$. The values of this statistic were also determined. By dividing the average $\sigma_{\%}$ (12.3 %) by the square root of the number of plants in the average pot ($\sqrt{18} = 4.243$) the value 2.90 is obtained as the average estimate of $\varepsilon_{\%}$. This means that if an indefinitely large series of replicate pots containing 18 plants each were used for a given treatment, the chances are 2: 1 that the mean of the series would be within ± 2.90 % of the means given in Table 5 and that 68 % of the mean plant weights of the individual pots in the series would lie within the range of about ± 2.90 % of the listed means. The values of ε and $\varepsilon_{\%}$ for the individual pots are given in the summary tables.

With the mean weights of the plants in the several pots thus reduced to a basis truly representative, the next step is to convert these mean weights to a value equivalent to the mean weights which would be found if the seedlings in all the pots were grown from seed of a single weight class. In an experiment where the increase in dry weight is the measure of growth, the weight of the plant at the start of the experiment is the base for the calculation. When plants are raised from seed, as in these experiments, the dry weight of the food reserve in the seed is the base. Discussion of the methods used for these calculations is given on pp. 629—633. For the present discussion it is sufficient to note that in the preparation of Table 5, the M, ε, and $\varepsilon_{\%}$ have been corrected by the appropriate factor listed on p. 631 to change them to values as of fresh seeds weighing 4.75 mg.

The mean weights of plants in various pots, refined and adjusted as described, are collected in the summary, Table 5. In it are also included the mean and standard error of the mean of the two duplicate pots pooled as a single sample. These grouped means are the values used in the graphical figures and in the discussions. This was done in spite of the fact that statistical analysis shows that in four cases out of fifteen there is a highly significant difference between the duplicate pots, and in one more instance, a significant difference. The significance of difference is estimated from the value of t as described by FISHER (1932). As will be shown later (p. 659), these dif-

Table 5. **Dry weights of three-months-old Scots pine seedlings grown in different radiation intensities and in various humus-sand mixtures. 1930.**

Torrvikter av tre månader gamla tallplantor, uppdragna vid olika solstrålningsintensiteter och i olika humussandblandningar. 1930.

Humus Humusslag	Radiation (Strålning) 4 % Pot Kruka	M mg	± ε mg	11 % Pot Kruka	M mg	± ε mg	22 % Pot Kruka	M mg	± ε mg	27 % Pot Kruka	M mg	± ε mg	50 % Pot Kruka	M mg	± ε mg
II. Good raw humus God råhumus	5	6.46	0.24	15	16.21	0.59	25	34.59	0.96				35	80.59	2.90
	6	6.69	0.18	16	20.30	0.57	26	38.45	0.82	46	50.70	1.37	36	92.27	3.49
			t = 0.74[2]			**t = 5.00**[2]			t = 2.98[2]						t = 2.54[2]
	mean[1]	*6.58*	*0.15*		*18.41*	*0.48*		*36.42*	*0.70*					*85.64*	*2.49*
III. Severely burnt raw humus Hårt bränd råhumus	7	6.95	0.18	17	18.33	0.45	27	29.32	0.52				37	44.21	1.74
	8	7.07	0.19	18	14.06	0.41	28	29.85	0.62	48	36.21	0.65	38	40.52	1.19
			t = 0.47[2]			**t = 6.91**			t = 0.61						t = 1.74
	mean[1]	*7.01*	*0.13*		*16.06*	*0.44*		*29.62*	*0.41*					*42.36*	*1.08*
I. Bad raw humus Dålig råhumus	3	6.46	0.31	13	13.85	0.34	23	21.96	0.53	43	26.32	0.61			
	4	6.60	0.16	14	13.61	0.30	24	21.13	0.31	44	27.08	0.74	34	29.86	0.45
			t = 0.38			t = 0.53			t = 1.22			t = 0.94			
	mean[1]	*6.57*	*0.15*		*13.72*	*0.22*		*21.45*	*0.28*		*26.63*	*0.47*			
IV. Inoculum humus Infektionshumus.	10	7.79	0.20	20	19.04	0.70	30	48.19	2.46	50	48.46	4.22	40	54.85	1.89
XIII. Mixture[3] Blandprov[3]	9	6.54	0.17	19	10.83	0.54	29	27.25	0.94	49	37.96	1.02	39	33.55	1.09
X. XI. XII. Sand	1	7.66	0.35	11	15.91	0.61	21	28.46	0.49				31	34.38	0.79
	2	7.80	0.16				22	28.01	0.96				32	31.05	0.94
			t = 0.58						t = 0.41						**t = 2.65**
	mean[1]	*7.73*	*0.18*					*28.24*	*0.53*					*32.60*	*0.56*

[1] Mean and standard error of the mean, ε, of the plants in the duplicate pots pooled as a single sample.

Medeltalet och medelfelet på medeltalet (ε) för de samtliga proven i parallellkrukorna.

[2] t was estimated by the formula of FISCHER (1932, Section 24 : 1, p. 107). By the style of type used in printing the value of t is indicated the probability that the plants in the duplicate pots can be considered random samples of a homogeneous population — that is, grown in similar environments:

t — probability of 0.05 or greater, such difference appears with a chance of 1 : 20 or more often, not significant difference.

t — probability between 0.05 and 0.01, such difference appears with a chance of 1 : 20 to 1 : 100, significant difference.

t — probability of 0.01 or less, such difference appears with a chance of 1 : 100 or less often, highly significant difference.

t uppskattades enligt FISHERS formel (1932, stycket 24 : 1, sid. 107). Genom bokstavstyperna hos t-värdet angives sannolikheten för att plantproven i parallellkrukorna kunna betraktas som slumpvis uttagna prov av en homogen population, m. a. o. att de uppvuxit under likartade betingelser:

t — sannolikheten 0.05 eller större; en sådan differens uppstår i fall på 20 eller mindre; icke signifikativ skillnad.

— sannolikheten 0.05—0.01; en sådan differens uppstår i fall på 20—100; signifikativ skillnad.

t — sannolikheten 0.01 eller mindre; en sådan differens uppstår i 1 fall på 100 eller mera: mycket signifikativ skillnad.

[3] Mixture of $^5/_6$ inoculum humus and $^1/_6$ bad raw humus.

Table 6. The differences between the dry weights of three-months-old Scots pine seedlings grown in unlike humus-sand mixtures compared for significance of difference. 1930. Data from Table 5.

Skillnaderna i vikt mellan 3 månader gamla tallplantor, uppdragna i olika slag av jord samt sannolikheten för, att de äro signifikativa.

Soil Jordslag	Radiation (Strålning)														
	4 %			11 %			22 %			27 %			50 %		
	Pots Krukor	*M* mg	± ε mg	Pots Krukor	*M* mg	± ε mg	Pots Krukor	*M* mg	± ε mg	Pots Krukor	*M* mg	± ε mg	Pots Krukor	*M* mg	± ε mg
II. Good raw humus	5+6	*6.58*	0.15	15+16	*18.41*	0.48	25+26	*36.42*	0.70	46	*50.70*	1.37	35+36	*85.64*	2.49
III. Severely burnt raw humus.	7+8	*7.01*	0.13	17+18	*16.06*	0.44	27+28	*29.62*	0.41	48	*36.21*	0.65	37+38	*42.36*	1.08
II. God råhumus.			*t* = 2.18[2]			***t* = 3.44**[2]			***t* = 8.04**[2]			***t* = 9.13**[2]			***t* = 16.1**[2]
III. Hårt bränd råhumus	*diff.*	*0.43*			*2.35*			*6.80*			*14.49*			*43.28*	
III. Severely burnt raw humus.	7+8	*7.01*	0.13	17+18	*16.06*	0.44	27+28	*29.62*	0.41	48	*36.21*	0.65	37+38	*42.36*	1.08
I. Bad raw humus.	3+4	*6.57*	0.15	13+14	*13.72*	0.22	23+24	*21.45*	0.28	43+44	*26.63*	0.47	34	*29.86*	0.45
III. Hård bränd råhumus.			*t* = 2.17			***t* = 4.42**			***t* = 16.4**			***t* = 12.0**			***t* = 8.00**
I. Dålig råhumus.	*diff.*	*0.44*			*2.34*			*8.17*			*9.58*			*12.50*	
III. Severely burnt raw humus.	7+8	*7.01*	0.13	17+18	*16.06*	0.44	27+28	*29.62*	0.41				37+38	*42.36*	1.08
X, XI, XII. Sand.	1+2	*7.73*	0.18	11	*15.91*	0.61	21+22	*28.24*	0.53				31+32	*32.60*	0.56
III. Hårt bränd råhumus.			***t* = 3.27**			*t* = 1.23			*t* = 1.80						***t* = 7.81**
X, XI, XIII. Sand.	*diff.*	*0.72*			*1.11*			*1.38*						*9.76*	
X, XI, XII. Sand.	1+2	*7.73*	0.18	11	*15.91*	0.61	21+22	*28.24*	0.53				31+32	*32.60*	0.56
I. Bad raw humus.	3+4	*6.57*	0.15	13+14	*13.72*	0.22	23+24	*21.45*	0.28				34	*29.86*	0.45
X, XI, XII. Sand.			***t* = 4.59**			***t* = 4.12**			***t* = 10.7**						***t* = 2.81**
I. Dålig råhumus.	*diff.*	*1.16*			*2.19*			*7.21*						*2.74*	

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[1] and [2]. See footnote of same number in Table 5.

ferences in yields can be explained on the basis of various quantities of nitrogen taken up by the seedlings in presumably duplicate pots.

The same *t* test can be employed to estimate whether the differences between mean weights of seedlings grown with varied nutrition in identical radiation intensities are significant. In Table 6 are entered the results of the tests. In 11 % or greater radiation intensities the three humus mixtures produced plants with highly significant differences. In 4 % radiation the plants grown in sand were the largest, the difference being highly significant. Comparison of the plants grown in sand and in bad raw humus indicates that in all cases the pure sand produced significantly larger plants than did the mixture of sand with bad raw humus. In two radiation intensities, the severely burnt (bad) raw humus and the sand produced plants which were not significantly different; only when the radiation reached 50 % was the higher fertility of the burnt raw humus evident.

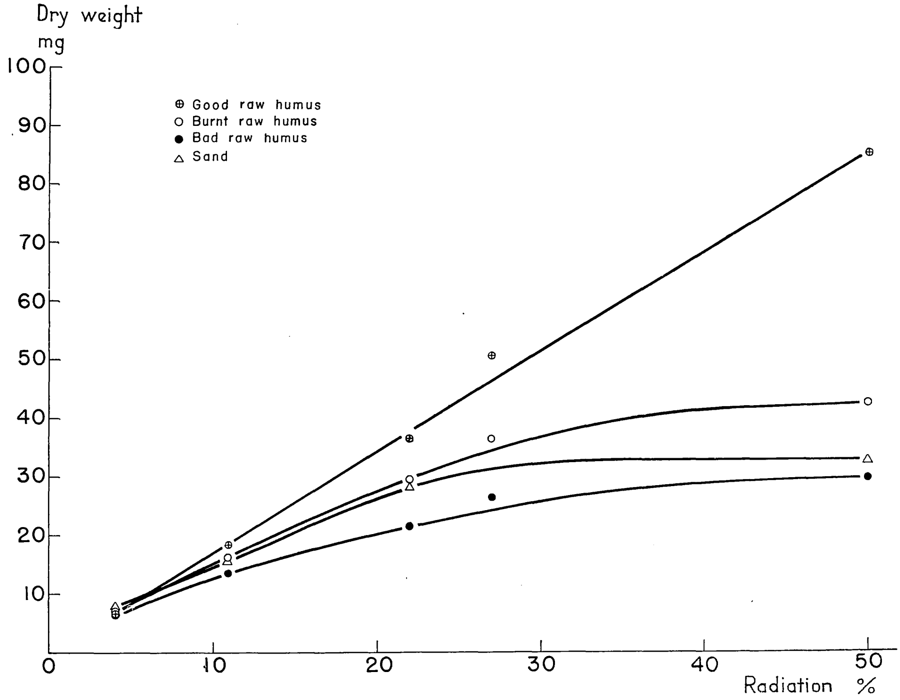


Fig. 5. The dry weights of three-months-old Scots pine seedlings grown in different radiation intensities in various humus-sand mixtures. Weights adjusted to values corresponding to a fresh seed weight of 4.75 mg. Skogsförsöksanstalt, 1930. See Table 5.

Torrvikt hos tre månader gamla tallplantor, som uppdragits vid olika bestrålningsintensiteter i olika humus-sandblandningar. Vikterna korrigerade till värden, motsvarande en friskvikt å fröet av 4,75 mg. Skogsförsöksanstalten, 1930. Se tab. 5.

In the later discussion of these experiments the emphasis will be placed on the nitrogen fertility of raw humus as evidenced by the nitrogen intake of the seedlings. It will be shown that the phosphorus and potassium contents in relation to the nitrogen in the seedlings were more than adequate. The nitrogen content of seedlings grown in bad raw humus was greater both in milligrams and in per cent than for those grown in sand. But the addition of bad raw humus to sand has the effect of decreasing its fertility since seedlings of lower weight result. This indicates a fundamental problem in the investigation of raw humus. It would seem that in the type of bad raw humus used in this experiment a parasitism, possibly due to mycorrhizal fungi (MELIN, 1925, p. 113), is responsible for removing food from the seedlings grown in it.

In Figure 5 are given smoothed curves of the variation of seedling weights with changing radiation intensities, the data for the three humus-sand cultures having been taken from Table 5. The weights of plants grown in the good raw humus soil with a high nitrogen mobilization are directly proportional to the increase in radiation intensity up to 50% of full sunlight. The weights of plants grown in the poorer soils increase with increasing radiation but tend to approach an upper limiting value which is lower, the lower the nitrogen mobilization.

Dry Matter Contents.

The fresh weights of tops and roots of the plants were taken at the time of harvesting. The ratios between dry weights and fresh weights of the individual plants were calculated and expressed as dry matter per cent.

In the study of the dry matter content of the roots no variation was found in the three-months-old plants grown under these conditions.

The dry matter content of the tops varied greatly in the plants grown with different radiation and different nutrition. As is shown in Fig. 6, the range of dry matter per cent is rather wide — from 18.8 % in the good raw humus under four per cent radiation to 31.6 % in sand under fifty per cent radiation. Distinct trends are evident. The diminishing content of dry matter as the radiation decreases reflects the succulence characteristic of etiolation. The less fertile the soil, the greater the content of dry matter of the seedlings grown in it. The changes brought about by different nitrogen supplies within a given radiation intensity are greater for high intensities than for low. The dry matter per cent of the tops of seedlings grown in good soils changes but little with changing radiation, provided it is greater than ten per cent; in poor soils, with radiation greater than twenty per cent. The influence of nutrition on the density of the plant tissues is clearly shown.

In the determination of the effect of radiation and other environmental factors on the growth of seedlings it is evident that size as measured by length or volume is to a certain extent misleading. Plants grown in moderately high radiation intensities in soils of different fertility are larger in the more fertile soils than would be expected by comparison of their dry weights. Similarly, plants grown in soils of the same fertility under different intensities of radiation are larger in the low intensities than would be expected by comparison of their dry weights.

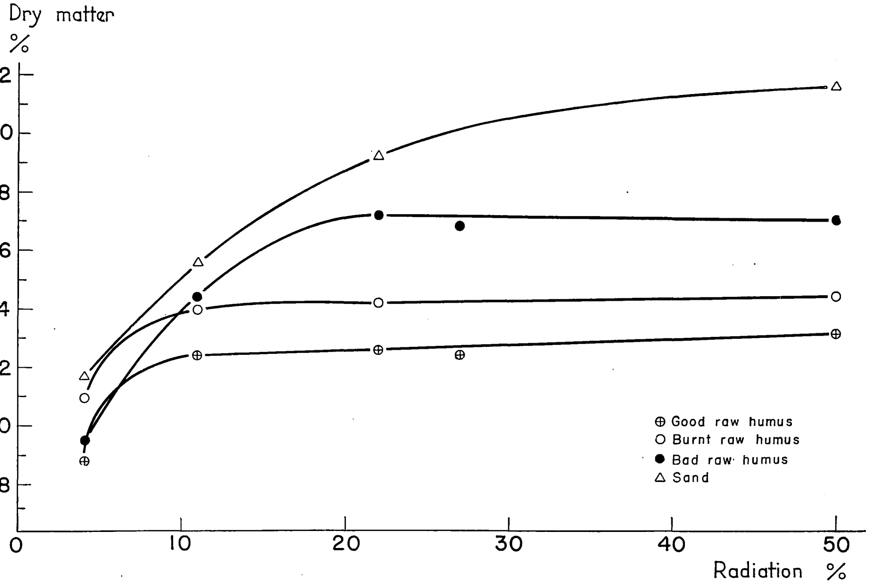


Fig. 6. The dry matter per cent in shoots of Scots pine seedlings grown in different radiation intensities in various humus-sand mixtures. Skogsförsöksanstalt, 1930.

Torrsubstanshalt i skott av tallplantor, som uppdragits vid olika bestrålningsstyrka i olika humus-sandblandningar. Skogsförsöksanstalten, 1930.

The plants grown in the more fertile soils were much lower in dry matter content than those grown in less fertile soils. The plants grown in low light intensities were much lower in dry matter content than those in higher light intensities. The diagnostic value of the dry matter content of pine seedlings in determining their hereditary frost hardiness has been shown by LANGLET (1934). It appears probable that soil fertility and radiation intensity may superimpose minor variations in frost hardiness — and possibly drought hardiness — upon the major differences due to hereditary qualities. In a series of experiments MARSHALL (1931) determined the water content of the seedling tops of a number of American conifers grown in sand as they progressively dried out to the point of wilting. In further studies of this sort it would seem well to take into account other environmental factors, such as radiation and nitrogen supply, in addition to the moisture content of the substrate.

An attack of aphids on plants growing in the 4 % radiation chamber has already been noted. It seems that the localization of the attack on the plants growing in this radiation intensity is of physiological importance, and probably associated with the low dry matter content and parallel high water content of these plants. To give substance to this suggested explanation an elaborate investigation is necessary, requiring the united work of a physiologist and an entomologist.

Number of Primary Needles.

In previous experiments HESSELMAN (1927) used the number of primary needles as an index of relative growth under varying conditions of nitrogen supply. The correlation between the number of primary needles and the dry weights of the plants is therefore of interest. For all the plants from all the pots, after discarding for the »second average» as described (p. 606), the correlation coefficient (*r*) between needle number and dry weight is .82. A correlation table showed that the plants from pots 35 and 36 were heavier than the proportionate number of needles indicated. By eliminating the plants from these two pots the correlation coefficient is raised to .87. But the dispersion is large throughout. Therefore growth as measured by numbers of needles is adequate to reveal only approximate quantitative relations and may be so used where lack of weighing equipment prohibits the use of the more precise index, dry weight.

Lengths and Numbers of Roots.

Following the terminology of ALDRICH-BLAKE (1930) and HATCH and DOAK (1933) the names used in this paper for the parts of the root system are radicle, laterals, and short roots. The radicle is the primary or tap root. The term lateral as here used includes those roots further distinguished as mother and pioneer roots; both are polyarch, containing two or more vascular strands. The short or monarch roots contain a single vascular strand; but the term as used in this report may include mother roots which might later become polyarch pioneers were their development not arrested by mycorrhizal infection. The monarch roots and slowly growing polyarch roots are subject to infection by mycorrhizal fungi. For measurement and

Table 7. **Total lateral root length per plant of three-months-old Scots pine grown in different radiation intensities and in various humus-sand mixtures. 1930. See Fig. 21.**

Totala sidorotlängder å tre månader gamla tallplantor uppdragna vid olika strålningsintensiteter och i olika humusformer. 1930. Se även Fig. 21.

Humus Humusslag	Radiation (Strålning)																			
	4 %				11 %				22 %				27 %				50 %			
	Pot Kruka	M cm	± ε cm	± ε %	Pot Kruka	M cm	± ε cm	± ε %	Pot Kruka	M cm	± ε cm	± ε %	Pot Kruka	M cm	± ε cm	± ε %	Pot Kruka	M cm	± ε cm	± ε %
III. Good raw humus. God råhumus.	5	0	—	—	15	2.2	0.72	32.7	25	15.1	1.40	9.3	46	43.9	2.28	5.2	35	59.2	2.88	4.9
	6	0	—	—	16	0.7	0.35	50.0	26	21.3	1.85	8.7					36	65.2	2.75	4.5
	Mean	0	—	—		*1.48*	*0.39*	*26.4*		*17.95*	*1.21*	*6.7*						*61.79*	*2.10*	*3.4*
III. Severely burnt raw humus. Hårt bränd råhumus.	7	0	—	—	17	1.6	0.48	30.0	27	11.6	1.43	12.3	48	22.8	1.18	5.2	37	27.2	2.07	7.6
	8	0	—	—	18	0.5	0.21	42.0	28	12.8	1.30	10.2					38	34.3	2.89	8.4
	Mean	0	—	—		*1.03*	*0.26*	*25.2*		*12.28*	*0.95*	*7.7*						*30.64*	*1.82*	*5.9*
I. Bad raw humus. Dålig råhumus.	3	0	—	—	13	2.1	0.50	23.6	23	13.2	0.96	7.3	43	23.3	1.36	5.8	34	33.8	1.51	4.5
	4	0	—	—	14	2.0	0.46	23.0	24	9.9	1.01	10.2	44	25.0	3.04	12.2				
	Mean	0	—	—		*2.01*	*0.27*	*13.4*		*11.29*	*0.75*	*6.6*		*23.97*	*1.43*	*6.0*				
IV. Inoc. humus. Inf. humus.	10	0	—	—	20	1.6	0.46	28.8	30	26.1	2.24	8.6	50	30.4	3.55	11.7	40	19.3	3.93	3.6
XIII. Mixture. Blandprov.	9	0	—	—	19	0.1	0.08	80.0	29	14.7	1.25	11.8	49	29.0	2.37	8.2	39	17.3	1.31	7.6
X. XI. XII. Sand.	1	0	—	—	11	1.5	0.58	38.7	21	15.1	1.04	6.9					31	20.8	1.75	8.4
	2	0	—	—					22	15.3	1.47	9.6					32	18.4	2.10	11.4
	Mean	0	—	—						*15.21*	*1.10*	*7.2*						*20.46*	*1.20*	*5.9*

count, the roots less than 5 mm in length were arbitrarily classed as short roots, those 5 mm or longer as laterals.

Numerous kinds of measurements were taken to describe the root development — length of radicle, length and number of long roots, fresh and dry weights, and observations on the character of mycorrhizal development of the short roots. Of these, the data on root lengths are considered to be the most important for discussion. With increasing radiation longer radicles were

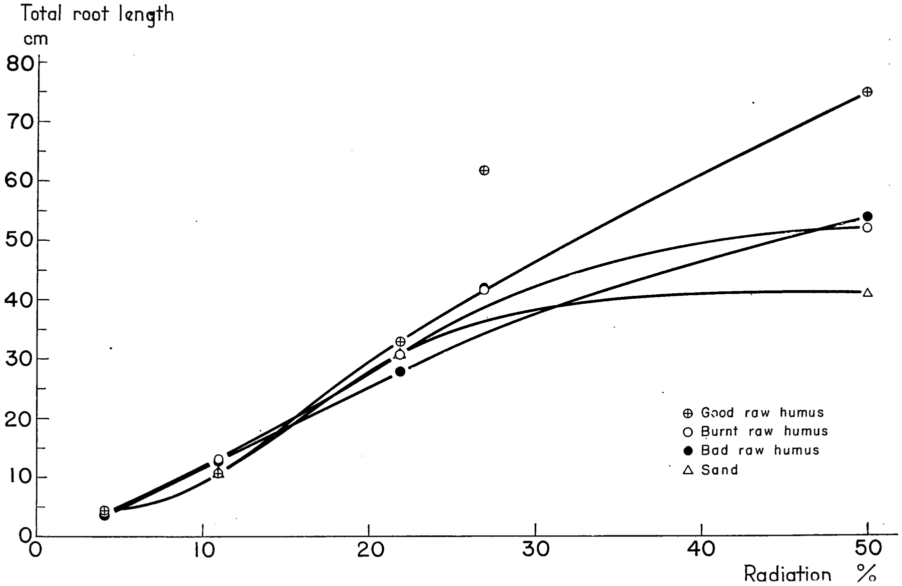


Fig. 7. The total root length per plant of Scots pine seedlings grown in different radiation intensities in various humus-sand mixtures. Lengths adjusted to values corresponding to a fresh seed weight of 4.75 mg. Skogsförsöksanstalt, 1930.

Totala rotlängden per planta hos tallplantor, som uppdragits vid olika bestrålningsstyrka i olika humus-sandblandningar. Längderna korrigerade till värden motsvarande en friskvikt å fröet av 4,75 mg. Skogsförsöksanstalten, 1930.

produced, as is evident from Fig. 3. But of even more interest are the data on the increase in the total length of the roots. These are summarized in Table 7, and Figs. 7 and 21. In tabulating the data for plants grown from seeds weighing 4.25 and 5.25 mg, the root lengths were adjusted to the equivalent of plants from 4.75 mg seed by the correction factor used for dry weights.

Observation of the data on total root length (Fig. 7) reveals trends which are quite smooth except for the 27 % radiation values. In the discussion of the dry weights and the dry matter contents, the plants grown under the water screen — in the so-called 27 % radiation intensity — received no special attention. That they received no special attention is in itself noteworthy, since the quality of the radiation they received was altered by the removal of infra-red. But inasmuch as they were apparently not out of line with the plants grown in lower and higher intensities more than might be due to experimental error, discussion of the significance of this fact was purposely postponed. In the case of root lengths, however, the curves in Fig. 7 were drawn ignoring the data on the plants grown in the 27 % radiation. The roots of the plants grown in this special quality of radiation are much longer and more numerous than would be expected for plants under this radiation intensity, but of the same quality as that received by the plants in the 22 % and 50 % chambers.

These data show that the development of roots is influenced very much by the radiation. Plants grown under the low intensities develop a root system only poorly furnished with lateral roots. In the four per cent radiation intensity the seedlings did not produce lateral roots. In the eleven per cent radiation, some of the plants developed lateral roots, others did not. The fertility of the soil affects root development but slightly under these conditions, only the length of the radicle being influenced. If the radiation intensity is about twenty per cent, the effect of the fertility of the soil then becomes significant, and at fifty per cent the differences in the root development associated with fertility are great. These changes in root development with various levels of radiation intensity and fertility are highly important in the survival of seedlings started under a shelterwood.

Shoot/Root Ratios.

The ratio between the distribution of dry matter to the shoot and the root is of interest in connection with all the problems involving seedling trees. Nursery stock planted in the field which does not have a good shoot/root balance succumbs because of inability to supply the transpiration demand. (See Aldrich-Blake, 1932, for extensive citations.) For the same reason reproduction under an overwood may fail when the tree canopy is removed. The mean of the quotients of the shoot dry weights divided by the root dry weights for the individual plants grown in each condition was calculated. The data for the plants grown in the humus-sand mixtures are given in Fig. 8 in graphical form. Again the plants grown under the water screen — in the 27 % radiation — are out of line and the curves drawn ignore them, necessitating a later detailed discussion (p. 663).

It appears that the shoot/root ratio is markedly influenced by both radiation and the fertility of the soil. This is to be expected from what has already been shown about root development and dry matter contents at the various levels of radiation and fertility. Evidently the non-development of the root systems in radiation intensities lower than twenty per cent is attributable to the extensive development of the top. The fertility of the soil is not without influence at this radiation intensity, however. At higher intensities the influence of the soil fertility becomes more important, the radiation less so: the shoot/root ratios remain more or less constant with changing radiation, although markedly different for the various nutritional levels, the soil with the higher fertility having the higher shoot/root ratio.

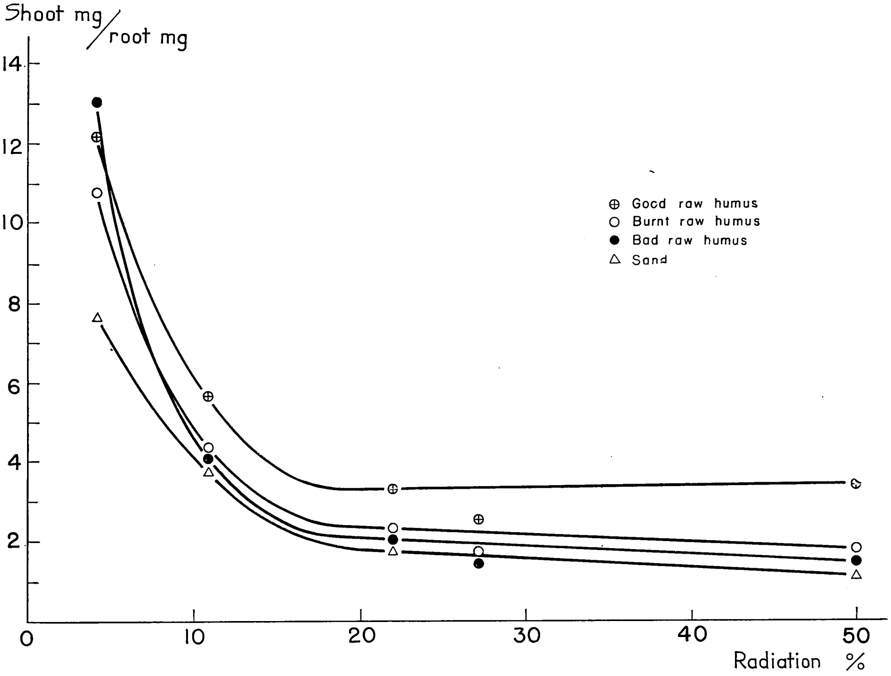


Fig. 8. The shoot/root ratios of Scots pine seedlings grown in different radiation intensities in various humus-sand mixtures. Skogsförsöksanstalt, 1930.
Förhållandet mellan skott och rot hos tallplantor, som uppdragits vid olika bestrålningsstyrka i olika humus-sandblandningar. Skogsförsöksanstalten, 1930.

Field examination of seedlings in dry sites indicates that the moisture supply is also of importance to the shoot/root ratio, but to the writer's knowledge there have been no exact experiments to separate the effects of radiation intensity, nutrient supply, and water supply on this important attribute.

SECTION III, Nutrient-sand Culture Experiments.

Study of the dry weight data obtained in the Försöksanstalt experiment indicated the possibility of explanation in terms of algebraic formulæ. Such would facilitate a quantitative estimate and generalization of the influence of radiation and fertility on cumulative growth. It is desirable to distinguish between cumulative growth, — conveniently designated as yield — and the growth rate. The latter is the derivative with respect to time of the former. As will be shown, the cumulative dry weight must be corrected for the original size of the plants. Only yield has been studied in the experiments reported in this paper; the measure used was the ultimate dry weight of a seedling corrected for the initial material with which it started.

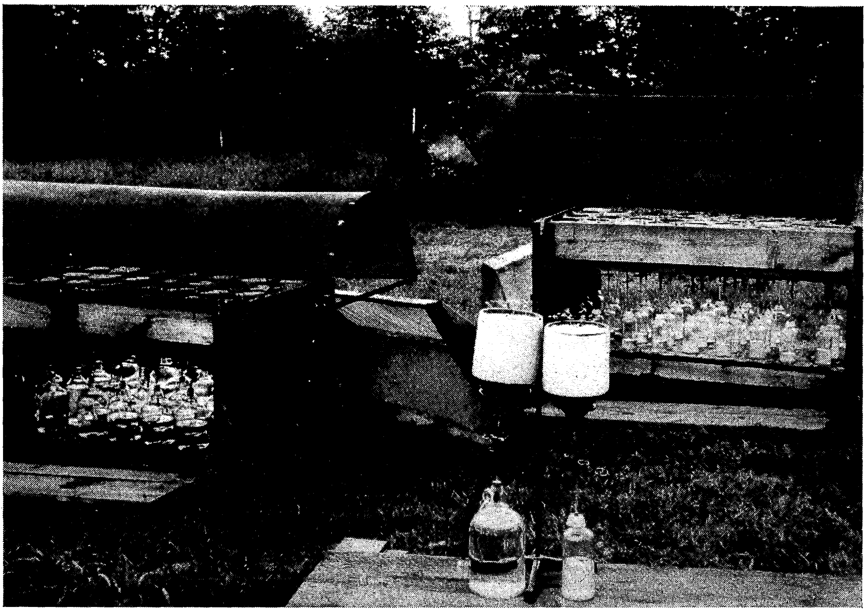
After the Försöksanstalt experiment was completed in the autumn of 1930, the writer discussed with Mr. ALDRICH-BLAKE the experiments which he was preparing for publication. At that time the application of the BLACKMAN (1919) compound interest law as applied to plant growth was mentioned. The writer was shown a graph in which the cumulative result of periodic compounding was utilized to explain the weights arrived at by the seedlings with various supplies of nitrogen. This graph was not included in the Oxford Forestry Memoir Number 12 (1930) but has since been published by him (1935). In another paper (1932) he gives additional evidence that the yield is logarithmically related to dry weight.

On the basis of the Försöksanstalt experiment and with the ALDRICH-BLAKE data in hand, the subsequent work with nutrient-sand cultures was planned. As will be shown, the logarithmic relation between yield and nutrient supply was fully and precisely substantiated, and its use makes possible a better understanding of the fertility of the humus-sand mixtures of the Försöksanstalt experiment.

Pot Culture Methods.

Various devices have been used in culturing plants in soil, nutrient-sand, and sand mixed with humus or soil. They may be briefly reviewed here.

In many experiments in Europe the pot devised by NEUBAUER (1925) has been used; it is about ten inches in diameter and fourteen inches deep. A slot in the bottom permits drainage into a pan, from which the excess solution may be returned to the soil. ALDRICH-BLAKE (1930) used a cream glazed pot thirteen inches in diameter and eighteen inches deep furnished with a tubulature near the bottom. Into this was fitted a T-tube, the upper arm of which served as a water level gauge and the lower permitted drainage of the excess solution, which was poured over the top every second day. The pots were filled with sand having a pore volume equal to one-third of the total volume and the water level »was maintained constant in all the pots at four to five inches from the base». This would approximate a



From the Harvard Forest collection. Photo by P. R. GAST.

Fig. 9. The arrangements at Petersham, Mass., 1934. To the left in the foregrouud are the pot and jug used in refluxing the nutrient solution in nutrient-sand cultures; to the right are the pot and bottle used in soil- and clay-sand cultures. (See MITCHELL, 1934, Plate I, p. 14.) On the wooden frames are the brass wire cloth shades. In the rear are the Cello-Glass screens used for protection against rain.

Anordningarna vid Petersham, Mass., 1934. Till vänster i förgrunden kärl och krukor, som använts för att hålla näringslösningen i rörelse genom sanden vid kulturförsöken, till höger kärl och flaska som använts vid jord-sand eller ler-sandkulturförsöken. På fackverk mässingsduksskärmar och i bakgrunden cellofan-skärmar, vilka senare nyttjats som regnskydd.

total volume of about 3.6 liters of solution, with a possible variation of fifteen per cent. In a later and less precise experiment, ALDRICH-BLAKE (1932) has used special boxes for rearing large numbers of seedlings, the boxes being fitted with an easily detachable side to facilitate removal of the whole plants.

The methods used by HESSELMAN (1927) were followed by the writer in the G-'30 experiment, and have already been described above (pp. 592, 599). In the next experiment (GM-'31) the arrangement employed was an adaptation of the device of ALDRICH-BLAKE (1930) and a large flooding tray described by EATON (1931). A detailed description has been given by MITCHELL (1934). Briefly, it was an asphalt-painted pail holding 7.6 liters (8 quarts) with a top diameter of twenty-four centimeters (9.5 inches), a bottom diameter of nineteen centimeters (7.5 inches) and a depth of twenty centimeters (8 inches). It was furnished with tubulature and T-tube, the upper arm serving as a water level gauge and the lower arm as an entrance by which the nutrient solution could be forced into the pail from a lower jug by the application of air pressure. It was found that in the case of humus sand mixtures a definite anaerobic condition existed. In the next experiments (see MITCHELL, 1934, p. 13—16) an attempt was made to overcome this difficulty by inserting unglazed clay pots in the pails. The apparatus served very well. In a later experiment it was thought advisable to guard against possible loss of nutrients in the porous walls of the pot by having the pot glazed. While this end was undoubtedly gained, it was found (HATCH, personal communication) that under high insolation the temperature might rise as much as 7° F (3.9° C) higher in the glazed than in the unglazed pots, with consequent undesirable effects on the soil flora, there being some evidence that the mycorrhizal development was affected. The cooling effect of the unglazed pot is attributed to the evaporation of water from the porous clay. The glazed inserted pots were used in the M-'33 experiment only. In the spring of 1934, stoneware gallon jugs (Fig. 9) without bottoms covered with an acid-proof glaze were obtained. These when inverted in a rack packed with sphagnum moss supplanted the previous pail and inner pot. They were used in the G-'34 experiment. The maximum difference between the noontime temperatures of pots exposed to full radiation and to twenty-five per cent radiation respectively was 9° F (5° C), the average 4° F (2.2° C). At other times the differences were much less.

In the earlier experiment the total supplies of nutrients available to the plant were less than in the later ones. In the first tests (GM-'31) 2.25 liters of solution with the stated parts per million (ppm) of nutrients were used. Later, in the G-'32, M-'32 and G-'34 experiments, the volume was increased to 3.5 liters, providing a larger reserve. In the M-'33 work, 4.5 liters were used.

Methods for the Modification of Radiation.

Intensity Reduction Shades.

The chief materials which have been used for the reduction of the intensity of solar radiation have been wooden shades, cheese cloth, and metal wire cloth.

The device of the wooden lath shades used in the Försöksanstalt experiment (p. 592) was adopted following CIESLAR (1909, pp. 5-6). In America numerous workers have used shades of cheese cloth, an inexpensive coarse mesh cloth easily available. When the series of experiments at Petersham was started, it was anticipated that they would continue for a number of years. Notwithstanding the high first cost, it was thought advantageous to purchase brass cloth screen made of wires drawn to an exact dimension and precisely spaced. Such material has several advantages. With brass screen a difficulty encountered in the use of cheese cloth does not arise: the openings in the latter are often blocked by loose fibres, inadequate aeration results, and the temperature rise is abnormal. Also, by reason of its high heat conductivity the metal screen is not heated above air temperature and cannot re-radiate the energy characteristic of a warmer body. The so-called open-area of the brass screen, the value of which is stated in catalogs of accurately made screen, is a precise measure of the transmission to be expected. Numerous tests at Petersham have proved this to our satisfaction. It is therefore possible to prescribe exactly the working conditions and to anticipate that the equipment will give uniform transmission over a number of years.

The brass wire cloth has the further advantage that it can be readily shaped into a hemi-cylinder which permits the optimum use of its precise transmission.

In the GM-'31 and the G-'32 experiments (MITCHELL, 1934, Plate VIII, p. 26) long east-west radii were used to cover pits with long east-west dimensions in which the pots were placed. Semi-circular pieces of screen tipped at an angle of about 45° were placed over the southern ends. The northern ends were closed by similar vertical semi-circles of wire cloth.

In the experiment G-'34 (Fig. 9) it seemed better to return to the older style of shade with narrow east-west dimensions and long north-south. An overhang projecting over each end ensured a constant intensity to the extreme limits of the area within which the plants were placed. The pots were originally put into the earth with the expectation that they would thus be kept cooler than in a more exposed position, but it was found that the temperatures were equalized much more efficiently by placing the pots in the raised frames at waist height and packing the openings between them with sphagnum moss. In the elevated position adopted in 1934 the pots and flooding arrangements were much easier to work with.

Algal development is always a difficulty in nutrient-sand cultures. By boxing in the glass jugs it is possible to inhibit practically all growth of algae in them. No difficulty is encountered with development in the top of the sand, if care is taken in flooding not to wet the top of the sand with the nutrient and if, after flooding, the top of the sand is occasionally rinsed by lightly spraying with some of the distilled water added to replace that lost by transpiration and evaporation.

To allow access of full solar radiation to the plants, no provision for glass shelter was made. For protection against rain Cello Glass screen — cellophane precipitated onto a wire mesh — has been used. Since it transmits only about 40 % of the radiation, this diminution must be taken into account when the plants are thus covered. Either a continuous record of the radiation received by the plants must be kept or else the continuous record of radiation, registered by a fully exposed radiometer must be corrected for the hours during which the plants are covered. On different occasions either one or the other of these two methods has been used.

Water Screen for Infra-red Filter.

Most physiologists who do not approve of even reconnaissance with devices measuring total radiation in the attempt to correlate radiation with plant growth object to the inclusion of infra-red radiation. In an attempt to obtain data concerning its influence on the growth of tree seedlings a water screen to absorb the infra-red was placed over some of the seedlings. Its design was based on the fact that eight centimeters of water absorbs more than 97 % of radiation longer than λ 1.0 μ.

The glass-bottomed tray (Fig. 1) was constructed by a mechanic under the direction of Mr. A. W. KARLSSON. It was 120 cm (47 inches) long, 70 cm (28 inches) wide, and 10 cm (4 inches) deep. It was made longer than the width of the bench so that the ends would not cast shadows on the plants. For the same reason the pots were not placed under its extreme southern portion. Thus for the greater part of the day the plants were fully exposed to the radiation which passed through the filter.

When similar trays were constructed at Petersham, they were furnished with wheels to run on a track and with a plate glass top (see Plate VIII, MITCHELL, 1934, p. 26). The top obviated some of the difficulty with dust and debris, which proved troublesome in the first design. The tray was also furnished with openings which made it possible to fill entirely the space between the bottom and top with water. Unfortunately it is impossible to state the physical characteristics of such a tray; determinations of the reflection and absorption of visible and infra-red radiation of solar intensities, though attempted, have not been completed with satisfactory precision.

Discussion of the Measurement of Radiation Intensities.

In these studies various types of equipment have been used for the determination of the radiation intensities to which the seedlings were exposed. The measurement of radiation as a factor in plant physiology still remains a vexatious problem. Various questions are raised: what part of the solar radiation spectrum is effective, what weight should be given to its various portions, and how should the radiation be integrated. As they are approached from either the theoretical or the experimental angle, various conclusions are reached.

Those who approach the problem from the theoretical viewpoint stress the fact that, so far as is now known, only the visible energy is effective in photosynthesis. (Parenthetically it is to be noted that to the writer's knowledge no study has ever been made of the effect on photosynthesis of adding to a known and constant intensity of monochromatic visible energy various quantities of »monochromatic» infra-red energy.) Yet since the visible energy is readily estimated by the human eye, or by devices which have the same or nearly the same relative efficiency over identical wave lengths, such measurements are most frequently used and advocated. For clarity these should be distinguished as illumination measurements, since the term light has become so indefinite by indiscriminate use.

Those who approach the problem of radiation measurement in physiological studies from the empirical viewpoint remark that photosynthesis is but one of the processes in the plant essential to growth as measured, for instance, by dry weight increase. Information as to the photo-sensitivity of the other physiological processes is lacking. Therefore a device without any special spectral photo-sensitivity is adopted. The temperature rise of a »black body» exposed to radiant energy is a measure of its intensity. Methods based on this fact have been in use for the last century. Numerous ways to measure the temperature rise have been contrived. Of these, thermoelectric devices have offered the greatest advantages in facility of recording and integrating. With the aid of these devices, measurements of total radiation are made.

During these experiments both total radiation and illumination records have been kept. For the total radiation measurements have been used both the spherical radiometer (GAST, 1930) and the U. S. Weather Bureau pyrheliometer manufactured by the Eppley Laboratory, Inc., Newport, R. I., U. S. A. Both are thermopiles designed specifically for continuous exposure to solar radiation. The spherical radiometer was contrived to record radiation from all points of the sky, both sky and sun radiation, as of normal incidence. The pyrheliometer as manufactured by the Eppley Laboratory is essentially the design described by KIMBALL and HOBBS (1923) but with somewhat smaller receiving surfaces so that it can be enclosed in a conveniently small bulb having glass seals throughout. The maximum diameter of the bulb is 7.6 cm (2 inches), and the glass is especially thin for maximum transmission. Carbon smoke and magnesium oxide smoke are used on the black and white surfaces respectively, and the sensitivity to radiant energy is therefore limited to the spectral region of wave lengths λ 0.3 μ to 1.5 μ.

Records from these thermopiles have been taken by both the Engelhard recording microammeter (KIMBALL, 1923, 1931; GAST, 1930, pp. 38—46) and the curve-drawing recording potentiometer manufactured by the Leeds and Northrup Company of Philadelphia, Pa., U. S. A. Such records have been summed with a planimeter. Beginning with the 1933 experiments at the Black Rock Forest and the 1934 experiments at the Harvard Forest, the potentiometers used have been equipped with an integrating device which permits direct reading of the cumulative radiation. The precision of the records obtained in the later work has been considerably increased.

The progressive improvement in the quality of the observations resulted from continuous critical study of the methods. Thus the adoption of the recording potentiometer was a consequence of maturing views on the relative merits of the deflection galvanometer and the potentiometer for measuring the thermoelectric energy. The galvanometer measures the current which results from the voltage generated by the thermopile. The passage of the current is accompanied by a transfer of energy from the hot to the cold junctions. and thus there is a tendency to neutralize the temperature difference which is the result of the differential absorption of radiant energy by the black and white surfaces respectively. The current registered by the galvanometer depends not only on the voltage of the thermopile but also on the resistance of the circuit. Whenever the resistance of the circuit is altered, a new factor must be determined for the conversion of ampere-hours into units of radiant energy. Temperature changes in the circuit result in changing resistances depending upon the temperature coefficient of the conductor affected. For these reasons the apparatus using the galvanometer deflection method is less accurate and less flexible than that using the potentiometric method. The latter does not draw current and is independent of changes in the circuit resistance. In conclusion it is only fair to say that in 1924 when the galvanometric method was adopted by the writer, the recording potentiometers on the market were not as sensitive and mechanically robust as the designs now available.

Attempts have also been made to obtain continuous records of illumination. AURÉN (1930, 1933) has had considerable success with such measurements. Unfortunately at Petersham no records have been obtained which satisfied critical examination as to reliability. Continuous exposure to full irradiation in all sorts of weather invariably resulted in change in the constants of the photo-electric cell, possibly due to inadequate design of the weather-proof case, possibly due to continuous exposure of the cells to high intensities, a combination of conditions to which they are not adapted. However, the experiments with photo-electric cells are being optimistically continued. Selenium cells of a new type used in the early part of the summer of 1935, which have apparently remained constant, have afforded an opportunity to study the differences between illumination and total radiation under changing sky conditions. The records which have been made give preliminary evidence that in a single locality in a single day the relative changes in illumination and total radiation are identical as passing clouds cover the sun. Previous evidence is against a direct proportionality between total radiation and illumination (KIMBALL, 1924; GRASOVSKY, 1929; AURÉN, 1930, 1933).

A question which still remains unanswered is how the sensitive surface should be exposed to incoming energy. The choice is between a surface mounted in a fixed horizontal plane and a surface which will integrate radiation from all points of the heavens at normal incidence. The first method is illustrated by the usual method of mounting the pyrheliometer (MITCHELL, 1934, Plate III, p. 16, Plate VIII, p. 26). The alternative method is illustrated by the so-called spherical radiometer. This device is not perfect (GAST, 1930, pp. 35—37, curve D in Fig. 9), but indicates that progress can be made in devising a mechanical method of integrating direct and sky radiation as of normal incidence.

The values of radiation intensity may be reported either in units of the total energy received in a given period (work) or of the average energy per unit of time (power). For total radiation the work unit used in this report is a kilogram calorie per square centimeter per growing season. For certain purposes the gram calories per square centimeter per day, week, or ten-day period might have been used. When comparisons between like periods are made in this way, the values become relative power units; the absolute power unit usually employed is the gram calorie per square centimeter per minute. The power unit of illumination is the lux or the foot-candle; the corresponding work units would be foot-candle-minute, foot-candle-hour, lux-minute, lux-hour or some similar convenient product of a power unit and time.

Unfortunately records are not available for stating exactly the sum of radiant energy received by the plants during the growing season for earlier experiments in this series. Unless qualified by specific statement, the values given for total radiation measurements are believed to be correct within ± 3%.

Corsican Pine Experiment, ALDRICH-BLAKE, 1929.

The 1929 experiment of ALDRICH-BLAKE (1930) on *Pinus laricio* Poir. var. *corsicana* Loud. will be drawn upon to illustrate in detail (a) the corrections needed for seed size, and (b) the relation between the nitrogen supply in nutrient-sand cultures and the weight of the seedling grown.

The weights of the seedlings are reported on the basis of 2 mg weight classes of seed. These were made by combining equal numbers of seeds separated by fresh

Table 8. **Dry weights of Corsican pine seedlings from seeds of different weights grown in sand cultures with varying quantities of available nitrogen. (After Aldrich-Blake [1930] 1929 experiment, Table 14, p. 55.)**

Torrvikter av svarttallplantor uppdragna ur frö av olika vikt och i sandkulturer med varierande mängder tillgängligt kväve.

Seed fresh weight Fröets friskvikt		Mg nitrogen ($NH_4 + NO_3$) available per plant = N Tillgängligt kväve per planta = N						Average ratio %
		1	3	5	9	17	33	
		Approximate nitrogen concentration in ppm Approximativ kväve-koncentration i milliondelar						
mg		15	44	73	132	249	485	
		(1) Mean dry weight in mg Medel-torrvikt i mg *Calculated values from seed weights corrected by factor, f* $y = f \times \text{seed weight} \times \text{antiln}_e\,(2.604 + \log_{10} N)$						
23 $f = 0.9640$	found	295	486	622	805	1 039	1 329	
	calculated	*299.8*	*482.9*	*602.9*	*778.2*	*1 025.9*	*1 369.6*	
	ratio %[1]	98.4	100.6	103.2	103.4	101.3	97.0	100.7
21 $f = 0.9873$	found	273	437	560	750	966	1 217	
	calculated	*280.3*	*451.6*	*563.7*	*727.7*	*959.4*	*1 280.7*	
	ratio %	97.4	96.8	99.3	103.1	100.7	95.0	98.7
19 $f = 1.0135$	found	255	412	534	693	851	1 210	
	calculated	*260.4*	*419.4*	*525.6*	*675.9*	*891.0*	*1 189.4*	
	ratio %	97.9	98.2	101.6	102.5	95.5	101.7	99.6
17 $f = 1.0436$	found	245	363	501	620	826	1 108	
	calculated	*239.8*	*386.4*	*482.4*	*622.7*	*820.9*	*1 095.9*	
	ratio %	102.2	93.9	103.9	99.6	100.6	101.1	100.2
	Average ratio %	99.0	97.4	102.0	102.2	99.5	98.7	99.787[2]
		(2) Mean dry weight in mg Medel-torrvikt i mg *Calculated:* $y = \text{seed weight} \times \text{antiln}_e\,(2.604 + \log_{10} N)$						
23	found	295	486	622	805	1 039	1 329	
	calculated	*311.0*	*500.9*	*625.4*	*807.3*	*1 064.2*	*1 420.7*	
	ratio %	94.9	97.0	99.5	99.7	97.6	93.6	97.1
21	found	273	437	560	750	966	1 217	
	calculated	*283.9*	*457.4*	*571.0*	*737.1*	*971.7*	*1 297.2*	
	ratio %	96.2	95.5	98.1	101.8	99.4	93.8	97.4
19	found	255	412	534	693	851	1 210	
	calculated	*256.9*	*413.8*	*518.6*	*666.9*	*879.1*	*1 173.6*	
	ratio %	99.3	99.6	103.4	103.9	96.8	103.1	101.0
17	found	245	363	501	620	826	1 108	
	calculated	*229.8*	*370.3*	*462.2*	*596.7*	*786.6*	*1 050.1*	
	ratio %	106.6	98.0	108.4	103.9	105.0	105.5	104.7
	Average ratio %	99.3	97.5	102.3	102.3	99.7	99.1	100.03

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[1] Ratio % = found divided by *calculated* × 100.

[2] Standard deviation of ratios (in %) = 2.80.

Table 8 continued.

Seed fresh weight Fröets friskvikt		Mg nitrogen (NH_4 + NO_3) available per plant = N Tillgängligt kväve per planta = N					
		1	3	5	9	17	33
		Approximate nitrogen concentration in ppm Approximativ kväve-koncentration i milliondelar					
mg		15	44	73	132	249	485
(3) Mean dry weight in mg per mg of fresh seed weight Medel-torrvikt i mg per mg av fröets friskvikt *Calculated: $y = \text{antiln}_e\,(2.604 + \log_{10}$ mg N available per plant)*							
23	found	12.83	21.13	27.04	35.00	45.17	57.78
21	found	13.00	20.81	26.67	35.71	46.00	57.95
19	found	13.42	21.68	28.10	36.47	44.79	63.68
17	found	14.41	21.35	29.47	36.47	48.59	65.17
	calculated	*13.52*	*21.78*	*27.19*	*35.10*	*46.27*	*61.77*
(4) Natural logarithm of mean dry weight in mg per mg fresh seed weight Naturliga logaritmen för medel-torrvikten i mg per mg av fröets friskvikt *Calculated: $\text{Ln}_e y = 2.604 + \log_{10}$ mg nitrogen available per plant*							
23	found	2.552	3.051	3.297	3.535	3.810	4.057
21	found	2.565	3.035	3.284	3.575	3.829	4.060
19	found	2.597	3.076	3.336	3.597	3.802	4.154
17	found	2.668	3.061	3.383	3.597	3.884	4.177
	calculated	*2.604*	*3.081*	*3.303*	*3.558*	*3.834*	*4.123*
	Log_{10} mg N	0.0	0.477	0.699	0.954	1.230	1.519

weight into 1 mg classes. Any discussion of standard deviation of the mean of the group weights of the seed must therefore be based on class limits separated by 1 mg. No data on the moisture content of the seeds or the weights of the seed coats are available. From the data of Table 14 (loc. cit., p. 55) are taken the values entered in Table 8 for the »mg nitrogen available per plant» and for the »found» values for plant weights in parts (1) and (2) of the table, which are merely repetitions of each other. From the quantity of NH_4NO_3 supplied to each pot and the approximate volume of solution (see p. 617) the »approximate nitrogen concentrations in parts per million» were calculated and entered in their respective columns. Similar computations give the following values for the concentrations of the other nutrient elements in the basic solution.

Concentration in parts per million (ppm) — milligrams per liter.

N	K	P	Ca	Mg	Fe	S	Cl
varied 0—485	400	316	305	219	10	289	541

For the analysis of the relation in this experiment between the seedling dry weights, the amount of nitrogen supplied externally and the fresh weight of the seed, two different methods may be used.

The first possibility is the direct application of the method of multiple correlation with the use of an equation suggested by Mr. MANFRED NÄSLUND of the Institute. By plotting the logarithms of the dry weights of the seedlings against the logarithms of the supplies of nitrogen it is found that the two are directly proportional. For a reason which will appear later, it is also desirable to include in the multiple correlation equation an additional term which is the product of the seed weight and the logarithm of the nitrogen supply. In this way is obtained the equation

$$\log \text{plant weight} = 0.44901 \log \text{mg N/plant} + 0.016725 \text{ mg seed weight} \\ -0.00063190 \log \text{mg N/plant} \times \text{mg seed weight} + 2.09280 \quad \ldots \quad (1)$$

The estimates made with the aid of this equation are approximately the same as the *calculated* values in part (1) of Table 8. Actually they are slightly closer to the found values than are the calculated values of the table, the over-all average ratio between the found and estimated being 100.042 %, the standard deviation of the ratios (in %) being 1.55. The values are approximately the same as those of the solid lines in the upper and the lower left parts (*A* and *B*) of Figure 10.

The second possibility is not so satisfying mathematically. It consists of a stepwise simplification of the data and then the application of the formula to give the cumulative size reached by compound interest growth at a given rate. For many decades foresters have used the compound interest formula to estimate the rate of forest growth (WEBER, 1891); but to BLACKMAN (1919) is attributed the introduction of the concept into the literature of plant physiology.

The first step in the analysis of the data is to reduce the weights of the seedlings grown from seeds of various sizes to a common basis, the milligrams of mean dry weight of whole plant per milligram of fresh seed weight. These values, which are entered in the lines opposite the respective seed weights as »found» values in part (3) of Table 8, were obtained by dividing the »found» values of part (2) by the appropriate seed weights in milligrams.

The next step is to determine the relation between these values and the supplies of nitrogen, using the theory of compound interest growth. If the growth is reckoned as the assimilation of separate increments the formula is

$$\text{yield} = s\ (1.0p)^n$$

or

$$\log \text{yield} = n \cdot \log 1.0p + \log s$$

In the above, p is the interest rate, n is the number of compounding intervals, and s is the seed weight in milligrams. In the problem under discussion the »found» values in part (3) are given with $s = 1$. With the aid of this formula it is possible to proceed as did ALDRICH-BLAKE (1935) in the estimation of the yields. He arrived at the rates (p) 2.92, 3.46, 3.78, 4.05, 4.35 and 4.68 respectively, with $n = 90$. The number of compoundings, ninety, was adopted on the assumption that all the foods formed »during a day are at least mobilized in soluble form for the production of new tissues by the following morning», although the growth period was approximately 150 days — from May 16, 17, and 18 to between October 1 and November 4 (ALDRICH-BLAKE, 1930, pp. 52—53). His use of 90 rather than 150 days is undoubtedly an attempt to account for the non-functioning of the food synthetic processes during germination and after the onset of cool weather in the autumn.

Instead of the assumption that the increments of food are assimilated into new

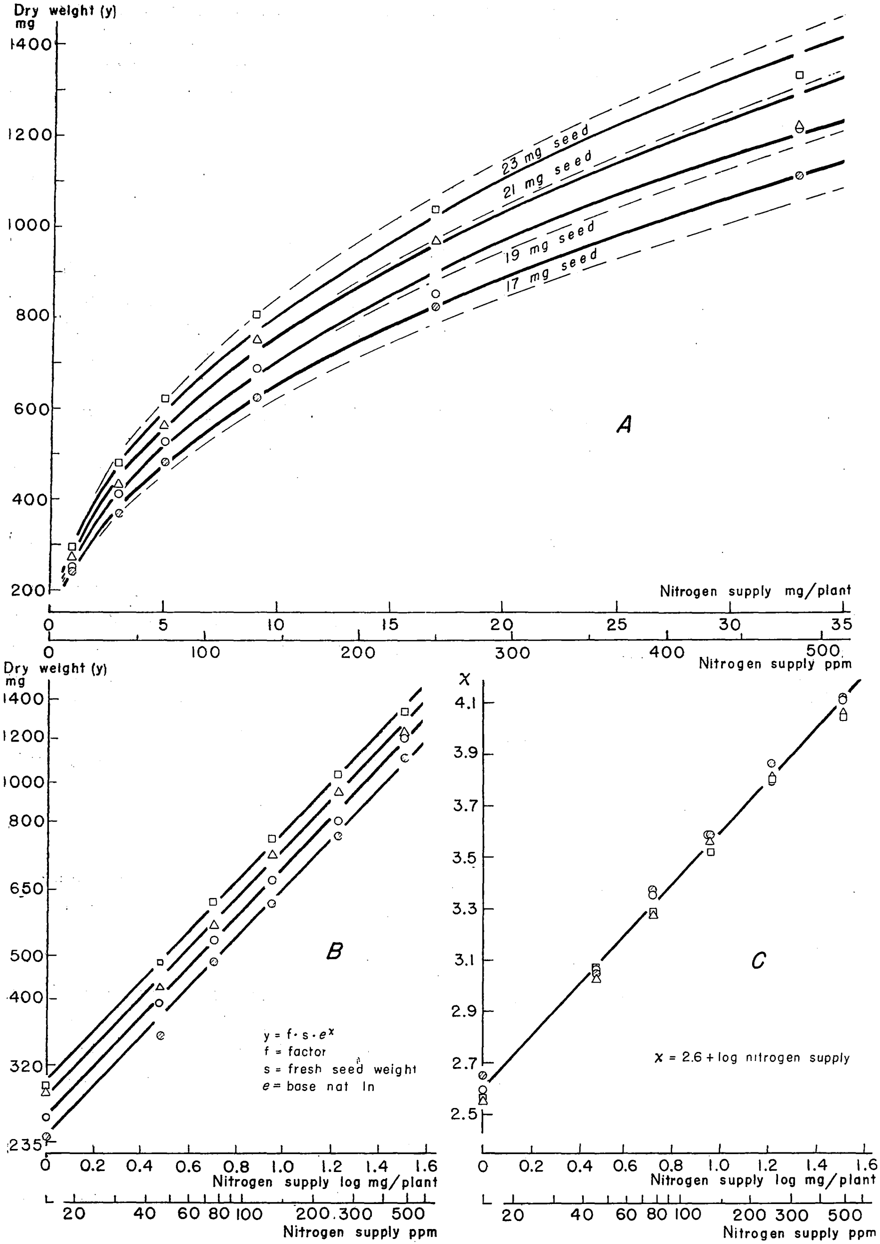

Fig. 10. The dry weights of Corsican pine seedlings from seeds of different weights grown in nutrient-sand cultures with various quantities of nitrogen. The curves ——— in *A* and *B* are the »*calculated*» data from (1), Table 8, plotted on arithmetic: arithmetic and logarithmic: logarithmic axes respectively. The curves — — — in *A* are the »*calculated*» data from (2), Table 8. The curve in *C* shows the relation between the exponent *x* and the external nitrogen supply, see (4), Table 8.

Torrvikt av svarttallplantor ur frö av olika friskvikt och vilka uppdragits i närsalttillsatt sand med kväve i olika mängd. Kurvorna ——— i *A* and *B* representera beräknade torrvikter från (1), tab. 8, vilka inprickats i aritmetiska resp. logaritmiska koordinatsystem. Kurvorna — — — i *A* representera beräknade torrvikter från (2), tab. 8. Kurvan i *C* visar sambandet mellan exponenten *x* och den tillförda kvävemängden, se även (4), tab. 8.

tissues daily or at similar long intervals it may be considered that they are immediately used for the production of new tissues which immediately assist in the formation of food. That is, instead of being compounded each day the interval of compounding is so small as to approach zero as a limit. The appropriate formula may then be given:

$$\left.\begin{array}{ll} & \text{yield} = s \cdot e^{x} \\ \text{or} & \ln \text{yield} = x + \ln s \end{array}\right\} \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (2)$$

where s is the seed weight in milligrams as before, but e is the base of the natural system of logarithms, and x is the rate of continuous compounding. The »found» values in part (4) of Table 8 are such rates (x) of growth of the seedlings with various supplies of nitrogen. Since in part (3) $s = 1$, then $\ln s = 0$, and the logarithms to the base e of the »found» values of part (3) are entered directly in the appropriate rows and columns of part (4).

These »found» values in part (4) were solved for their relation to the nitrogen supplies by the method of least mean squares. But in this case the log mg N/plant — the last line in Table 8 — is used instead of the mg N/plant — the first line in the table. Thus is obtained the formula

$$\ln y_{s=1} = x = 2.604 + \log \text{mg N/plant} \quad \ldots\ldots\ldots\ldots \quad (3)$$

which is graphically shown in the lower right part C of Figure 10. The average rates for the different supplies of nitrogen are the »*calculated*» values in the second from the bottom line of Table 8. With the smallest supply of nitrogen ($N = 1$) the average rate of growth with continuous compounding is 2.604; with the maximum external supply ($N = 33$) the rate is 4.123. These are equivalent to the rates of 2.92 and 4.68 for 90 discontinuous compoundings given above.

Had the plants been grown for shorter or longer periods, or the plant weights or N supplies been given in different units, formula 3 would appear as

$$\ln y_{s=1} = k_1 + k_2 \log \text{mg N/plant} \quad \ldots\ldots\ldots\ldots \quad (4)$$

That the above k_2 term is in formula 3 equal to unity — at least it is sufficiently close to unity for the purpose of present estimation — is merely a remarkable coincidence, for usually k_2 would appear as a constant term in any estimating formula.

The «*calculated*« values in part (3) are the antilogarithms of the »*calculated*» values in part (4). From the »*calculated*» values in part (3) are obtained the »*calculated*» values in part (2) by multiplying by the appropriate fresh seed weight in milligrams. The values so obtained are represented by the dashed lines in the upper part A of Figure 10. This estimating formula is

$$\text{yield}_{s=17,\,19,\,21,\,23} = s \cdot \text{antiln}\,(2.604 + \log \text{mg N/plant}) \quad \ldots\ldots \quad (5)$$

For the survey of the estimates obtained with the aid of the formula the ratios between the found and calculated are given as per cent in part (2):

$$\frac{\text{»found»}}{\text{»}\mathit{calculated}\text{»}} \times 100 = \text{ratio } \%$$

Scrutiny of these average ratios indicates that the intermediate nitrogen supplies gave, on the average, slightly higher yields than anticipated by the formula, while the yields from extreme supplies are low. There is no consistent trend. But the average ratios at the right of part (2) indicate that the yields are not exactly proportional to the fresh seed weights. A pronounced trend is to be observed. The plants from seeds larger than 20 mg were overestimated, and from those smaller than 20 mg, under-estimated. By the method of least mean squares were obtained decimal factors f ($f = 1.0$ for the median 20 mg seed) by which to correct the respective seed weights for this discrepancy. By the multiplication of the »*calculated*» values in part (2) by the values of f in the seed weight column of part (1) were obtained the »*calculated*» values of part (1). They are shown as the heavy lines in the upper and lower left parts, *A* and *B*, of Figure 10. The final equation used may be written

$$\text{yield}_s = f_s \cdot s \cdot \text{antiln } (2.604 + \log \text{mg N/plant}) \quad \ldots\ldots\ldots \quad (6)$$

or

$$\ln y_s = \log \text{N} + \log s + \ln f_s + k$$

where N is the nitrogen supply and k is a constant.
If written in logarithms to the base 10 this equation is

$$\log y_s = k_1 \log \text{N} + \log s + \log f_s + k_2 \quad \ldots\ldots\ldots \quad (7)$$

As has been remarked, equation 6 gives almost the same estimates as 1.
The latter, written in the same form as equation 7, is

$$\log y = k_1 \log \text{N} + k_2\, s + k_3 \cdot s \cdot \log \text{N} + k_4 \quad \ldots\ldots\ldots \quad (8)$$

Study of the results of this experiment by ALDRICH-BLAKE demonstrates two important principles. The first important deduction is that for precise work on the effects of environmental conditions on seedling growth, the work should be so planned that correction may be made for the food reserves in the seeds, because they are the initial amounts of capital which are increased by continuous compounding during growth.

The second important deduction is that over the range of supplies of available nitrogen used in the experiment, a formula for estimating the yield of tree seedlings based upon the theory of continuously compounded growth may be used to predict ultimate dry weight with extraordinarily accurate results. The logarithms of the two variables, weight and nitrogen supply, are linearly related.

Discussion of Seed Size Correction.

Study of the Corsican pine experiment reveals the indispensable nature of the seed size correction. During the winter experiment of 1929—30 the writer had learned that the correction for seed size would be a necessary refinement in precise work. In the so-called Försöksanstalt or G-'30 experiment of the following summer it was proved essential. The influence of seed size was shown by a series of plants grown in 22 % radiation in pure sand without nutrients. Two additional series of plants were grown with weak irradiation in pure sand with nutrients at the Harvard

Forest in 1931. The results of these experiments have been described by MITCHELL (1934, pp. 30—32).

A provision for estimating the effect of seed size on the dry weights of seedlings raised from seed of various weights was given in equations 7 and 8 on p. 629. The values of the correction terms ($\log s + \log f_s$ and $k_2 s + k_3 \cdot s \cdot \log N$) in the two equations are naturally not the same. The difference is due to the difference in the methods of correcting for the effect of seed weights on the cumulative size of the plants. In equation 8 the correction factors are derived from a multiple correlation equation making use of the observation that there is a linear relation between the logarithm of the yield and the logarithm of the nitrogen supply. In equation 7 the argument has involved the use of the continuously augmented compound interest relation in which the rate is proportional to the logarithm of the external nitrogen supply. The effect of the seed size on yield is almost directly proportional to its fresh weight, but not exactly.

The explanation for the lack of exact proportionality is as follows. If the seedling weights were exactly proportional to the fresh seed weights, it would be because the food reserves in the seed were a constant per cent of the fresh weight. It is seen from Table 10 that this is not true. If this were so, the relation between the dry food reserve (g) and the fresh seed weight (s) would be

$$g = k \cdot s$$

Rather, the relation is

$$g = k_1 + k_2 \cdot s$$

Experimentally, the value of g may be found either by subtracting from the dry weight of the seed the dry weight of the seed coat or by determining the value of r as described on p. 631.

In the preceding discussion an argument of ALDRICH-BLAKE (1935) against the use of seed-size corrections has been answered indirectly. By examination of the same yield data as have just been analyzed he came to the conclusion (p. 57): »factors derived from a linear graph expressing the relation between seed weight and resulting weight of seedlings . . . cannot yield accurate results». The difficulty arose from the fact that he had no information on the food reserves in the Corsican pine seed used. Nevertheless, had he proceeded to observe the relation between estimate and yield as was done in part (2) of Table 8 he would have observed the desirability of a constant factor f. By the computation of such a factor his estimates would have been improved. His conclusions must therefore be revised. The employment of correction factors derived from a linear relation between the food reserves and seedling weights do yield accurate results. This relation can be used when it is not expedient to distribute seeds of all sizes through all of the treatments. That this is true can be shown in the course of such excellent experiments as ALDRICH-BLAKE himself performed in 1929. No additional experiment is required. It is only necessary to make provision for such a factor in deriving the estimation equation. Such a factor may be based on the demonstrated fact that amounts of capital (g) with which the plants start from seed of various sizes are not directly proportional to the fresh weights of the seed but are linearly related to them.

It has been shown that a correction for seed size is possible and necessary. But a further problem remains: the choice of the unit of seed size to which the yield is to be referred. In summarizing the effect of a given environmental factor on yield, the yield might be expressed as the weight produced per milligram of fresh seed weight, per milligram of dry seed weight or per milligram of reserve food. But a probably more useful expression, because more easily correlated with the forester's experience as a result of examination of seedlings in the field, is the dry weight of the plant grown with stated nitrogen supply from the seed of a stated fresh weight. In the case of Corsican pine, the weight of the average seed sown was 20 mg. For each of the four classes of seed weight — S_{17}, S_{19}, S_{21} and S_{23} — each differing from the next by 2 mg, a ratio r can be obtained by which to convert the various weights to equivalents of the median 20 mg seed weight, S_{20}. For example,

$$r_{\frac{S_{20}}{s_{19}}} = \frac{20}{19 \times 1.0135} = 1.039$$

The values to convert the other plant weights to weights equivalent to 20 mg seed would be similarly computed.

An alternative method for estimating r can be used. In the case of the Försöksanstalt experiment of 1930, the values of r can be obtained from the ratios of the weights estimated from the smoothed regression curve of the sand grown seedlings. This method was used in deriving the ratios given by MITCHELL (1934, p. 32). Still another method can be used. In fourteen of the treatments, seeds of the median weight were planted in one pot and seed of another weight class in the second. The ratios between the duplicates may be computed. The arithmetic mean of the ratios may then be found. If it is desired to smooth the values by the method of least mean squares, it is advantageous to take logarithms of the seed weights and the logarithms of the ratios. In the case of the data given, the two methods result in ratios differing from each other by about one per cent. Where more than three weight classes are involved, the second method is to be preferred. The values of r obtained by the method of least mean squares — 1.034 for the 4.25 mg seed and 0.9670 for the 5.25 mg seed — were used in changing the found weights to the equivalents of 4.75 mg seed shown in Table 5.

Table 9. **The mean fresh weight of Scots pine seeds of various sizes. The »found mean weight» is the average of 20 groups of 30 seeds each. 1932.**
Medeltal av friskvikten av tallfrön av olika storlek. Den »funna medelvikten» är ett medeltal för 20 grupper om 30 frön i vardera.

Theoretical mean fresh weight Teoretisk medelfriskvikt	Found mean fresh weight Funnen medelfriskvikt			Difference Skillnad
M mg	M mg	± σ mg	 %	(1)—(2) mg
(1)	(2)	(3)	(4)	(5)
4.75	4.719	0.048	1.0	— 0.031
5.25	5.208	0.076	1.5	— 0.042
5.75	5.684	0.040	0.7	— 0.066
6.25	6.161	0.051	0.8	— 0.089
Mean..			*1.0*	—

Occasional gross inconsistencies are found in that the plants from the smaller seed are larger than the companion plants from the larger seed. Such can be explained only as mistakes or as untoward differences in fertility of different pots, which might result from the differential development of microflora. That duplicate pots showed different fertilities is proved on p. 606. An additional possibility may also be pointed out. It will not account for the large errors, but will indicate how smaller errors may arise. In column (1) of Table 9 are given the theoretical mean fresh weights expected by sorting into the respective classes with limits at 4.5, 5.0, 5.5, 6.0 and 6.5 mg respectively. From several hundred seeds so weighed, 20 groups of 30 seeds each were removed and the average of each group determined. The found means, standard deviations, σ, and the coefficients of variation, $\sigma_{\%}$, were calculated and entered in columns (2), (3), and (4) respectively. The coefficient of variation averaged for all classes was about one per cent. That is, 68 out of 100 groups of 30 seeds each will have mean weights lying within one per cent of the mean; but 32 out of 100 groups will have mean weights deviating from the mean by more than one per cent of the mean. In the Corsican pine experiment, the standard error of estimate obtained by equation 6, p. 629, was 2.85 %: 32 out of 100 trials would differ from the estimate by a possible value greater than 2.85 % of the estimate. Since the correction for seed weight enters with a $\sigma_{\%}$ of 1, such would account for a third of the error in the predicted values obtained by the use of equation 6. If the better estimates obtained from equation 1, p. 626, are used, the possibility of the error in the mean weight of the seed sample will account for a still greater part of the error of estimate.

In the nutrient-sand experiments later reported in this paper, the standard error of estimate was also on the order of 3 %. It seems reasonable to expect that by narrowing the class limits into which the seeds are separated by weight, the error of estimate may be decreased. For comparison of the class limits they may be calculated as per cents of the mean seed weights. Thus for the larger seeds

$$\frac{\text{class limits} = 1 \text{ mg apart}}{\text{mean weight} = 20 \text{ mg}} = 5 \ \% \ \text{»seed class limit».}$$

For the smaller seeds

$$\frac{\text{class limits} = 0.5 \text{ mg apart}}{\text{mean weight} = 5.0 \text{ mg}} = 10 \ \% \ \text{»seed class limit».}$$

An experiment has been started to determine whether by narrowing the seed class limit to 2 % the standard error of estimate is decreased.

The difference between the theoretical and found mean fresh weights reported in column (5) of Table 9 is believed to be due to moisture loss and inaccuracy in weighing. In later experiments more care has been taken after weighing quickly to return the seed to the chamber containing the stock, thereby providing an atmosphere of constant moisture content. Also, a more precise balance is now available for weighing swiftly seed up to 30 mg.

While the methods elaborated above are satisfactory for converting the data from a single lot of seed used in a given year to a common basis, a fundamental problem remains as yet undiscussed. A correction for the food reserve of seeds of different species from varied sources and used under varied conditions is needed. Since the dry weights of the plants are taken as the measures of growth, a similar

Table 10. **Reserve dry weights in the same lot of white pine (*Pinus strobus* L.) seed in two samplings separated by a year's storage.**

Reserv-torrvikt av samma parti weymouths-tallfrö, bestämd omedelbart och efter 1 års lagring.

Class	Fresh weight Frisk-vikt	1932[1]				1933[2]			
		Dry weight Torr-vikt	Reserve dry weight[3] Reserv-torrvikt		$r = \frac{g_{25.5}}{g_x}$	Dry weight Torr-vikt	Reserve dry weight[3] Reserv-torrvikt		$r = \frac{g_{25.5}}{g_x}$
	mg	mg	g mg	% (4)/(3)	(in 4)	mg	g mg	% (8)/(7)	in (8)
(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)
0	20.5	19.05	12.43	65.2	1.204	19.04	11.92	62.6	1.238
1	21.5	19.89	12.94	65.1	1.157	19.89	12.49	62.8	1.182
2	22.5	20.73	13.44	64.8	1.114	20.74	13.06	63.0	1.130
3	23.5	21.57	13.95	64.7	1.073	21.58	13.62	63.1	1.084
4	24.5	22.42	14.46	64.4	1.035	22.43	14.19	63.3	1.040
5	25.5	23.26	14.97	64.4	1.000	23.28	14.76	63.4	1.000
6	26.5	24.10	15.47	64.2	0.9677	24.12	15.33	63.6	0.9628
7	27.5	24.94	15.98	64,1	0.9368	24.97	15.90	63.7	0.9283
8	28.5	25.78	16.48	63.9	0.9084	25.82	16.47	63.8	0.8962

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[1] Data from Mitchell (1934) Table 17, p. 120. Columns (1), (2), (3), (4), above are columns (1), (2), (7), (8) respectively in table cited; (4), (5), (8) and (9) are smoothed values estimated from regression equations.

[2] Data from Mitchell, Black Rock Forest, unpublished, calculated as in 1932.

[3] Dry weight of seed minus dry weight of seed coat = reserve dry weight (g).

measure of the original capital would be the dry weight of the seed minus the dry weight of the seed coat. This datum represents the dry weight of embryo plus endosperm and may be called the reserve dry weight (g). In MITCHELL's Table 17 (1934, p. 120) is evidence, amply substantiated by later experiments, that the values of r for the reserve dry weight and for the seedlings raised from corresponding weight classes are identical within the limits of experimental error.

Yet the values of r correct for the lot of seed in 1932 are not correct for the same lot of seed in 1933. From results obtained by MITCHELL (in part published as indicated and in part personal communication) was prepared Table 10. The reserve dry weight in the same lot of seed is shown to have diminished after a year's storage. Not only are the values of r different for the two years, but also the reserve dry weights of the median weight classes of 25.5 mg. In 1932 the reserve dry weight was 14.97 mg; in 1933, 14.76 mg. The weights of the seedlings equivalent to the 25.5 mg fresh weight class in 1933 should be multiplied by 1.014 to make them comparable to those of the 25.5 mg fresh weight class of 1932. By a similar method, growth from seeds of many origins can be reduced to a common basis.

Scots and White Pine Experiments, GAST and MITCHELL, 1931—1933.

Further evidence concerning the validity of the correction for seed size and of the logarithmic relation between increase in dry weight and nitrogen supply in nutrient-sand culture is obtained from experiments during the period 1931 to 1933. The mechanical arrangements used have been briefly described on pp. 617—621. Other details of the experiments, including the preliminary after-ripening desirable for white pine, are described in detail in MITCHELL (1934).

In all these experiments chemically pure salts were dissolved in distilled water to form a solution not much different from that used by ALDRICH-BLAKE (loc. cit. see p. 48). A description of various combinations and associated pH values is given by MITCHELL (1934, Tables 2—4, p. 110 and inserted tables). By the use

Table 11. **Range of various fresh weights of seeds, the fresh weight of the representative seed to which all plants are calculated and the corresponding reserve dry weight, and the seasonal *total radiation* intensities of the different culture experiments. See also table A, p. 590.**

Amplituden av fröets friskvikt, friskvikten å det representativa frö till vilken alla plantor äro beräknade och motsvarande reservtorrvikt, och den totala strålningsintensiteten under en vegetationsperiod för de olika kulturförsöken. Se även tab. A, p. 590.

Experiment Abbreviated designation Försöket utfört av	Species of pine Tallart	Range [1] of seed fresh weights Amplitud av fröets friskvikt mg	Moisture content Fuktighet %	Representative seed		Radiation for growing period Strålning under vegetationsperioden kg cal/cm²
				Fresh weight Friskvikt mg	Reserve dry weight Reserv-torrvikt mg	
A—B —'29	Corsican *P. laricio* Poir. var. *corsicana* Loud.	16—24	—	20	—	—
G —'30	Scots *P. silvestris* L.	4.0—5.5	7.21	4.75	2.93	— [2]
GM —'31	Scots	5.5—6.5	—	5.25	3.4 [3]	30.2 [4]
G —'32	Scots	4.5—6.5	5.10	5.25	3,20	32 [5]
G —'32	White *P. strobus* L.	20—27	7.79	25.5	14.97	32 [5]
M —'32	White	22—26	7.79	25.5	14.97	38.9
M —'33	White	20—25	7.55	22.5	13.77	38.1 [6]
G—'34	White	15—23	6.51	18.5	11.32	22.0 [6]
M —'34	White	19—21	6.82	20.5	12.66	32.5

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[1] *Range* includes the plants used with various nutrients, not those for seed size correction.
[2] See Tab. 3, p. 597.
[3] Approximate.
[4] A fair value obtained by planimetering the records from deflection galvanometer.
[5] Approximate value only from discontinuous records.
[6] Beginning in 1933 the continuously recording and integrating recorders were used.

of KH_2PO_4, $MgSO_4 \cdot 7H_2O$, $CaCl_2 \cdot 6H_2O$ and ferric citrate (approximately $FeC_6H_5O_7 \cdot 3H_2O$) the following concentrations were obtained for the basic solutions.

Concentration in parts per million (ppm) — milligrams per liter

N	K	P	Ca	Mg	Fe	S	Cl
varied	319	254	244	176	3.4	231	412

By the use of NH_4NO_3 the nitrogen concentration, half as ammonium and half as nitrate, was varied to give different supplies. As a separate part of the 1933 experiment, as yet unpublished, MITCHELL varied potassium and phosphorus. He found that under the conditions of the experiment, the optimum for potassium was about 100 ppm, the optimum for phosphorus lay between 200 and 300 ppm, and the optimum for calcium lay between 150 and 250 ppm. These values were found under

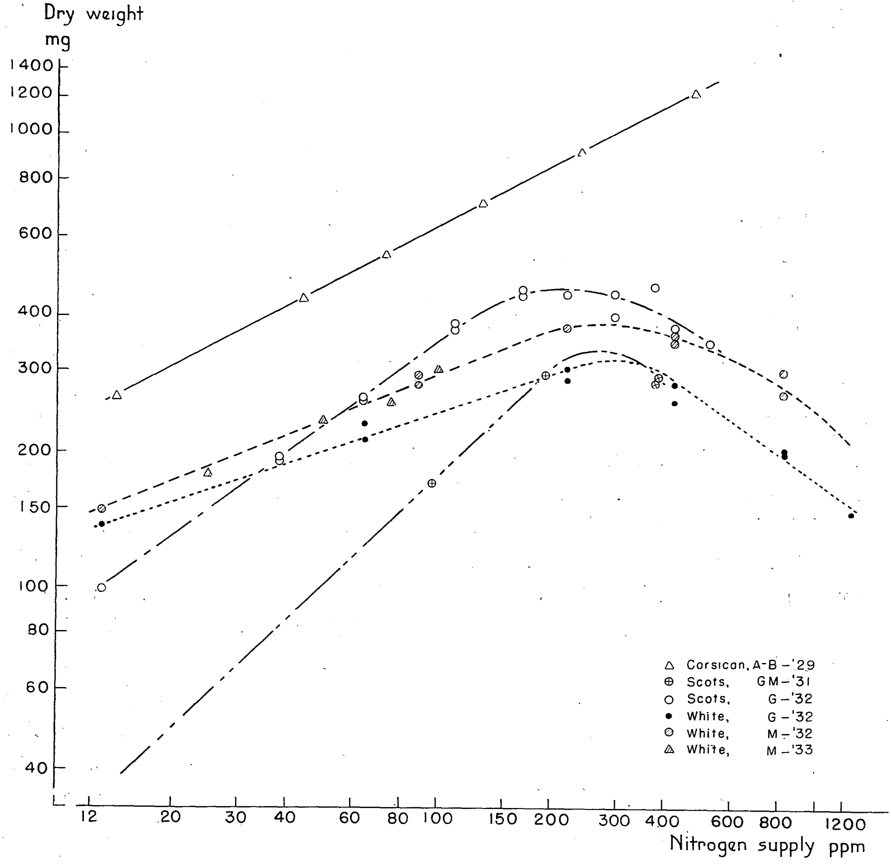

Fig. 11. The dry weights of Scots, white, and Corsican pine grown in nutrient-sand cultures with different amounts of nitrogen. From various experiments, see Table 11. Yield and nutrient concentration on logarithmic: logarithmic axes.

Torrvikt av tall, weymouthtall, och svarttall, som uppdragits i närsalttillsatt sand med kväve i olika mängd. Olika experiment, se tab. 11. Logaritmiskt koordinatsystem.

the following conditions: nitrogen was supplied at a concentration of 300 ppm, half as ammonium and half as nitrate; supplies of other nutrient elements not varied were as listed above; the plants received during the growing period a cumulative radiation (visible plus infra-red) of about 38 kilogram-calories per square centimeter measured on a fixed horizontal surface. It seems that 319 ppm of potassium in the '31—'33 experiments with nitrogen was far too high. The concentration of the other elements was approximately optimum, although a slight excess of calcium was afforded.

The information on seed and radiation which is an important part of the data of the '31—'33 experiments is listed in Table 11. In reporting the results of these experiments the yields are adjusted to values equivalent to plants grown from seed of representative size.

The results of the '31—'33 and the A-B-'29 experiments are summarized by curves plotted on logarithmic co-ordinate axes in Figure 11. In the case of Scots pine and white pine the curves are linear up to about 175 to 200 ppm nitrogen. Thereafter follows a more or less flat portion, where there is negligible change in weight with increasing concentration. Beyond that the dry weights decrease as the concentrations increase. For the purposes of discussion, the total range of concentrations can be arbitrarily divided into four regions. The first two regions are those in which the logarithmic: logarithmic curve is linear. The low concentrations up to 25—50 ppm might be called the range of minima. From 25 to 50 and increasing up to 175 to 200 might be called the working range. The region of concentrations in which no increase of weight is exhibited might be called the range of tension, and higher concentrations, the toxic range. As will be shown, the parts per million nitrogen concentrations thus delimited within the specific ranges are not independent of but are conditioned by the intensity levels of other factors, such as the potassium concentration and the radiation intensity.

Quite evidently the reactions of the various species to changing nitrogen supply are very different. Of the three, Scots pine shows the greatest relative increase with the same change in concentration, the white pine shows the least, and the Corsican pine is intermediate. But, whereas in the case of the first two species at concentrations of 175 to 200 ppm the toxic effects of nitrogen excess appear, the Corsican pine benefits by concentrations of more than 400. As a point for later discussion, it should be noted that the Corsican pine plants yielded dry weights of 800 to 1 000 mg at 250 ppm, and 1 110 to 1 300 mg at 485 ppm. The white pines yielded 380 mg at 250 ppm nitrogen, the Scots pine yielded 300 mg. The fresh weights of the white and Corsican pine seeds, which are approximately the same, are about four times that of the Scots pine seeds. Yet because of differing efficiencies of the seedlings in the use of nitrogen and of radiation, the toxic effect of nitrogen appears at about the same external concentrations in the case of the Scots and white pine, while at the same external concentration the Corsican pine yield curve gives no evidence of toxic depression.

The Mitscherlich Formula.

It has been shown that the compound interest formula can be advantageously used in the examination of the effect of varying external supplies of nitrogen on the yields of coniferous seedlings. But this formula can be used only for what have above been called the range of minima and the working range. To estimate the yields over the extensive range of nitrogen supplies which may be used in pot cultures, the logarithmic formula of Mitscherlich with the depression constant can be employed successfully (MITCHELL, 1934).

An ever-increasing literature about the MITSCHERLICH curve, its possible biological significance and its usefulness and limitations in pot and field experiments is to be found (NIKLAS and HOCK, 1934; SPILLMAN and LANG, 1924; WILLCOX, 1930; SPILLMAN, 1933; LUNDEGÅRDH, 1934). A discussion of these questions is not essential here. It is only desirable to point out that the curves for the yields of white and Scots pine shown in Fig. 11 were smoothed with the aid of the MITSCHERLICH equation. In the lower ranges of nitrogen supplies, the logarithms of these values and the logarithms of the corresponding estimates of the yields obtained from the MITSCHERLICH formula are linearly related. These ranges are the most important since they cover, as the names imply, the conditions under which the seedlings grow in nature.

Since for most pot culture work with coniferous seedlings the compound interest formula is a simpler estimating formula than that of MITSCHERLICH, its use is advisable. But with appropriate constants the MITSCHERLICH formula gives approximately the same estimates as does the compound interest formula for the ranges in which the use of the latter is proper.

The concept of various ranges — minimal, working, tensional and toxic — is useful in describing physiological effects as exhibited in the changing morphology of plants. Mere description of the external supplies and internal amounts of nutrients in terms of concentrations is not sufficient. Identical concentrations, either internal or external, have different effects on different plant species and varieties. Such differing effects in terms of yield are shown in Fig. 11 by graphical comparisons. If comparisons of structure associated with changing external conditions are to be made between different varieties of plants it is not sufficient to describe the environment in units of intensity. But by delimiting the ranges as suggested it is possible to make comparisons on the basis of the physiological effect. The physiological effects determine the various growth rates which result in differing yields. By using a scale of ranges related to yield, comparisons on a common basis are possible.

White Pine Experiment, Gast, 1934.

In the nutrient-sand culture experiment of 1934, the three factors of radiation, nitrogen, and potassium were simultaneously varied in a study of the yield of white pine seedlings. Except for the details noted below, the method of experiment was the same as used earlier.

Three levels of radiation intensity and three of nitrogen concentration were used. Four levels of potassium concentration were used in the two higher radiation intensities and three in the lowest. In all, thirty-one combinations of the three environmental factors resulted. The seed were from the same lot, obtained from a single mother tree, as those used by Mitchell in his 1933 experiment. (This experiment is as yet unpublished. From it are taken the data on the effects on yield of varying nitrogen, shown by the triangular symbols in Fig. 11; they were kindly furnished in advance of publication.) The three radiation intensities were obtained by the use of brass wire cloth. After the various corrections were applied, the cumulative »total radiation» per square centimeter for the summer, corresponding to »full», »half», and »quarter» sunshine were 21.95, 13.02, and 6.89 kilogram calories respectively. These are believed to be accurate within ± 3 %.

The concentrations of the various nutrients in ppm are as listed:

Varied	Varied	Not Varied					Varied with changing values of K	
N	K	P	Ca	Mg	Fe	S	Cl	Na
—	25	200	60	179	3.4	232	—	65
50	50	—	—	—	—	—	—	50
100	100	—	—	—	—	—	—	7
250	200	—	—	—	—	—	30	—

The total volume of solution for each pot was 3.5 liters. In this experiment, as previously, the solutions were not supplied immediately but were strengthened gradually in three steps, supplementing the original concentration of 10 %. The concentrations in which the seedlings grew for successive periods of about two weeks were therefore respectively 10 %, 30 % and 60 % of the final concentration. In this experiment the glazed jugs packed in sphagnum (p. 619) were used for the first time. A watering schedule evolved by Mitchell for the 1933 experiment was adopted. The pots were flooded at 8 AM and the solution drained immediately. Between 11 AM and 12 noon they were again flooded and the solutions allowed to stand at half height through the warmest part of the day, after which they were drained off. At 5 PM they were again flooded and drained immediately. Just after the seedlings were transplanted to the pots, the solutions were allowed to stand at half height for longer periods, if the weather was clear, the sunshine bright, and the air hot and dry.

The pine seeds were divided into 0.5 mg classes, the ranges 15 to 22 mg being used. For conversion to a common base the seedling weights were calculated to the equivalents of 18.5 mg fresh weight, corresponding to 11.32 mg of reserve dry weight.

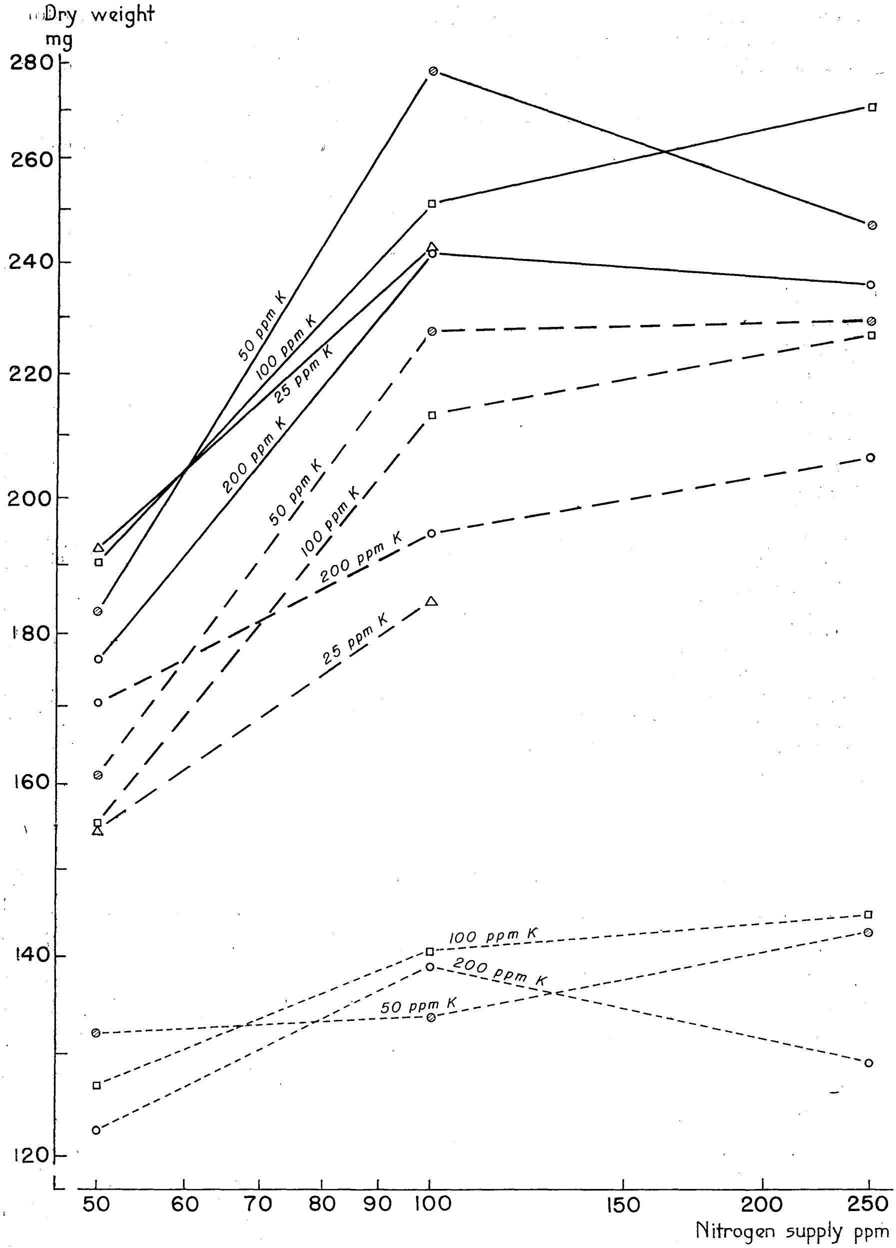

Fig. 12. The dry weights of white pine grown in nutrient-sand cultures with different nitrogen supplies at various levels of potassium supply and radiation intensity. Experiment in Petersham, 1934. Yield and nutrient concentration on logarithmic: logarithmic axes.
——— full radiation, — — — — half radiation, - - - - quarter radiation.

Torrvikt av weymouthtall, som uppdragits i närsalttillsatt sand med kväve i olika mängd och olika kalihalter och bestrålningsstyrkor. Försök i Petersham, 1934. Logmaritmiskt koordinatsystem.
——— full bestrålning, — — — —1/2, - - - - 1/4.

Table 12. **Seedling weights from M—'32 and M—'33 experiments corrected for *reserve dry weight* for comparison with the G—'34 experiment.**
Frövikter från M—'32 och M—'33:s experiment korrigerade för reserv-torrvikten för jämförelse med G—'34 experiment.

	Nitrogen concentrations in parts per million (ppm)[1] N-koncentrationen i milliondelar		
	50	100	250
Dry weights, M—'32[2] Torrvikter	233.1	305.6	380.6
Dry weights, M—'33[3] Torrvikter	237.9	303.6	—
Mean of M—'32 and M—'33 Medeltal	235.5	304.6	380.6
Adjusted[4] Korrigerade	178.1	230.3	287.8

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[1] In M—'32 and M—'33 the concentrations were K: 319 ppm, Ca: 364 ppm, P: 253 ppm; other concentrations (See MITCHELL, 1934, Table 1, p. 108) were the same as in G—'34 (See table, p. 638).

[2] Interpolated values, see MITCHELL (loc. cit., Table 19, p. 122). Cumulative radiation over growing season 38.9 kg cal. cm^{-2}.

[3] Values actually found at nitrogen concentrations given, MITCHELL (personal communication). Cumulative radiation over growing season 38.1 kg cal. cm^{-2}.

[4] In the M—'32 experiment the seedlings were grown from No. 5 seed; in the M—'33 experiment the seedlings were adjusted to the equivalents of No. 5 seed of 25.5 mg fresh weight, equal to 14.97 mg reserve dry weight. In the G—'34 the reserve dry weight was 11.32 mg. Compare Table 11, p. 634. The following correction factor results: $\frac{11.32}{14.97} = 0.7562$.

In Fig. 12 are shown the data plotted as the logarithms of the seedling dry weights against the logarithms of the nitrogen concentrations. The four solid lines above represent the yields for each of the four potassium levels as they changed with the three nitrogen concentrations when grown in the »full» sunshine; the four dashed lines below represent the identical combination of potassium and nitrogen in »half» sunshine, and the three finely dashed lines at the bottom represent the three potassium levels varying through the three nitrogen concentrations in »quarter» sunshine.

The same data are plotted in Fig. 13, but in this case against the logarithms of the potassium concentrations. As before, the upper solid lines, dashed lines and lower finely dashed lines represent the »full», »half» and »quarter» radiation intensities respectively, the three lines of each kind indicating the three nitrogen levels in each intensity.

The experimental results are not entirely satisfactory. Because the seeds were smaller than those used in previous experiments, and because the radiation intensity was less, the nitrogen concentrations approximating 250 ppm

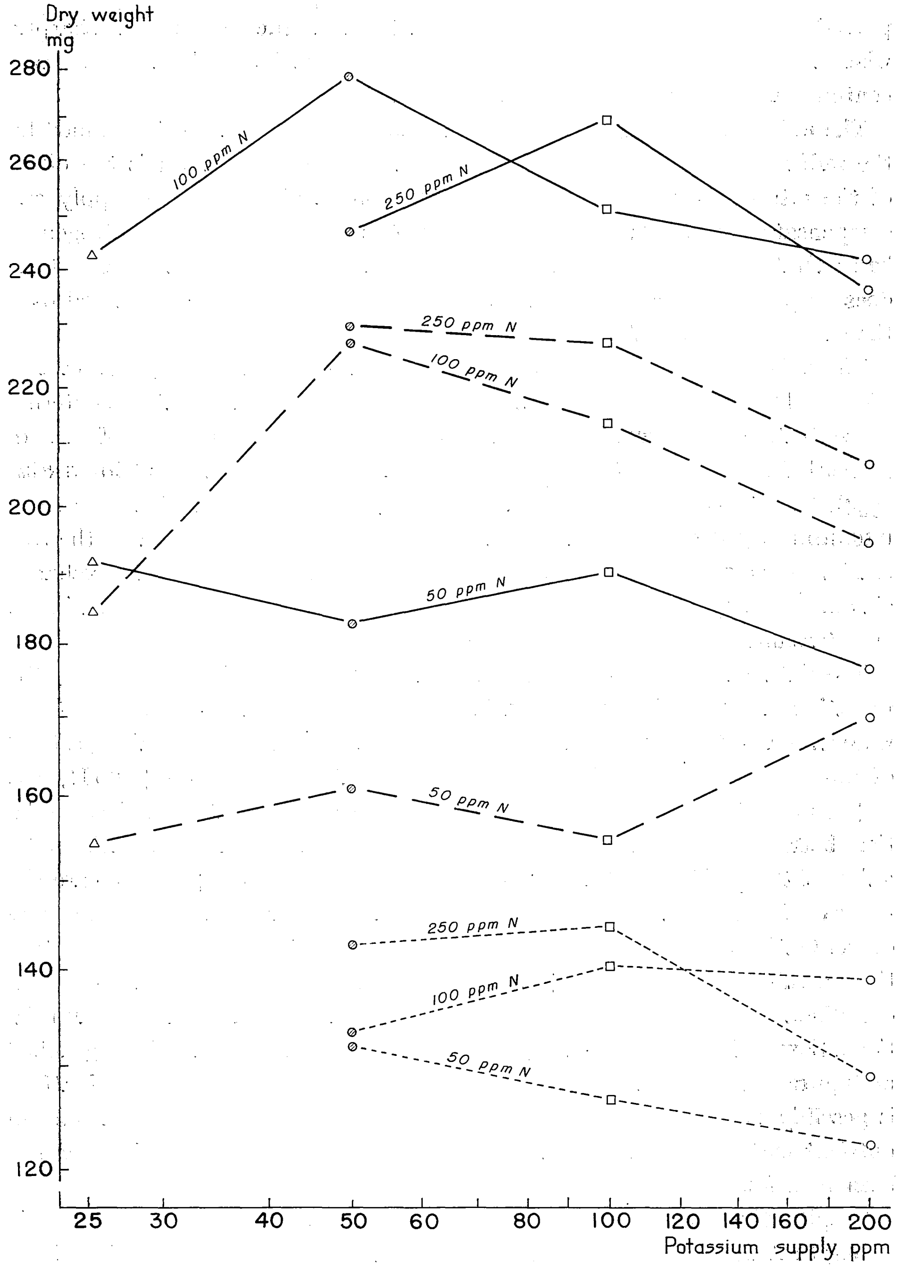

Fig. 13. The dry weights of white pine grown in nutrient-sand cultures with different potassium supplies at various levels of nitrogen supply and radiation intensity. Same data as Fig. 12, experiment Petersham, 1934. Yield and nutrient concentration on logarithmic: logarithmic axes.
——— full radiation, — — — — half radiation, - - - - quarter radiation.

Torrvikt av weymouthtall, som uppdragits i närsalttillsatt sand med kali i olika mängd och olika kvävehalt och bestrålningsstyrka. Samma uppgifter som fig. 12, försök i Petersham, 1934. Logaritmiskt koordinatsystem.
——— full bestrålning, — — — — 1/2, - - - - 1/4.

proved to be toxic. This is shown by the fact that all the curves break sharply, whereas in previous experiments (see Fig. 11) graphs on logarithmic axes continue as straight lines up to approximately 250 ppm.

The evidence is strong, however, that the yield is primarily determined by the radiation intensity. Second in importance to the radiation is the effect of the nitrogen supply. Under some conditions a high nitrogen supply can compensate for low radiation intensities. A supply of 100 ppm nitrogen in half radiation gives larger plants — with 50 and 100 ppm potassium — than does 50 ppm nitrogen in full radiation. Of importance, but less marked over the range of concentrations tried, is the supply of potassium.

The difficulties in working with potassium are emphasized by the data in Fig. 13. The lack of regular relations is evident. It appears that the external concentrations used were too great. There is also the possibility of lack of proper balance between the potassium and calcium concentrations (BURSTRÖM, 1934). In pot experiments with oats using varying supplies of potassium LUNDEGÅRDH (1934) showed that the addition of colloidal SiO_2 increased the regularity of the results. It is possible that some mechanism such as base exchange clay is necessary in nutrient culture experiments where the effect of variation in potassium is being studied.

The data can be represented graphically in a third figure by using the radiation as the independent variable. For three radiation intensities there were available three levels of nitrogen and three of potassium, making a total of nine combinations. Of these, four combinations — 100 K+250 N, 100 K+100 N, 50 K+100 N, 50 K+50 N — show approximately a linear relation between the logarithm of the radiation intensity and the arithmetic value of the yield. Two values — 50 K+250 N and 200 K+50 N — are depressed in full radiation, possibly indicating that the excess internal concentrations become toxic only in high radiation intensities. The other three combinations — 200 K+250 N, 200 K+200 N, 100 K+50 N — suggest curvilinear relations between the quantities, rather than exact linear relations. Some of both the linear and the non-linear relations have been graphed in Figure 14. The reason for the non-linearity of three of the combinations is possibly to be sought in the difficulty of experimenting with potassium in nutrient cultures containing large amounts of potassium as free ions, as has been mentioned.

Despite the shortcomings of the experiments, the evidence is exceedingly strong that the dry weights of the seedlings are proportional to the logarithm of the cumulative radiation. It is of further interest to try to bring the data of the M-'32 and the M-'33 experiments into line with this hypothesis. The essential data are assembled in Table 12. The corrected values from these experiments are entered in Figure 14 and the lines through the G-'34 values continued to them by the dashed line. In two cases, those for the lowest and highest values of nitrogen — 50 and 250 ppm respectively — the extrapolation is exact; for the median concentration of 100 ppm the data are out of line. The importance of the difference between the potassium concentrations (319 ppm in the earlier as against 200 ppm in the later) and between the calcium concentrations (364 ppm in the earlier as against 60 ppm in the later) is problematical. The increase from 100 ppm potassium to 200 ppm brought about a decrease in dry weight in the '34 experiment. How much

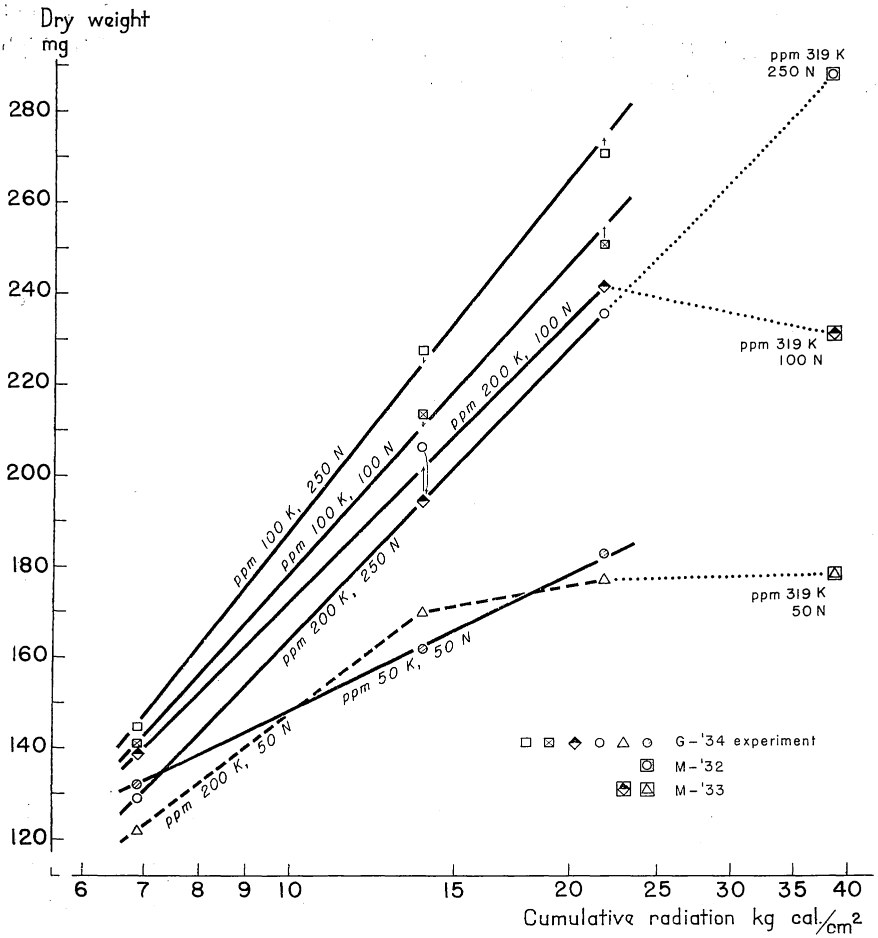

Fig. 14. The dry weights of white pine grown in different radiation intensities at various levels of nitrogen and potassium in nutrient-sand cultures. Same data as in Figs. 12 and 13, Petersham, 1934; further data in Table 12. Radiation on logarithmic and yield on arithmetic axes.

Torrvikt vid olika bestrålningsstyrka hos weymouthtall, som uppdragits i närsalttillsatt sand med kväve och kali i olika mängd. Samma uppgifter som fig. 12 och 13, försök i Petersham, 1934; ytterligare uppgifter tab. 12. x-axeln logaritmisk, y-axeln aritmetisk.

of a decrease would be caused by a further increase from 200 ppm to 319 ppm it is difficult to say. In the '33 experiment of MITCHELL (unpublished), increases of potassium above 200 ppm gave exceedingly discordant results. It is to be noted that it is the median concentrations (100 ppm) which do not fall into line in these experiments. Trials with the low (50 ppm) and the high (250 ppm) potassium concentrations are consistent.

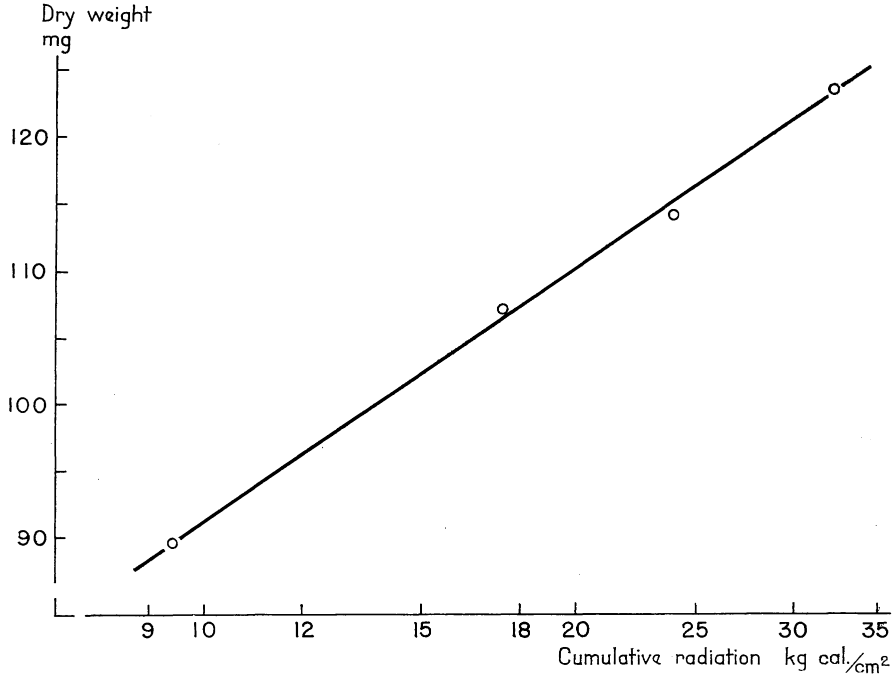

Fig. 15. The dry weights of white pine grown in nursery soil under brass wire cloth screens. Data from MITCHELL (1936), experiment of 1934, at the Black Rock Forest. Radiation on logarithmic and yield on arithmetic axes.

Torrvikt av weymouthtall, som uppdragits i plantskolejord under mässingsduksskärm. Material från MITCHELL (1936). x-axeln logaritmisk, y-axeln aritmetisk.

Additional evidence for the validity of the logarithmic estimate of the per cent cumulative radiation intensities is obtained from an experiment at the Black Rock Forest which was recently published. Under a series of brass wire cloth screens transmitting 29 %, 53 %, and 74 % of the radiation about four hundred seedlings were grown in each intensity, in poor garden soil with no other attention than initial cultivation and occasional watering. An additional sample was grown in the open in the same soil. From the data, described in detail by MITCHELL in another publication (1936), are quoted in Fig. 15 the dry weights of the seedlings plotted as arithmetic values against the logarithms of radiation intensities. The same linear relation discovered in the G-'34 experiment is shown.

In the examination of data as given graphically in Fig. 14 the increasing slope of the curves with changing radiation levels for the same supplies of nitrogen is noticed. This effect has been observed in all the experiments in which radiation and nitrogen have been varied simultaneously. The effect of nitrogen supply is always dominated by the level of radiation intensity. The whole series of experiments furnishes positive evidence that between nitrogen supply and dry weight there is a logarithmic : logarithmic relation. Between radiation intensity and dry weight there is a logarithmic : arithmetic relation valid under certain nutrient conditions when the radiant energy measurement used is that of total radiation. It may be well to emphasize that measurement of illumination would have served as well within the G-'34 experiment. This is true because the radiation screens diminish the total radiation and the illumination by the same amounts. But even if further tests should show that the logarithm of the total radiation serves to correct exactly for the differences between years or between localities under all conditions, it would still be necessary to show by experiment that illumination measurements serve as well.

Discussion of the Internal Concentration of Nitrogen.

The relation between the supplies of nitrogen and the yields of seedling conifers heretofore discussed has been based on the external concentration of the supplies. If instead of external supplies one were able to use the internal concentrations, it is to be expected that the effects of the nitrogen on the physiological processes in the plants would be more closely approximated. In an approach to this problem the first step is to learn if there is any constant relation between the external and internal concentrations; the second, if there is any relation between the internal concentration and the yield.

In the description of the '29 experiment on Corsican pine, ALDRICH-BLAKE (bottom of Table 14, p. 55; discussion, p. 56—57) states, »The results do not yield any certain conclusions on the availability of nitrogen in the several treatments.» Insofar as the separation between the relative availabilities of ammonical and nitrate nitrogen are concerned, this is true. But a logarithmic : logarithmic relation can be shown between the total nitrogen and the nitrogen content as per cent of dry weight, with the exception of treatment 4 (0.643% N) which is obviously discordant.

For evidence of a similar relation, the per cent nitrogen contents of the seedlings raised in the series of nutrient-sand cultures at the Harvard Forest and the Black Rock Forest have been examined. In the Scots pine experiment of '31, a simple linear relation between the arithmetic values of external and internal concentrations was found (MITCHELL, Fig. 5, p. 48; Table 5, p. 111; discussion pp. 46—49). For white pine in the M-'32 experiments the logarithmic relation true for the Corsican pine experiment was again found, and MITCHELL (loc. cit.) was able to show that the limit logarithmic-decrement or asymptotic logarithmic formula — the Mitscherlich formula, but without the depression term used in determining yield — could be employed to estimate the nitrogen content as per cent of dry weight at time of harvesting. This formula holds over the ranges of minimal and working concentrations; in the toxic range of concentrations, the nitrogen content of the seedlings expressed as per cent of the dry weight remains constant.

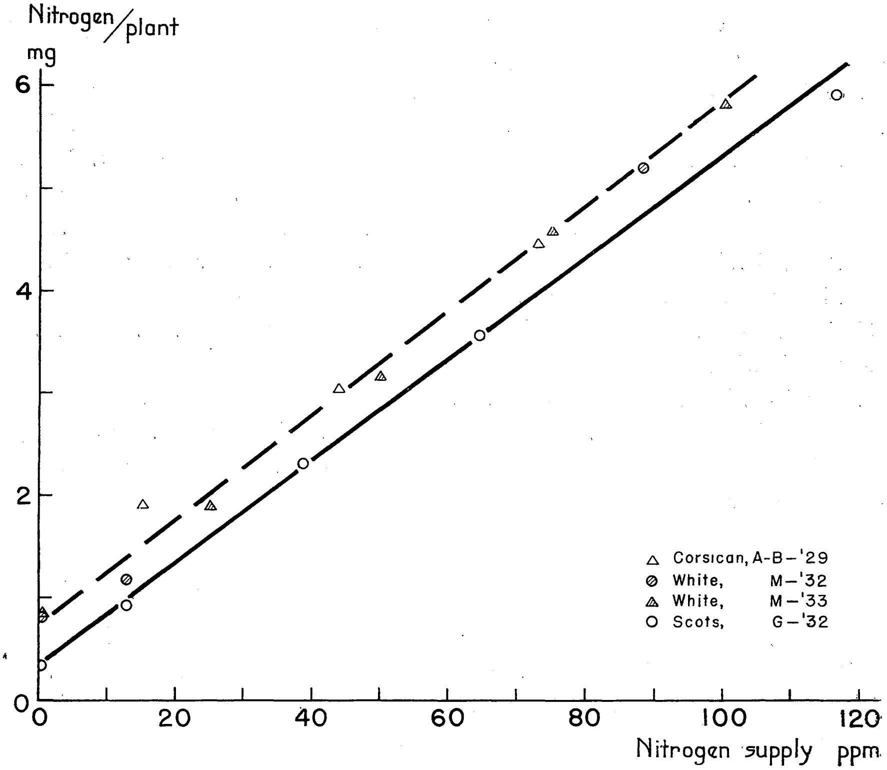

Fig. 16. The arithmetic: arithmetic relation between the external nitrogen concentration in nutrient-sand cultures and the miligrams nitrogen content per plant. This relation holds only for relatively low concentrations of external supplies — the so-called *minimal* and *working* ranges.

Sambandet mellan kvävehalten i närsalttillsatt sand och kvävehalten i plantan i mg.

The nitrogen content of the seedlings expressed in milligrams decreases in the toxic ranges at about the same rate as does the dry weight, as evidenced by the fact that the per cent nitrogen content on dry weight remains constant. It has been found (MITCHELL, loc. cit.) that the Mitscherlich formula with depression constant provides a satisfactory formula for estimation of the milligrams nitrogen internal concentration appropriate to the external concentrations through the range of tension, but that a linear depression fits as well as any other relation through the toxic range.

Although the asymptotic logarithmic formula is necessary to account for the relation between internal nitrogen content in milligrams and the external concentration over the entire range, for the dilute concentrations a simpler relation is adequate. Up to 120 ppm the relation is a linear function of the arithmetic values of the two quantities (Fig. 16). It is of further interest that notwithstanding the large differences in the sizes of the plants and the corresponding root systems, the internal contents in milligrams in plants grown under widely differing radiation intensities are very close. It would seem that a sort of partition coefficient between the two phases — the plant and the external supply — is involved.

Since constant relations are shown to exist between the external and the internal concentrations in either absolute units or per cent on dry weight, it is to be expected that relations should be found between the internal contents and the yield. This relation takes the form of a linear proportion between the arithmetic values of the yield plotted against the logarithmic values of the internal nitrogen concentration expressed as per cent of dry weight. That the internal concentration of nitrogen expressed as per cent of dry weight apparently has the same relation to yield as does radiation intensity is worthy of note. Since both conclusions deserve further study in extended experiments the point will not be further emphasized.

The relations between the external concentration and the internal content of nitrogen have been used by MITCHELL (loc. cit. p. 84—87) to estimate the nitrogen availability of forest soils. Since it was planned that the pot culture tests should be repeated every few years in order to demonstrate the results of various forest treatments, it was necessary to devise some reference scale which would remain constant and would serve to correct for the differences in insolation, temperature and seedling genotypes in the different experiments. The results discussed on pp. 617—645 indicate that the nutrient-sand culture experiments fully justify the expectations, in that they can be replicated quite exactly if proper accounting is made for the various factors.

But the nutrient-sand culture method is far from the ideal medium. The high free ionic concentrations of the nutrient-sand cultures which contain no reserve supplies of exchangeable bases are perhaps not the best standards with which to compare the soil-sand cultures. Vageler and Alten (1933) stress the importance of hydrogen ions liberated from carbonic acid formed by the solution of respiratory carbon dioxide. These may act as an exchangeable base to free nutrient bases. A process of this nature provides an automatic mechanism for increasing the rate of supply of nutrients to the plants as they grow. Although some adjustment for the size of plants has been made in the nutrient-sand cultures by gradually increasing the external concentration, this adjustment is but crude at best.

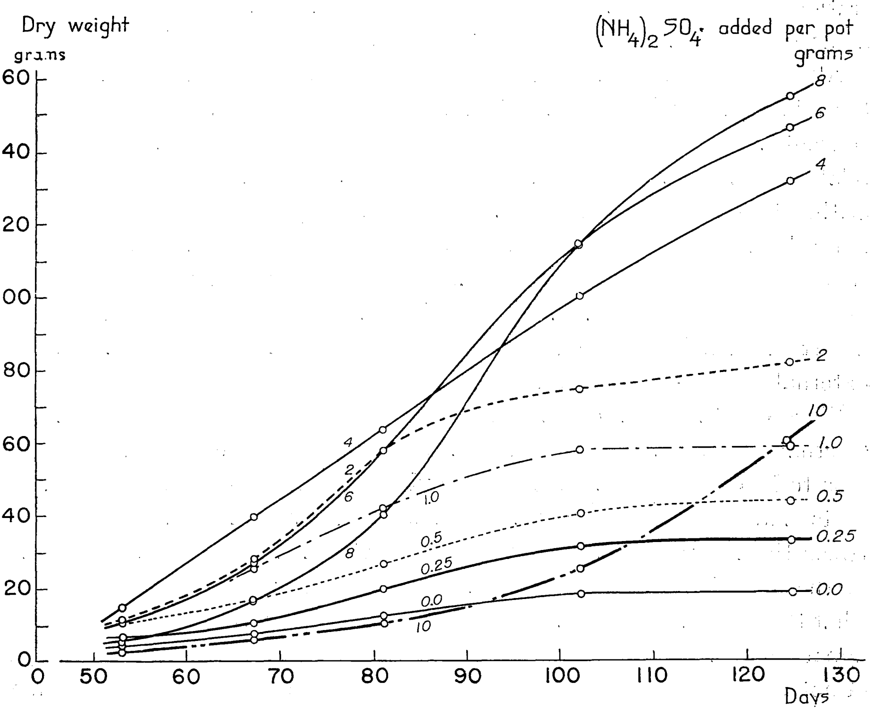

Fig. 17. The changing optimal external concentrations of nitrogen with increasing size of oat plants. Data from Rippel (1931, Fig. 12). Plants harvested at various intervals after having been grown in pots of soils to which differing amounts of ammonium sulfate were added.

Den med ökad storlek hos havreplantor förändrade optimala kvävekoncentrationen. Efter Rippel (1931, fig. 12). Plantorna hava skördats efter olika antal dagar, sedan de vuxit i krukor till vilka tillsatts olika mängd ammoniumsulfat.

Evidence that nutrient supply rates which are either too low or too high for plants of a given size may be optimum for smaller or larger plants can be obtained from the work of Mayr (see Rippel 1931) on oats. In Fig. 17 are data estimated from his figure 12 (loc. cit.) redrawn as in his figure 14. These results are interpreted as showing that between the 50th and 86th days, when the dry plants in a pot weighed between 18 and 70 grams, 4 grams of $(NH_4)_2SO_4$ was the optimum addition to a pot of soil, 2 grams and 6 grams being respectively too little and too much. Between the 87th and the 102nd days, the plants having grown to between 70 and 118 grams dry weight, a supply furnished by 4 grams of $(NH_4)_2SO_4$ per pot is not enough; 6 grams are better and 8 grams are too much. In the next period, from the 103rd day to the end of the experiment on the 125th day, for plants with a dry weight of 118 to 158 grams, a 6 gram supply of the same salt proved insufficient, and the plants with an addition of 8 grams achieved the greatest dry weight. A supply of 10 grams per pot proved so concentrated that the plants never recovered from the excess supply; the final dry weight was the same as that of plants grown in a pot to which only 1 gram had been supplied. A particular external concentration is apparently necessary for the maximum rate of dry weight increase, the optimum changing with the size of the plant. Explicit evidence for this is not to be obtained from the nutrient-sand cultures of pine seedlings at present, but is implicit in the relations between yield and nitrogen content expressed as milligrams per plant and per cent of dry weight.

An example of an unfavorable relation between plant size and external supply of nitrogen, such as has just been discussed, is shown in Fig. 14. Over the range of radiation intensities in the G-'34 experiment (7 to 22 kg cal. cm^{-2}) a supply of 100 ppm nitrogen gives greater yields than does 250 ppm. With the latter external supply the internal concentration is probably toxic. But with a radiation intensity of 38 kg cal. cm^{-2} for the season the greater external supply of nitrogen is beneficial rather than injurious. The curve for the 100 ppm supply breaks at a radiation intensity of twenty kilogram calories for the same reason that the 50 ppm supply breaks at about fifteen kilogram calories. The nitrogen supply is limiting. A similar case has already been shown for Scots pine (Fig. 5) when grown in humus-sand mixtures at different radiation intensities.

From the experience with Scots and white pine obtained in the experiments just discussed, and from the data furnished by Aldrich-Blake (loc. cit.) for Corsican pine, it appears that an internal nitrogen concentration of about three per cent of the dry weight is most favorable for the maximum yield of these pines in the seedling stage.

The effects of external supplies of nutrients on growth rates are often studied by the use of flowing culture solutions with low concentrations. But the discussion of the last paragraph indicates that if flowing nutrient cultures are used, they must be so adjusted that the concentration is increased as the plants become larger. That is, since the logarithm of the internal concentration in per cent is proportional to the logarithm of the external concentration, in order to maintain a constant internal concentration in terms of per cent content, the external concentration must be increased by an amount which is proportional — again a logarithmic function — to the size of the plant. The efficiency of the nutrient in affecting the growth of the plant should be studied in relation to the internal concentration, which should be maintained constant.

With these thoughts in mind it is profitable to return to the data on the change in yield with change in nitrogen supply, as shown in Fig. 11. When these were under discussion (p. 636), attention was called to the fact that the Corsican pine were not supplied with external concentrations sufficiently large to extend beyond the working range. The nitrogen content of these plants as per cent of dry weight varied from 0.7 to 1.1 (ALDRICH-BLAKE, loc. cit., bottom of Table 14, p. 55). This is much less than the similar values for white and Scots pine in the ranges of tension and toxicity, namely, 3.2%. It is believed that the efficiency of the radiant energy use by the Corsican pine must be much greater, and therefore much larger supplies of nitrogen would have to be provided to increase the internal concentration to the point where it might become injurious. Further, it is to be noted that the efficiency of nitrogen use by the Scots pine is much greater than the efficiency in white pine. Thus, even though the Scots pine plants start with smaller reserve dry weights, and with low nitrogen supplies under low radiation intensities result in smaller seedlings, with high levels of radiation and nitrogen they can in a single growing season accumulate a dry weight greater than that of white pine. Control of the external concentrations to give a desired internal concentration therefore depends upon the growth rate of the seedlings. This in turn is determined by the efficiency of the photosynthetic process and the efficiency of the plant in its use of radiation and the various nutrients.

There is every reason to believe that the criteria of exact experimentation as analyzed in the last paragraphs are not satisfied in these nutrient-sand culture experiments. Therefore, helpful, suggestive, and illuminating as they are, they provide merely a first approach to the problems of the yield and growth rate of coniferous seedlings, which deserve further study. Experiments with tree seedlings are desirable from two points of view. They will furnish scientific knowledge to serve as a background for improvement in silvicultural practice, and they provide unique material for the study of vegetative growth uncomplicated by the fruiting phases of development.

SECTION IV. Discussion of the Growth of Scots Pine in Raw Humus Soils under Varied Radiation Intensities.

Highly exact relations between external nitrogen supply, internal nitrogen concentration, radiation and yield have been found in the experiments using nutrient-sand cultures. These relations may be utilized in the interpretation of the results of the Försöksanstalt experiment to disclose the differences between pot cultures of sand flowed with mineral nutrients and sand mixed with humus and soil. In beginning the discussion it is to be noted that the radiation intensities are, in general, lower in the Experimentalfältet trial than in the later nutrient-sand culture experiments. Again, the nutrient-sand cultures are a much simpler growth medium than are the humus substrates. To the nutrient-sand cultures known amounts of ammonium and nitrate are added. In the humus the supplies of ammonium and nitrate are the result of microbiological activity. About this activity we know only that the reciprocal influences of the organisms are complex, and the methods for determining the nutrients released by their activity and available to the higher plants can as yet be considered to give only approximate values. Further, the effective nutrient concentrations must be quite different in the nutrient-sand cultures from those in the humus-sand tests. These facts limit the application of the relations since the nitrogen mobilization values found in the storage tests are used as the measures of the external supplies of nitrogen.

Logarithmic: Logarithmic Relation between Yield and Nitrogen Supply.

The linear relation between dry weights of the seedlings and the external nitrogen supplies, both plotted on logarithmic scales, was the first relation examined. For measures of external nitrogen supplies were used the mobilization coefficients in milligrams of nitrogen per kilogram ($N_{NH_4+NO_3}$) of the humus mixed with sand. This linear relation found for the nutrient-sand cultures cannot be used to generalize the results of the humus-sand cultures. The yields from the good raw humus are relatively high in comparison with the yields from the other humus types. It might be suspected that some essential nutrient other than nitrogen is deficient and therefore limiting to the growth of the plants, especially in the burnt raw humus and the bad raw humus. To determine whether this was the case, analyses were made for nitrogen, phosphorus and potassium. Analytical methods were adapted from those published in the literature: for nitrogen, after PREGL but with the addition of salicylic acid (see MITCHELL, 1934, p. 28); phosphorus, after FISKE and SUBBAROW (1925); potassium, after HOFFMAN and JACOBS (1931). In the latter two cases digestion with perchloric acid preceded the use of the methods noted. The results of the analyses are summarized in classified form in Tables 13—16.

The phosphorus contents as per cent of dry weight varied comparatively little in the plants grown under the different radiations in the humus-sand cultures (Table 15); the averages in the 22 % radiation were about 0.34 % phosphorus, and in the 50 % radiation they ranged from 0.29 % to 0.34 %.

Table 13. **Nitrogen content in milligrams per plant of three-months-old Scots pine seedlings grown in different radiation intensities and in various humus-sand mixtures. 1930.**

Kväve i milligram per planta i tre månader gamla tallplantor, uppdragna vid olika strålningsintensiteter och i olika humusslag. 1930.

Humus Humusslag	Radiation (Strålning)																			
	4 %				11 %				22 %				27 %				50 %			
	Pot Kruka	M mg	± ε mg	± ε %	Pot Kruka	M mg	± ε mg	± ε %	Pot Kruka	M mg	± ε mg	± ε %	Pot Kruka	M mg	± ε mg	± ε %	Pot Kruka	M mg	± ε mg	± ε %
II. Good raw humus God råhumus	5	0.249	0.014	5.6	15	0.435	0.040	9.2	25	1.032	0.046	4.5					35	2.421	0.170	7.0
	6	0.225	0.003	1.3	16	0.553	0.017	3.1	26	1.141	0.046	4.0	46	1.813	0.090	5.0	36	2.914	0.169	5.8
	Mean	*0.237*	*0.009*	*3.8*		*0.485*	*0.027*	*5.6*		*1.092*	*0.033*	*3.0*						*2.733*	*0.058*	*2.1*
III. Severely burnt raw humus Hårt bränd råhumus	7	0.243	0.013	5.3	17	0.383	0.015	3.9	27	0.686	0.031	4.5					37	1.278	0.124	9.7
	8	0.178	0.011	6.2	18	0.264	0.008	3.0	28	0.643	0.032	5.0	48	0.859	0.051	5.9	38	0.953	0.047	4.9
	Mean	*0.214*	*0.014*	*6.5*		*0.326*	*0.014*	*4.3*		*0.659*	*0.054*	*8.2*						*1.075*	*0.065*	*6.0*
I. Bad raw humus Dålig råhumus	3	0.207	0.013	6.3	13	0.230	0.006	2.6	23	0.229	0.008	3.5	43	0.262	0.007	2.7				
	4	0.231	0.006	2.6	14	0.195	0.007	3.6	24	0.241	0.008	3.3	44	0.276	0.012	4.3	34	0.349	0.007	2.0
	Mean	*0.219*	*0.008*	*3.7*		*0.213*	*0.006*	*2.8*		*0.235*	*0.006*	*2.6*		*0.267*	*0.002*	*0.7*				
IV. Inoc. humus Inf. humus	10	0.235	0.021	8.9	20	0.459	0.015	3.3	30	1.238	0.153	12.4	50	1.292	0.103	8.0	40	1.135	0.049	4.3
XIII. Mixture Blandprov	9	0.174	0.004	2.3	19	0.239	0.012	5.0	29	0.556	0.044	7.9	49	0.887	0.033	3.7	39	0.712	0.006	0.8
X. XI. XII. Sand	1	0.188	0.024	12.8	11	0.220	0.006	2.6	21	0.229	0.006	2.6					31	0.258	0.003	1.2
	2	0.186	0.010	5.4					22	0.225	0.006	2.7					32	0.295	0.013	4.4
	Mean	*0.187*	*0.015*	*8.0*						*0.227*	*0.004*	*1.8*						*0.276*	*0.010*	*3.6*

Table 14. **Nitrogen content in per cent of three-months-old Scots pine seedlings grown in different radiation intensities and in various humus-sand mixtures. 1930.**

Kvävehalt i procent i tre månader gamla tallplantor, uppdragna vid olika strålningsintensiteter och i olika humusslag. 1930.

Humus Humusslag	Radiation (Strålning)																			
	4 %				11 %				22 %				27 %				50 %			
	Pot Kruka	M %	± %	ε %	Pot Kruka	M %	± %	ε %	Pot Kruka	M %	± %	ε %	Pot Kruka	M %	± %	ε %	Pot Kruka	M %	± %	ε %
II. Good raw humus God råhumus	5	3.51	0.17	4.8	15	2.61	0.05	1.9	25	2.92	0.08	2.7	46	3.28	0.07	2.1	35	3.05	0.06	2.0
	6	3.51	0.06	1.7	16	2.76	0.04	1.4	26	2.85	0.06	2.1					36	2.81	0.05	1.8
	Mean	*3.508*	*0.081*	*2.3*		*2.674*	*0.035*	*1.3*		*2.881*	*0.047*	*1.6*						*2.897*	*0.047*	*1.6*
III. Severely burnt raw humus Hårt bränd råhumus	7	3.34	0.26	7.8	17	2.11	0.04	1.9	27	2.31	0.01	0.4	48	2.28	0.08	3.5	37	2.66	0.07	2.6
	8	2.62	0.23	8.8	18	1.90	0.06	3.2	28	2.02	0.06	3.0					38	2.29	0.06	2.6
	Mean	*3.024*	*0.209*	*6.9*		*2.010*	*0.041*	*2.0*		*2.079*	*0.090*	*4.3*						*2.379*	*0.047*	*2.0*
I. Bad raw humus Dålig råhumus	3	3.25	0.27	8.3	13	1.65	0.04	2.4	23	1.06	0.03	2.8	43	0.98	0.03	3.1	34	1.14	0.01	0.8
	4	3.63	0.48	13.2	14	1.48	0.04	2.7	24	1.18	0.03	2.5	44	0.95	0.02	2.1				
	Mean	*3.386*	*0.115*	*3.4*		*1.569*	*0.104*	*6.6*		*1.125*	*0.024*	*2.1*		*0.970*	*0.021*	*2.2*				
IV. Inoc. humus Inf. humus	10	3.07	0.31	10.1	20	2.36	0.12	5.1	30	2.52	0.08	3.2	50	2.54	0.08	3.1	40	1.96	0.05	2.6
XIII. Mixture Blandprov	9	2.55	0.13	5.1	19	2.36	0.12	5.1	29	2.01	0.16	8.0	49	2.24	0.08	3.6	39	2.15	0.01	0.5
X. XI. XII. Sand	1	2.52	0.21	8.3	11	1.51	0.09	6.0	21	0.81	0.02	2.5					31	0.76	0.02	2.6
	2	2.47	0.14	5.7					22	0.80	0.02	2.5					32	0.92	0.05	5.4
	Mean	*2.501*	*0.137*	*5.5*						*0.805*	*0.012*	*1.5*						*0.842*	*0.039*	*4.6*

Table 15. **Phosphorus content in milligrams per plant and in per cent in three-months-old Scots pine seedlings grown in different radiation intensities and in various humus-sand mixtures. 1930.**

Fosforhalt i milligram och i procent per planta i tre månader gamla tallplantor, uppdragna vid olika strålningsintensiteter och i olika humusslag.

Humus Humusslag	Radiation (Strålning)													
	22 %							50 %						
	Pot Kruka	Absolute			In per cent			Pot Kruka	Absolute			In per cent		
		M	± ε		M	± ε			M	± ε		M	± ε	
		mg	mg	%	%	%	%		mg	mg	%	%	%	%
II. Good raw humus God råhumus	25	0.112	0.007	6.3	0.327	0.005	1.5	35	0.235	0.013	5.5	0.297	0.008	2.7
	26	0.144	0.009	7.9	0.363	0.014	3.9	36	0.210			0.281		
	Mean	*0.129*	*0.008*	*6.2*	*0.34*	*0.009*	*2.6*		*0.231*	*0.027*	*11.7*	*0.294*	*0.008*	*2.7*
III. Severely burnt raw humus Hårt bränd råhumus	27	0.109	0.013	11.9	0.356	0.013	3.7	37	0.187	0.037	2.0	0.340	0.042	12.4
I. Bad raw humus Dålig råhumus	24	0.072	0.006	8.3	0.343	0.011	3.2	34	0.106			0.316		

Table 16. **Potassium content in milligrams per plant and in per cent in three-months-old Scots pine seedlings grown in 27 % radiation intensity and in different humus-sand mixtures.**

Kalihalt i milligram och i procent per planta i 3 månader gamla tallplantor, uppdragna vid 27 % strålningsintensitet och i olika humusslag.

Humus Humusslag	Pot Kruka	Radiation Strålning 27 % (Water screen) (Vattenskärm)					
		Absolute			In per cent		
		mg	± ε		M	± ε	
			mg	%	%	%	%
II. God raw humus God råhumus	46	0.752	0.049	6.5	1.528	0,078	5.1
III. Severely burnt raw humus Hårt bränd råhumus	48	0.416	0.027	6.5	1.118	0.029	2.6
I. Bad raw humus Dålig råhumus	43	0.246	0.009	3.7	0.914	0.019	2.1
	44	0.283	0.024	8.5	1.029	0.033	3.2
	Mean	*0.265*	*0.010*	*3.8*	*0.972*	*0.026*	*2.7*

Naturally the weights of phosphorus per plant varied widely because of the differing dry weights, ranging from 0.07 to 0.23 mg.

The figures for the per cent potassium contents, on the other hand, are markedly different (Table 16). Unfortunately, since practically all of the plants were consumed in the nitrogen and phosphorus determinations, the potassium analyses were not as complete as could be desired. Only the plants grown under the water screen (27 % radiation) were available. Those grown in the good raw humus contained 1.5 % potassium on dry weight, in the burnt raw humus 1.1 %, and in the bad raw humus 1.0 %. These correspond to 0.75 mg, 0.41 mg, and 0.27 mg per plant respectively. The potassium contents, both as per cent and as milligrams, are greater by nearly a half in the plants grown in the good raw humus than in those from the burnt raw humus. The first thought is that the plants grown in the burnt raw humus and possibly those grown in the bad raw humus were deficient in potassium.

But another way of examining the data remains. The per cent contents of potassium and of phosphorus can be calculated as ratios to the nitrogen per cent content. These can be compared with the values similarly obtained by MANSHARD (1933, p. 120) for one- and two-year-old Scots pines grown in a nursery. He obtained ratios which are about the same as the average of the ratios he calculated from the results of SCHMITZ-DUMONT (1894) and BAUER (1910). For the oxides of phosphorus and potassium he secured the following:

P_2O_5 : K_2O : N
1 : 1.50 : 3.61

The above ratios may be expressed in terms of the elements instead of the oxides, using nitrogen as unity, as follows:

N : P : K
1 : 0.12 : 0.35

From Tables 15 and 14 may be taken the phosphorus and nitrogen values in per cent for the plants grown in the three humus substrates in 22 % and 50 % radiation intensities. With nitrogen equal to unity the following ratios may be computed.

	22 % Radiation			50 % Radiation		
	N	:	P	N	:	P
Good raw humus	2.88 %	:	0.346 %	2.90 %	:	0.294 %
	1	:	0.12	1	:	0.10
Burnt raw humus	2.08 %	:	0.356 %	2.38 %	:	0.340 %
	1	:	0.17	1	:	0.14
Bad raw humus	1.13 %	:	0.343 %	1.14 %	:	0.316 %
	1	:	0.30	1	:	0.28

From Tables 16 and 14 may be taken the potassium and nitrogen values in per cent for the plants grown in the three humus mixtures under the water screen transmitting 27 % radiation. For potassium the following ratios may be computed with nitrogen as unity.

	27 % Radiation		
	N	:	K
Good raw humus	3.28 %	:	1.53 %
	1	:	0.47
Burnt raw humus	2.28 %	:	1.12 %
	1	:	0.49
Bad raw humus	0.97 %	:	0.97 %
	1	:	1

In the above there is no evidence of either phosphorus or potassium deficiency in the plants grown in the severely burnt bad raw humus or the bad raw humus. Only in the case of the plants grown in good raw humus in 50 % radiation does the phosphorus/nitrogen ratio fall below that found by MANSHARD. This slightly lower value can hardly be considered of importance to the growth of these plants, which are the largest of all. The potassium/nitrogen ratios are in all cases well above those which MANSHARD determined.

The intake of potassium and phosphorus in plants grown in soils of low nitrogen mobilization coefficients is proportionately much greater than the intake of nitrogen. It is clear then that the growth of the seedlings was limited not by the amount of phosphorus and potassium but by the amount of nitrogen supplied to the plants.

Arithmetic: Arithmetic Relation between the Nitrogen Content in Milligrams and the Nitrogen Supply.

A linear relation between the arithmetical values of the nitrogen supply and the arithmetical values of the internal nitrogen content in milligrams was found for the lower concentrations of external supplies in nutrient-sand cultures. If the results of the humus-sand cultures are examined for this relation it is found that the contents in milligrams are not linear functions of the nitrogen supplies as determined by the storage tests. The failure of this test shows only that the nitrogen mobilization value as determined in these particular storage tests did not provide the same measure of available nitrogen in the humus-sand cultures as does the concentration of free ions in the nutrient-sand cultures.

Arithmetic: Logarithmic Relation between Yield and Radiation.

The linear relation between the dry weights on an arithmetic scale and the radiation intensities on a logarithmic scale provides another test. Again the expected relation does not result. As the radiation intensity is increased, the relation, while approximately linear in the case of the two less fertile soils, is far from linear for the more fertile soil. The reasons for this are discussed in the next paragraphs.

Logarithmic: Logarithmic Relation between Yield and Internal Nitrogen Content.

In the nutrient-sand culture experiments it was found that the logarithms of the dry weights of the seedlings and the logarithms of their nitrogen contents in milligrams are linearly related. The plants from the humus-sand cultures are examined for this same relation in Fig. 18. In this, the logarithms of the dry weights and the logarithms of the milligrams nitrogen contents, based on the averages of the plants in the individual pots, are entered on logarithmic scales. As may be seen in the figure, the points lie for the most part along the straight lines representing the individual relations for the various soils. In this instance the relation found in the humus-sand cultures coincides with the experience from the nutrient-sand cultures.

It is evident that the data fall into two groups. The first group contains the plants grown in substrates with low nitrogen availability — the sand and the bad raw humus. The steep slopes of the graphed relations indicate large changes in yield with small changes in the internal content of nitrogen.

In the second group which can be distinguished the graphs are less steep.

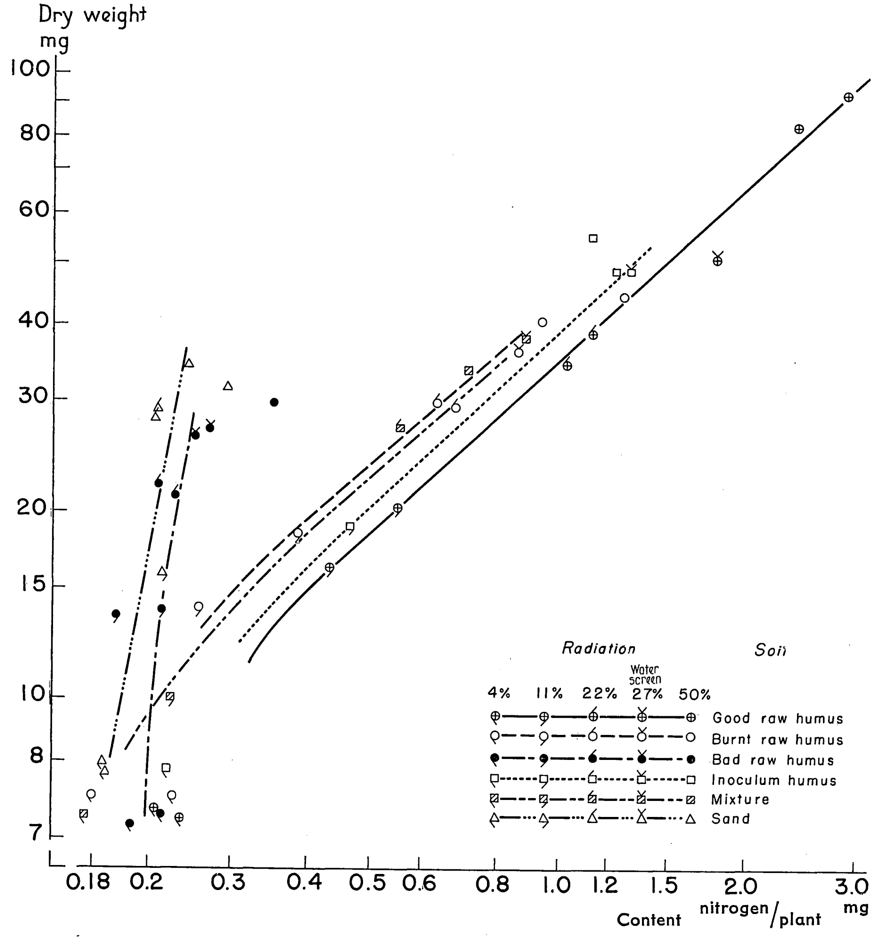

Fig. 18. The relation between the nitrogen content in milligrams per plant and the plant dry weight of Scots pine seedlings grown in humus sand cultures in varying radiation intensities. Data from Tables 5 and 13. Skogsförsöksanstalt, 1930. Yield and nitrogen content on logarithmic: logarithmic axes.

Sambandet mellan kvävehalten i mg per planta och torrvikten. Från experiment med tallplantor uppdragna i humus-sand vid olika bestrålningsstyrka. Uppgifter från tab. 5 och 13. Skogsförsöksanstalten, 1930. Logaritmiskt koordinatsystem.

The increases in yield with increasing nitrogen are smaller. Although the slopes of the graphed relations are more or less parallel, there is a displacement of the graphs to the right — toward higher nitrogen contents — as the nitrogen availability in the humus increases. These differences were clearly brought out by the storage mobilization tests. The comparatively simple relations for estimating yield and nitrogen contents from the external supply discovered in the nutrient-sand cultures did not hold when the attempt was made to use the nitrogen mobilization tests as a measure of external availability. A relation obviously exists but at the moment seems beyond mathematical analysis.

The above relations are very important. For qualitative determination of the nitrogen mobilization, the storage tests serve very well. According to the viewpoint of Professor HESSELMAN, the chief value of such tests is in characterizing the probable intensity of the reaction of the humus types to changes which may be brought about by silvicultural treatment. With this viewpoint the data fully agree.

It is now possible to show more clearly why the mobilization tests failed to give effective measures of the nitrogen availability. In the early discussion of the weights of plants from the duplicate pots (p. 606) it was pointed out that in certain of the duplicate pots — namely, 15 + 16, 17 + 18, 25 + 26, 31 + 32, and 35 + 36 — the yields differed sufficiently in their means and standard deviations to indicate that the plants were not grown under identical conditions. It is shown in Fig. 18 that the differences in the yields were due to differences in the internal nitrogen contents. Despite the care taken to treat all pots alike differences developed between duplicates, probably the result of differing nitrogen mobilizations. If the mobilization proceeded differently in duplicate pots, it is not to be expected that it would be the same in the pots as in Erlenmeyer flasks in the laboratory. It is for this reason that the storage tests of the humus-sand mixtures failed to give quantitative estimates of the nitrogen available to plants grown in pot cultures of the mixtures.

Although for five pairs of duplicates the amounts of nitrogen taken up were rather different, the means of the duplicates were sufficiently alike so that they can be used in assessing the differences between treatments. It is of interest to relate the uptake of nitrogen by the plants to the radiation intensity in which they were grown. This is accomplished in Table 17, but Fig. 18 can also be used to show the effect. As a first step the average nitrogen contents in milligrams per seedling grown in each of the substrates in the 22 % radiation intensity were taken as unity. The ratios of the nitrogen contents of the seedlings from the same substrate in each of the other radiation intensities were then calculated to the unit content in the 22 % radiation. The resulting ratios are seen to be dependent on the effects of both the radiation and the nitrogen availability in increasing the size of the plants. In the sterile sand the uptake of nitrogen by the seedlings grown in 50 % radiation is increased by about fifty per cent over the uptake of those grown in 4 % radiation. Compared with the median plants grown in the 22 % radiation a variation of about twenty per cent in either direction is noted. In the infertile bad raw humus for the values from 4 % to 27 % radiation only a very small change is noticed, but at 50 % radiation a large increase in the uptake by the seedlings is found. In the soil of higher nitrogen availability, the good raw humus, the uptake of nitrogen increases greatly as the size of the plant is increased by more intense radiation.

This variation in uptake of nitrogen with varying radiation is not characteristic of plants grown in nutrient-sand cultures. If provided with the same external concentrations, although their size may change as the radiation intensity is varied from 25 % to full, they have approximately the same internal content in milligrams. By bathing the roots in solutions containing comparatively large quantities of free ions, the internal content of nitrogen is governed by the external concentration.

Table 17. **The nitrogen content at various radiation levels relative to the nitrogen content at 22 % radiation of the Scots pine seedlings grown in humus-sand cultures in different radiation intensities. From table 13.**

Kvävehalt vid olika strålningsintensitet i förhållande till kvävehalten vid 22 % strålningsintensitet hos tallplantor uppdragna i humus-sandkulturer. Från tab. 13.

Humus Humusslag	Radiation Strålning									
	4 %		11 %		22 %		27 %		50 %	
	Pot Kruka	Relative content	Pot Kruka	Relative content	Pot Kruka	Relative content	Pot Kruka	Relative content	Pot Kruka	Relative content
II. Good raw humus	5	0.23	15	0.40	25	0.95	46	1.66	35	2.22
God råhumus	6	0.21	16	0.51	26	1.05			36	2.67
	Mean	*0.22*	*Mean*	*0.44*	*Mean*	*1.00*			*Mean*	*2.51*
III. Severely burnt raw humus	7	0.37	17	0.58	27	1.04	48	1.30	37	1.94
Hårt bränt råhumus	8	0.27	18	0.40	28	0.98			38	1.45
	Mean	*0.33*		*0.50*		*1.00*				*1.63*
I. Bad raw humus	3	0.88	13	0.98	23	0.97	43	1.12	34	1.49
Dålig råhumus	4	0.98	14	0.83	24	1.03	44	1.17		
	Mean	*0.93*		*0.91*		*1.00*		*1.14*		
IV. Inoculum humus Inf. humus	10	0.17	20	0.37	30	1.00	50	1.04	40	0.92
XIII. Mixture Blandprov	9	0.31	19	0.43	29	1.00	49	1.60	39	1.28
X.	1	0.83	11	0.97	21	1.01			31	1.14
XI. Sand	2	0.82			22	0.99			32	1.30
XII.	*Mean*	*0.82*				*1.00*				*1.22*

But in natural soils and in humus-sand cultures the plants have to obtain the nitrogen from a complex in which it is adsorbed in organic and inorganic base exchange compounds. Frequently the supply of inorganic nitrogen is increasing as the result of mobilization. The seedling uptake is acquired only in competition with the microflora of the soil. Under these conditions the internal concentration of nitrogen, together with its effect on yield, is quite different from that in nutrient-sand cultures of homologous »availabilities». In obtaining nutrients from substrates characterized by these complicating properties, tree seedlings are influenced by the intensity of the radiation. It affects the extension of the root system and thereby the amount of absorbing surface. There is every reason to believe that the development of mycorrhizae and their functioning is determined by the amount of food transferred to the roots; that the amount of food thus supplied is dependent on the radiation intensity is indicated by the shoot/root ratios. Such control of food supplied to the roots would also affect the liberation of adsorbed bases through its influence on the root and mycorrhizal respiration, if the exchange mechanism discussed on p. 648 is valid.

The arithmetic-logarithmic relation between yield and radiation appears to hold, therefore, only under the conditions where the uptake of bound nutrients is not affected to any large extent by the increase in plant size. The relation will not be found valid for large changes in radiation intensities where the proportion of absorbed nutrients is great and the proportion of nutrients present as free ions is small.

The results of these tests and comparisons between the nutrient-sand cultures and the humus-sand cultures emphasize what has been stated above about the inadequacy of nutrient-sand cultures as the sole bases for generalizations about the physiology of tree seedlings or their yield in relation to soil fertility. Conclusions from nutrient-sand cultures cannot be applied *in toto* to pot culture or nursery experiments which are complicated in that the nutrients are partly in ionic solution, partly in the adsorbed condition, and partly combined in less or more labile compounds. The need of more experiments of all kinds is evident; comparisons between work with nutrient-sand cultures, humus and soil cultures, and field trials must be continually employed to advance our understanding of the physiology of trees and the fertility of soils.

Inoculum Humus-Bad Raw Humus Mixtures.

The comparison of bad raw humus and sand culture yields gave evidence of a probable parasitism on the plants grown in the bad raw humus. In the discussion of the immediately preceding paragraphs it was pointed out that the mobilization tests indicated the approximate nitrogen availabilities in the various types of soils. While this is true, the mobilization values determined in the three types — inoculum humus, severely burnt bad raw humus and the mixture of five sixths inoculum humus with one sixth bad raw humus — were not much different. Yet the nitrogen intakes of the plants grown in them are quite different and closely associated with the yields. From all the experience of HESSELMAN it seems evident that the introduction of the bad raw humus into the inoculum humus should depress the yields, as indeed it does.

But the question may be asked why this depression was not revealed in the storage test of this material. The following explanation is suggested. In work shortly to be published HESSELMAN has observed that the course of mobilization proceeds at quite different rates during the decomposition of the material. This effect has also been noted in various other experiments involving microbiological composting. If mobilization did proceed at different rates during the storage tests of the mixture under discussion, the result may be easily explained. The decomposition in the Erlenmeyer flasks in the laboratory may have progressed so rapidly due to optimal temperature and moisture conditions that a new type of mobilization may have started toward the end of the three-month storage period. This was sufficiently intense to overcome the initial injurious effect of the addition of the bad raw humus. Analysis for total mobilized nitrogen therefore revealed as much as did the pure inoculum humus. In the mixture in the pots the progress of decomposition was possibly not so rapid due to less favorable temperature and moisture conditions. It did not arrive at the point of overcoming the effect of the initial addition of bad raw humus. And, even if it had, the effect of the less favorable fertility in the early development of the seedlings might well have been sufficient to handicap their later development.

The use of a mixture of this sort — material in what might be called a state of unstable equilibrium — was in one sense unfortunate. The experience with the severely burnt bad raw humus suggests the same criticism of that portion of the experiment. Yet in addition to pointing out possible pitfalls in experimenting with seedlings grown in raw humus, these trials do serve to emphasize an important aspect of raw humus fertility.

Discussion of the Yield and Development as Affected by the Quality of Radiation and the Fungi Parasitic on the Mycorrhizæ.

An additional interesting example of the complexity of the problem of estimating forest soil fertility is brought out by a study of the yields of the seedlings grown in the inoculum soils in the 27 % and the 50 % radiation intensities.

Attention has been previously directed (p. 614) to excess development of roots in the plants grown under a water screen. At the same time it was observed that the yields of seedlings grown in the good raw humus under the water screen were slightly larger than expected on the basis of the radiation intensity. From the reasoning of the previous paragraphs one would anticipate that the nitrogen content of the seedlings grown under the water screen would be increased because of the greater development of the root systems. This is found to be the case. The three samples, good, burnt and bad increase as much in nitrogen content (expressed as ratios, see Table 17) when the radiation is increased from 22 % to 27 % — with changed quality of radiation — as they do when the radiation is increased from 11 % to 22 %. Such increase in nitrogen content accounts for part of the increase of yield in comparing the plants grown in the 22 % radiation with those grown in 27 %. But in comparing the 50 % radiation intensity with the 27 %, it should be understood that the increase in energy is mostly in the infra-red region. The energy in the 50 % intensity consists of the radiation — mostly visible — transmitted by the water screen, a small additional amount of visible and much additional infra-red (longer then λ 1.0 μ, see p. 620). The further increase in yield under 50 % radiation must be attributed to the effect of mostly infra-red energy working together with the increased nitrogen content.

The experiments on varying the quality of radiation by the use of water screens have been repeated at the Harvard Forest using nutrient-sand cultures. In the summer of 1931 the improved water screen was used in the open. The intensity at the surface of the upper glass was that of full sunshine, not 50 % as in the Försöksanstalt experiment. In this trial the plants grown under the water screen had a greater yield than those grown in the »full» sunshine — this was actually 85 % of »full» (see Table 12, MITCHELL, 1934, p. 117). In 1932 the experiment was repeated with white pine, but a flat brass wire cloth screen transmitting 50 % radiation was laid over the upper glass of the tray. Thus radiation intensity in this experiment was more like that of the Försöksanstalt experiment. In this trial the yields under the tray were slightly lower than in the »50 %» intensity, but the duplicate pots did not check well. Tests for significance of difference indicated a barely significant probability — 0.05, a chance of 1 in 20 — that the yields were lower. This low probability and the fact that the intensities of visible and infra-red were not fully known render the interpretation not quite conclusive. But the results indicate that infra-red is important and probably can be substituted for visible energy when the visible energy is reduced to less than half of the solar intensity. In all cases the shoot/root ratio was changed, the root in relation to the shoot being relatively heavier than in solar radiation containing a full complement of infra-red longer than λ 1.0 μ. There is clear evidence that the change in the quality of the radiation as a result of the omission of infra-red greatly alters the relative development of shoot and root. But in experiments involving such tests the internal nutrient concentrations and the factors of size and metabolism in the roots which may influence the uptake of nutrients must be more fully known.

For seedlings grown in inoculum humus under the water screen, relatively large root systems and parallel increases in nitrogen content and in yields were anticipated. Instead of the expected results, the following observations were made. 1) The yields in the 4 %, 11 % and 22 % radiation intensities were larger for the inoculum humus than for any of the other humus substrates. 2) In the 27 % radiation intensity under the water screen the plants grown in inoculum humus were no larger than those in 22 % radiation in the same mixture; for no other substrate was this the case. 3) The standard deviations of the dry weights of the plants grown in the substrate into which the inoculum soil was introduced were for the most part large compared with the similar statistic for the others — in the case of pot 50 the $\sigma_{\%}$ was 39.0 %, compared with an average of 11.4 % for the rest of the pots in the same chamber. 4) A fungus, *Mycelium Radicis atrovirens*-type Melin, known to be parasitic on the mycorrhizae, was found on the plants from pots containing the inoculum humus (HATCH, 1934). 5) The nitrogen contents in milligrams per seedling from the inoculum soils in the 27 % and 50 % water screen (pots 50 and 40) were respectively about the same and smaller than the nitrogen content of plants from the same soil in the 22 % radiation (pot 30). 6) The per cent nitrogen contents of seedlings in pot 50 was somewhat greater and in pot 40 somewhat smaller than in the comparison pot 30.

Taken together these facts form a picture of plants in which at radiation intensities up to 22 % most of the food is being supplied to the shoots. When the elaboration of food materials is increased sufficiently in the higher radiation intensities, a greater proportion is provided for root use. In the inoculum soil are mycelia of the *M. R. atrovirens*-type which sporadically infect the mycorrhizae of the seedlings. The infestation is not uniform in the plants grown under the water screen, hence the wide standard deviation of the individual weights, the plants with many parasitized mycorrhizae being the more affected by the increased supply of nutrients to the roots as a result of the reduction in intensity of the infra-red energy. In these plants the food which would normally go to form a larger root system is diverted to the parasite. As a consequence the increased supply of nitrogen which would be expected is not available, and the plant weights are not increased proportionately to the radiation intensity. In the plants grown in the inoculum soil in the 50 % intensity, the infection is more uniform, the standard deviation correspondingly smaller, and the plants show a still smaller content of nitrogen.

This picture is little more than a sketch of what was apparently taking place in these experiments. To fill in the details and make the lines firm and true, more work is necessary. In such experiments, the reduction of the infra-red energy may prove a useful device for accentuating the injury caused by the parasites on mycorrhizae.

SECTION V. Conclusion.

The effect of simultaneously varying radiation intensities and nitrogen supplies on the early development of pine seedlings can be determined in nutrient-sand cultures quite precisely if due care is taken to account for the various other factors which affect the seedlings.

Such a factor is the seed weight. From the silvicultural point of view the seed weight will affect the plant for only a comparatively short time. After some years nutritional factors and plant competition will be far more important to plants growing in the field than the early size. But if the results of various experiments with various lots of seeds of different species and different origins are to be compared, it is necessary to be able to correct for the differences in seed size. The correction for seed size is derived from a linear relation between the fresh weight of the seeds and the plants grown from them. This relation between fresh weight and seedling size is not a direct proportion, because the amount of reserve food which determines the initial size of the seedling is not the same per cent of the fresh weight for seeds of various sizes. The measure of the reserve food can be obtained by subtracting the dry weight of the seed coat from the dry weight of the seed. This measure has been given the name reserve dry weight. There is a direct proportion between the reserve dry weight and the weights of seedlings grown from various sizes of seed.

Two quite different methods of controlling the mineral nutrition were used in these experiments. For comparison with the experiments in which samples of humus — a complex substrate — were used, cultures in which sand was flooded with pure chemical salts were employed. Under these latter simplified cultural conditions it is possible to predict quite accurately the dry weights to be anticipated from *Pinus* seeds of known weight of a single species and similar origins, when only the radiation and the nitrogen supplies are varied — potassium, phosphorus, magnesium, calcium, sulfur, and iron being supplied as chemically pure salts in constant amounts.

In such experiments definite relations can be shown between external nitrogen supply, internal nitrogen content and the dry weights of the seedlings. These empirical relations afford tools useful in physiological studies. Some are logarithmic and some are direct proportions. Some simple relations apply over a narrower range of concentrations and dry weights than do others; for the wider ranges of supply, more complicated formulae are necessary. The latter, attributable to MITSCHERLICH, contain quadratic terms deduced from experiments with crop plants. In nutrient-sand cultures, with the aid of the appropriate formula, the magnitude of any one of the following measures may be estimated from another: external supply, internal concentration in weight, internal concentration in per cent, yield.

Between the phosphorus supplies, the internal phosphorus concentrations, and the dry weights of seedlings, similar relations are found (MITCHELL, unpublished).

Experiments with potassium designed to provide similar information have proved rather unsatisfactory. The explanation advanced is that nitrogen and phosphorus are less easily translocated within the plant than is potassium. The latter is in the water soluble condition (KOSTYTSCHEW and ELIASBERG, 1920; JANSSEN and BARTHOLOMEW, 1929; MORRIS, 1933, TYNER, 1935) and does not enter into foods elaborated by the plant, as do nitrogen and phosphorus. It would seem necessary to present the potassium in a form in which its supply at high concentrations might be more adequately controlled. Such may be the base-exchange form in which it occurs in the soil. A further possibility is that the antagonistic requirements of basic elements have not been satisfied in the nutrient-sand culture experiments described.

The level of radiation intensity is shown to be of major importance in determining dry weight at intensities less than about twenty per cent of that received in temperate humid regions north of 40° latitude. At radiation intensities greater than thirty per cent, the factors of nutrition become more important. Where neutral screens are used for the reduction of the radiation intensities and under certain nutritional conditions, the seedling dry weights are found to be logarithmic functions of the cumulative radiation received on a fixed horizontal surface during the period of growth. This relation between yield and irradiation has been derived with the aid of a device measuring all the radiant energy between wave lengths λ 0.3 μ and 1.5 μ — the so-called total radiation. This correlation cannot be considered as conclusively established but is worthy of further study as an empirical relation providing a useful tool. As between yield and illumination (the measure of visible radiation — light), trials as yet not completed will be necessary to demonstrate the relation.

Comparisons between the effects of increasing quantities of nitrogen on three species of pine — Scots, Corsican and white — can be made from the results of nutrient-sand culture experiments. From Figure 11 are taken the slopes of the straight line portions of the curves which can be redrawn passing through the origin as in Fig. 19. This is equivalent to plotting the logarithms of the ratios between the yields against the logarithms of the ratios between the nutrient concentrations from which the yields were obtained. Any convenient low concentration and corresponding low yield may be taken as the divisors of the ratios. The relative slopes of the lines represent the relative efficiencies of nitrogen use. These indicate that equivalent increases in nitrogen supplies are much more effective in increasing the size of Scots and Corsican seedlings than in increasing the size of white pines. Part of the difference in the apparent efficiencies is due to differences in radiation for which the adjustments could not be made with accuracy in the early experiments.

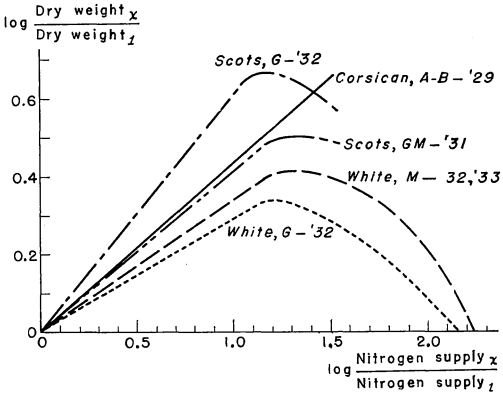

Fig. 19. Relative efficiencies in the use of nitrogen by Scots, Corsican, and white pine grown in nutrient-sand cultures. Compare Fig. 11. Nitrogen supply$_1$ = 13 ppm nitrogen.

Den relativa effekten av kvävegödsling å tall, svarttall och weymothtall i närsalttillsatta sandkulturer. Jfr fig. 11. Nitrogen supply$_1$ = 13 milliondelar kväve-koncentration.

For the effectiveness of radiation, of potassium, or any other nutrient in increasing yield, similar »efficiency» measures can be derived. It is to be expected that even for water use such an efficiency rating is possible. When such efficiency coefficients are established, numerical measures of »tolerance» will have been obtained.

At this point the writer would like to make some recommendations concerning the standardization of technique in pot cultures. It seems probable that this method can be extensively utilized in silvical and soils research with advantageous results. The cumulative benefits from such studies can be obtained only if all workers invariably give full details of the experiment. As many as possible of the following measurements should be given: 1) the seed weights and corresponding reserve dry weights of all seeds used in the experiments; 2) the supplies of mineral nutrients, so far as possible in terms of milligrams or milliequivalents per million; 3) the dry weights, in addition to any other measures of growth or yield; and 4) some measures of the cumulative radiant energy, either of illumination or total radiation. For each measure the worker should so present the data that it is possible to estimate the precision from the standard deviation.

From the results of the early experiments with the various humus-sand mixtures at the Skogsförsöksanstalt are obtained a set of three curves showing the relation between yields and varying radiation intensities for good raw humus, burnt raw humus, bad raw humus and sand (Fig. 5). It has been shown that in proportion to the nitrogen these plants were supplied adequate amounts of phosphorus and potassium. They were well supplied with water. The curves may therefore be considered to represent the influence of varying nitrogen supplies on yields at given radiation intensities. But if these yields are to be quantitatively related to the nitrogen availability in the substrates, the amount available must in some way be estimated.

As a measure of nitrogen availability the use of the nitrogen mobilization value as found in storage experiments in the laboratory was at first attempted. The storage mobilization test was found to give a qualitative separation of the nitrogen availability of the substrates into two classes and a relative separation between soils of higher fertility. But it could not be used to provide a quantitative estimate of the nitrogen supplied to the seedlings in these particular experiments. The difficulties of comparing the nitrogen mobilization in humus samples in Erlenmeyer flasks with the mobilization of nitrogen in pot cultures of humus in the glasshouse become apparent. Even in duplicate pots in the glasshouse marked differences in mobilization occur which result in significantly different contents of nitrogen in the plants and in the yields correlated therewith.

As a measure of the nitrogen availability it is therefore necessary to use the quantities of nitrogen in the seedlings themselves. The external supplies of available nitrogen are then assumed to be directly proportional to the nitrogen content in milligrams in the seedlings. By supplies of available nitrogen in the humus cultures are meant in this instance the quantities available to plants under the complicated conditions which exist in the humus mixtures. The importance of the competition for nitrogen between the bacterial and fungal flora and the higher plants is well known. This competition is for the most part determined by the condition of the humus. The introduction of a small portion of bad raw humus into the sample of inoculum humus was shown to decrease considerably the amount of nitrogen available. Also of importance is the function of the mycorrhizae in obtaining nitrogen from the various sources. The mycorrhizae probably not only increase the absorbing surface of the roots (STAHL, 1904, HATCH, 1935) but also aid in making the nitrogen available (MELIN, 1925). Another factor is the proportion of the nitrogen which is bound in the absorbed form in the organic and inorganic base-exchange materials as compared with the amounts present as free ions.

To represent the concurrent influences of various values of radiation and nitrogen, the surface shown in Fig. 20 is constructed from the data in Tables 3, 5, och 13 (see also Figs. 5 and 18). The dry weights scaled on the vertical axis represent the sizes of plants which may be expected from seed of 4.75 milligrams fresh weight with a reserve dry weight of 2.93 milligrams.

The spacing on the axis representing the effective nitrogen is partly determined from the nitrogen content of the seedlings grown in the 50% radiation intensity. But the scale is modified to satisfy the condition that the greater the content or supply the less the effect of further increases; the surface is shaped to follow the exponential law for yield verified in the extensive nutrient-sand culture experiments. The term supply is not used for the scale because it does not stress the part played by the plant and the carbohydrate/nitrogen content of the humus. The term available is but little better. Relative potential nitrogen uptake might well have been used as a designation.

For the radiation values the axis is scaled in per cent radiation and also in total gram calories per square centimeter as measured on a fixed horizontal surface for the growing season from June first to September first. The above values cannot be said to be more than approximate. But they may be helpful in comparing the results of this experiment with later repetitions.

By imagining a plane parallel to either of the axes on which radiation and nitrogen supply are scaled off and picturing the intercept of the vertical plane with the surface, the reader can obtain an idea of the influence of either radiation or nitrogen as the other is kept constant. It is apparent that in moderately high radiation intensities an increase in nitrogen availability can offset a deficiency in radiation.

In one respect the information gained from Fig. 20 may be misleading. From Fig. 5 and Tables 5 and 6 it is noted that the plants grown in the bad raw humus were in all cases significantly smaller than those grown in the infertile sand. An hypothesis to explain this is suggested. It is known that in the decomposition of bad raw humus such as this, both the supplies of nitrogen and the carbohydrates available to the microflora are important. It seems probable that the microflora are able to obtain supplies of carbohydrates from the seedlings. The weights of the seedlings grown in bad raw humus are therefore smaller then those grown in sand. Parasitism of the microflora on the seedlings in bad raw humus, when conclusively demonstrated, will add another important argument in favor of the rational management of the humus layer in the forest floor. It is possible that another soil providing an available supply of one milligram of nitrogen per kilogram of soil might grow slightly heavier plants because of a more favorable relation between the non-nitrogenous and the nitrogenous ingredients. Yet for the purpose for which this experiment was undertaken, it is believed that the data will not result in serious error. But it should be emphasized that the weights of the seedlings grown in slowly mobilizing raw humus are apparently conditioned by the degree of this apparent parasitism. The geometric surface in Fig. 20 is drawn as concave toward the plane of the radiation and nitrogen axes. This form of surface is drawn as a result of extensive experience with nutrient-sand cultures. But experience with certain types of humus indicate that with some of them certain portions of the surface may be convex toward the plane of the nitrogen and radiation axes. The area of the surface which is thus debatable is that area in which plants grown in a slowly mobilizing bad raw humus necessarily can have only a small nitrogen uptake. Only in this type of humus would there be extensive parasitism. Certain portions of the geometric surface in Fig. 20 are therefore conditioned by the type of humus; this is another factor not as yet adequately accounted for which must be considered in further refining in later experiments the data represented by the figure.

By study of the figure it is seen that the importance of nitrogen to young seedlings as emphasized by HESSELMAN has not been overstressed. If for any given low value of nitrogen the radiation is increased to moderately large amounts, further increases in the radiation intensity result in but comparatively small increases in seedling size. The nitrogen supply is the critical factor. If a slightly larger supply of nitrogen is provided it is possible to obtain somewhat larger plants at the same radiation intensities. As the nitrogen is increased the benefit of higher radiation levels is obtained and the radiation intensity may be raised to increasingly higher levels before the »limiting effect» of inadequate nitrogen supply appears.

The data shown in the figure apply only over approximately half of the radiation intensity available to plants growing in the open. Experiments in nutrient-sand cultures (MITCHELL, 1934) show that with sufficient supplies of nitrogen the radiation may be increased to the full intensity of sunlight with exponentially proportional increases in plant weight.

If the figure is examined with a view to the effect of changing intensities of radiation with constant supplies of nitrogen, new information is gained about the old viewpoints concerning the importance of radiation to the early development of reproduction. At low radiation intensities the variation in nitrogen supplies is not of practical importance. The size of the seedlings as measured by dry weight is almost wholly dependent on the radiation intensity. Apparently there are enough of the necessary mineral elements stored in the seed to supply the requirements of the seedlings grown in low intensities. Only when the radiation is increased to values approximating at least twenty per cent of full sunlight — about five to seven kilogram calories per square centimeter totaled between June first and September first and measured on a fixed horizontal surface — does the nitrogen supply become important. With increases in the radiation up to thirty per cent of full — approximately eight to eleven kilogram calories per square centimeter for the three summer months — only comparatively small increases in the nitrogen supply can be used before the radiation becomes »limiting». Only with eighteen or more kilogram calories per square centimeter during the three summer months can the Scots pine seedlings use to advantage the relatively high nitrogen supplies which are available in a rapidly mobilizing raw humus.

Under the conditions in the humus-sand mixtures, in which the nitrogen is being mobilized as the plant size increases, is found a quite different relation between the yield and the radiation from that in the nutrient-sand cultures. In the latter the exponential law applies — the yield is proportional to the logarithm of the radiation intensity. In the humus cultures, increasing root surface and food supplies which parallel the increase in radiation enable the plants growing in humus with a rapid nitrogen mobilization to obtain more nitrogen from it. A linear relation between the radiation and the yield is the result. This result answers the question raised in an earlier study of the growth of white pine seedlings under a shelterwood (GAST, 1930, pp. 57—59) concerning the probable effect of woods operations in altering simultaneously radiation intensity and the biological conditions in the forest floor. By thinning or clear-cutting a stand of timber the radiation intensity to which the seedlings have access is increased. But at the same time the biological conditions in the forest floor are altered. The rapid transformation of the litter and *F*-layer which follows immediately greatly increases nutrient availability. The changes in root competition, the decomposition of root remnants, and the higher temperature also contribute to a higher rate of nitrogen mobilization and consequent availability. Both the increased nitrogen availability and the higher radiation intensities on the seedlings affect their growth rate.

Two additional three-dimensional figures help explain the reason why radiation exerts the primary control at low intensities. They describe two important qualities of the plants grown with differing supplies of radiation and nutrition. Thus Fig. 21 showing the lengths of the lateral roots is complementary to Fig. 22 showing the shoot/root ratios. These were derived in

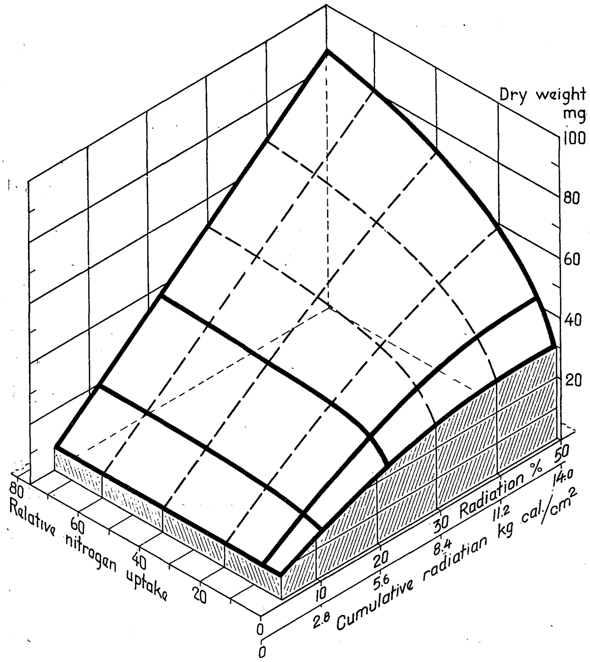

Fig. 20. The dry weights of three months old Scots pine seedlings as affected by radiation and nitrogen. Seedling weights adjusted to the equivalent of plants grown from seeds of 4.75 mg fresh weight. The radiation given as 1) per cent of full, 2) an approximate value in kg-cal. as measured on a horizontal surface. The nitrogen determined from the nitrogen uptake of the plants in the Skogsförsöksanstalt 1930 experiment, with intermediate values (— — —) interpolated from the nutrient-sand culture experiments. See Tables 5 and 13, and Figs. 3 and 5.

Inflytande av bestrålning och kväveupptagning på torrvikten av tre månader gamla tallplantor. Plantvikterna korrigerade till värden motsvarande en friskvikt å fröet av 4,75 mg. Bestrålningen uttryckt 1) i % av det fulla värdet, 2) approximativt mätt i kg-kalorier infallande på en horisontal yta. Kväve bestämt genom kväveupptagningen i plantorna i Skogsförsöksanstaltens experiment av 1930, med interpolerade värden (— — —) från närsalttillsatta sandkulturer. Jfr. även tab. 5 och 13, och fig. 3 och 5.

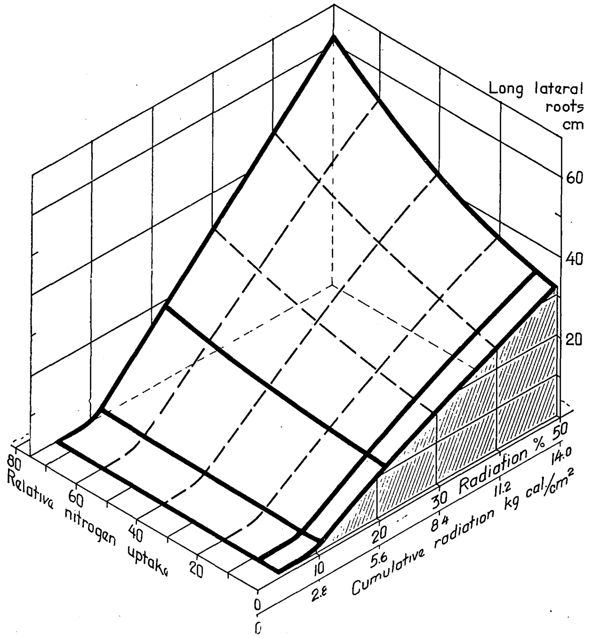

Fig. 21. The development of long lateral roots of three months old Scots pine seedlings as affected by radiation and nitrogen. See Table 7. Compare description for Fig. 20.

Inflytandet av bestrålning och kväveupptagning på utvecklingen av långa sidorötter hos tre månader gamla tallplantor. Jfr. tab. 7 och texten till fig. 20.

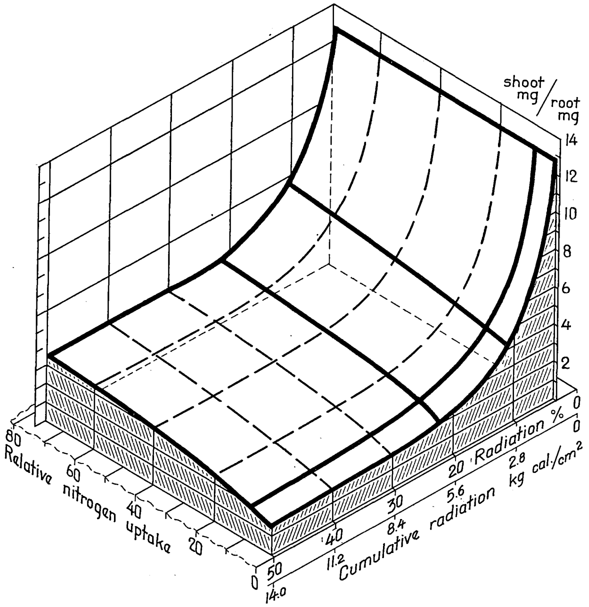

Fig. 22. The shoot-root ratios of three months old Scots pine seedlings as affected by radiation and nitrogen. See Fig. 8. Compare description for Fig. 20.

Inflytandet av bestrålning och kväveupptagning på förhållandet mellan skott och rot hos tre månader gamla tallplantor. Jfr. fig. 8 och texten till fig. 20.

the same way as Fig. 20 was derived from Table 5. In Fig. 22 it was necessary to reverse the direction of the radiation scale used in the two earlier figures in order to avoid drawing a surface which would be awkwardly represented in the figure.

In 4 % radiation it appears that most of the food is used in the production of shoot tissues. A high shoot/root ratio results and there is no development of lateral roots. At 11 % radiation intensity the plants are somewhat better proportioned: the shoot/root ratios are distinctly lower and the plants are provided with a few short lateral roots. At 22 % radiation intensity the shoot/root ratios approach values which show but slight further decrease as the radiation is increased above 22 %. At 11 % and higher intensities the nitrogen supply as well as the radiation supply affect the distribution of the food between the shoot and the root. Adjustments in the sizes of the absorbing surfaces of needle and root to compensate for lower supplies of radiation and of nitrogen are evidenced. At a given nitrogen supply the total lengths of lateral roots increase almost in direct proportion to the radiation. But at high levels of nitrogen supply the increase in length with increasing radiation is very much greater. This helps to explain why the yields of seedlings grown in humus with high nitrogen mobilization are proportional to the radiation intensities over the experimental range — an apparent violation of the law of diminishing returns.

A radiation intensity of about twenty per cent of full sunlight, equivalent to approximately five to seven kilogram calories per square centimeter on a fixed horizontal surface through June, July and August is the minimum supply with which Scots pine will develop a vigorous root system and a well balanced shoot/root ratio. Even though all the other factors, such as moisture supply and the supplies of the mineral nutrients are favorable, seedlings rooted in raw humus and growing in radiation intensities less than these are unlikely to be an effective means of reproducing a stand.

Such seedlings will be provided with a meagre root system, mostly developed in the *H*-layer and reaching up into the *F*-layer. When the overwood responsible for the reduction in radiation is removed, the seedlings and the humus surface will be exposed to full insolation. In the strong radiation the humus will be quickly dried out. At the very time when an increased transpiration due to the increased insolation is to be expected, less water will be available to the seedlings because of the inadequate root system.

The observations of TIRÉN (1934) on the hazards of dessication which attend seedlings immediately after germination apply no less to older seedlings rooted in raw humus. In dry periods, and especially if the insolation has been increased by cutting, injury to natural reproduction with an unfavorable shoot/root ratio may be expected. Four equivalent measures of the critical ratio for Scots pine as obtained in these experiments can be used. Thus seedlings with a shoot weighing more than 3.0 to 3.5 times the weight of the root, or with a shoot weighing more than 75 % of the whole plant, or with a root weighing less than 25 % of the whole plant, or with a root weighing less than 30 % of the top — such seedlings can be considered to have an improperly balanced development. Only under unusually favorable circumstances will they be able to survive when exposed to the hazards of dry periods, especially if they occur soon after cutting of the overwood.

The reasons for the various steps which experience has shown to be desirable in securing pine reproduction under an overwood, for example in the shelterwood method, are more clearly understood when viewed in the light of these experiments. The preparatory cuttings accelerate the decomposition of the forest floor. Such accelerated decomposition has been shown by HESSELMAN to be accompanied by increased nitrogen mobilization, which increases nitrogen availability to the plants. But where a non-nitrifying bad raw humus is found, any steps which will transform it are important for another reason. From seedlings rooted in such a bad raw humus apparently are drained a part of the food which they have formed.

The seeding cutting for Scots and white pine should be such as to supply the seedlings with a radiation intensity of at least twenty per cent. Seedlings grown under an overwood absorbing eighty per cent or more of the radiation cannot take advantage of the nitrogen being mobilized. Weak irradiation results in a meagre food supply, and without adequate food supply the seedlings are at a disadvantage in the competition with the soil flora for nutrients. Other factors permitting, intensities of thirty per cent or more should be supplied at the time of the seeding cutting. As the reproduction develops, progressively greater intensities are necessary for maximum growth; such are supplied by the removal cuttings (secondary fellings). For both Scots and white pine, intensities up to the full value of sunlight increase the growth rate.

The particular advantage to Scots pine of a high nitrogen mobilization rate is apparent. An increase in the supply of nitrogen to Scots pine has a greater effect on the rate of growth than does an equal increase in supply to white pine; apparently for Scots pine the »use efficiency» of nitrogen is greater. When the radiation intensity is adequate and the nitrogen supply optimal, Scots pine can in a single growing season produce seedlings with a weight as great as that of white pine seedlings which start from seeds weighing four times as much.

The work summarized in this paper attempted to push to the limit throughgoing quantitative methods in the study of the growth and development of pine seedlings under various environmental conditions. Every factor was not controlled or measured with the utmost refinement because of the difficulties, mostly the cost, of so doing. It is apparent that only by using the experience gained alternately from field observation and laboratory, in each case using such precision as is appropriate, are the complex problems involved in forest soil fertility to be solved. Progress has been made, much work remains to be done.

References.

ADAMS, W. R. 1934. Studies in Tolerance of New England Forest Trees. XI. The Influence of Soil Temperature on the Germination and Development of White Pine Seedlings. Vermont Agr. Exp. Sta. Bul. 379, pp. 1—18.

ALDRICH-BLAKE, R. N. 1930. The Plasticity of the Root System of Corsican Pine in Early Life. Oxford Forest Memoir No. 12, pp. 1—64.

—— 1932. The Influence of Nutrition on the Relative Root and Shoot Development of Forest-tree Seedlings. Forestry *6:* 40—52.

—— 1935. A Note on the Influence of Seed Weight on Plant Weight. Forestry *9* (1): 54—57.

AURÉN, T. E. 1930. Illumination from Sun and Sky in the Neighbourhood of Stockholm in 1928. Medd. från Statens Meteorologisk-Hydrografiska Anstalt *5* (4): 1—24.

—— 1933. Illumination from Sun and Sky. Arkiv för Matematik, Astronomi och Fysik *24 A* (4): 1—55.

BALLS, LAWRENCE 1929. Discussion: Yield, Field Tests, Cotton. Conf. Empire Meteorologists *2:* 31—32.

BAUER, H. 1910. Stoffbildung und Stoffaufnahme in jungen Nadelhölzern. Naturw. Ztschr. f. Forst- und Landw. *8:* 457—498.

BLACKMAN, V. H. 1919. The Compound Interest Law and Plant Growth. Ann. of Bot. *33:* 353—360.

BURSTRÖM, HANS 1934. Über antagonistische Erscheinungen bei der Kationenaufnahme des Hafers. Svensk Bot. Tidskrift *28* (2): 157—263.

CIESLAR, A. 1909. Licht- und Schattholzarten, Lichtgenuss und Bodenfeuchtigkeit. Centralb. f. d. g. Forst. *35:* 4—22.

EATON, FRANK M. 1931. A Large Sand Culture Apparatus. Soil Science *31:* 235—242.

FISHER, R. A. 1932. Statistical Methods for Research Workers. (4th ed.) London.

FISKE, C. H. and SUBBAROW, Y. 1925. The Colorimetric Determination of Phosphorus. Jour. Biol. Chem. *66* (2): 375—400.

GAST, P. R. 1930. A Thermoelectric Radiometer for Silvical Research with Preliminary Results on the Relation of Insolation to the Growth of White Pine. Harvard Forest Bulletin 14, pp. 1—76. Petersham, Mass.

GRASOVSKY, A. Some Aspects of Light in the Forest. Yale Univ. School of Forestry Bull. 23. New Haven, Conn.

GREGORY, F. G. 1929. Discussion: Yield, Statistics, Pot Cultures, Field Tests. Conf. Empire Meteorologists *2:* 29—33.

HATCH, A. B. and DOAK, K. D. 1933. Mycorrhizal and Other Features of the Root Systems of *Pinus*. Jour. Arnold Arboretum *14*: 85—99.

HATCH, A. B. 1934. A Jet-black Mycelium forming Ectotrophic Mycorrhizae. Svensk Bot. Tidskrift *28* (3): 369—383.

—— 1935. The Physical Basis of Mycotrophy in *Pinus*. Dissertation, Harvard University. To be published by the Arnold Arboretum.

HESSELMAN, H. 1917 a. Studier över salpeterbildningen i naturliga jordmåner och dess betydelse i växtekologiskt avseende. (Resümee: Studien über die Nitratbildung in natürlichen Böden und ihre Bedeutung in pflanzenekologischer Hinsicht.) Medd. från Statens Skogsförsöksanstalt *13—14* (1): 297—528.

—— 1917 b. Om våra skogsföryngringsåtgärders inverkan på salpeterbildningen i marken och dess betydelse för barrskogens föryngring. (Summary: On the Effect of our Regeneration Measures on the Formation of Saltpetre in the Ground and its Importance in the Regeneration of Coniferous Forests.) Medd. från Statens Skogsförsöksanstalt *13—14* (2): 923—1076.

—— 1917 c. Studier över de norrländska tallhedarnas föryngringsvillkor. (Resümee: Studien über die Verjüngungsbedingungen der norrländischen Kiefernheiden.) Medd. från Statens Skogsförsöksanstalt *13—14* (2): 1221—1286.

—— 1926. Studier över barrskogens humustäcke, dess egenskaper och beroende av skogsvården. (Resümee: Studien über die Humusdecke des Nadelwaldes, ihre Eigenschaften und deren Abhängigkeit vom Waldbau.) Medd. från Statens Skogsförsöksanstalt *22* (5): 169—552.

—— 1927. Studier över barrträdsplantans utveckling i råhumus. I. Betydelsen av kvävemobiliseringen i råhumustäcket för tall- och granplantans första utveckling. (Resümee: Studien über die Entwicklung der Nadelbaumpflanze in Rohhumus. I. Die Bedeutung der Stickstoffmobilisierung in der Rohhumusdecke für die erste Entwicklung der Kiefern- und Fichtenpflanze.) Medd. från Statens Skogsförsöksanstalt *23:* 337—432.

HOFFMAN, WM. S. and JACOBS, H. R. D. 1931. A New Colorimetric Method for the Estimation of Potassium. Jour. Biol. Chem. *93:* 685—691.

JANSSEN, GEORGE and BARTHOLOMEW, R. P. 1929. The Translocation of Potassium in Tomato Plants and its Relation to their Carbohydrate and Nitrogen Distribution. Jour. Agr. Res. *38:* 447—465.

KIMBALL, H. H. and HOBBS, H. E. 1923. A New Form of Thermoelectric Recording Pyrheliometer. Mon. Wea. Rev. *51:* 239—242.

—— 1924. Records of Total Solar Radiation Intensity and their Relation to Daylight Intensity. Mon. Wea. Rev. *52:* 473—479.

—— 1931. Pyrheliometers and Pyrheliometric Measurements. U. S. Dept. of Agr. Weather Bureau Circular Q: 1—28.

KOSTYTSCHEW, S. and ELIASBERG, P. 1920. Über die Form der Kaliumverbindungen in lebenden Pflanzengeweben. Ztschr. Physiol. Chem. *111:* 228—235.

LANGLET, OLOF 1934. Om variationen hos tallen (*Pinus silvestris* L.) och dess samband med klimatet. (Zusammenfassung: Über die Variation der Kiefer (*Pinus silvestris* L.) und deren Zusammenhang mit dem Klima.) — Svenska Skogsvårdsföreningens Tidskrift 32 (*I—II*): 87—110.

LUNDEGÅRDH, H. 1934. Markbeskaffenhet och gödslingsbehov. (Summary: Studies on the Relations between Soil Conditions and the Absorption of Nutrient Salts by Plants.) Medd. från Centralanst. för försöksväsendet på jordbruksområdet *444:* 1—67.

MANSHARD, E. 1933. Untersuchungen über den Nährstoffgehalt der Aschen forstlicher Kulturpflanzen aus den Halstenbeker Forstbaumschulen. Tharandter Forst. Jahrb. *84:* 105—158.

MARSHALL, ROBERT 1931. An Experimental Study of the Water Relations of Seedling Conifers with Special Reference to Wilting. Ecological Monographs *1:* 38—98.

MELIN, E. 1925. Untersuchungen über die Bedeutung der Baummykorrhiza, eine Öklogisch-Physiologische Studie. Jena.

—— 1927. Studier över barrträdsplantans utveckling i råhumus. II. Mykorrhizans utbildning hos tallplantan i olika råhumusformer. (Resümee: Studien über die Entwicklung der Nadelbaumpflanze in Rohhumus. II. Die Ausbildung der Mykorrhiza bei der Kiefernpflanze in verschiedenen Rohhumusformen.) Medd. från Statens Skogsförsöksanstalt *23:* 433—494.

MITCHELL, HAROLD L. 1934. Pot Culture Tests of Forest Soil Fertility with Observations on the Effect of Varied Solar Radiation and Nutrient Supply on the Growth and Nitrogen Content of Scots and White Pine Seedlings. Black Rock Forest, Bulletin 5: 1—138. Cornwall-on-the-Hudson, N. Y.

—— 1936. The Effect of Varied Solar Radiation upon the Growth, Development and Nutrient Content of White Pine Seedlings Grown under Nursery Conditions. Black Rock Forest Papers *1* (4): 16—22.

MORRIS, V. H. 1933. Form of Potassium in Corn Tissue. Ohio Agr. Exp. Sta. Bul. 616: 35—36.

NIKLAS, H. and HOCK, A. 1934. Literatursammlung aus dem Gesamtgebiet der Agriculturchemie. Bd. III. Pflanzenernährung. München. In pp. 937—983 is given an extensive bibliography of the literature on yield estimation and cultural experiments.

ODÉN, SVEN 1929. Växtodling i elektriskt ljus. Medd. från Lantbruksakademiens Vetenskapsavdelning N:r 1.

PALMER, A. deF. 1912. The Theory of Measurements. New York.

PREGL, FRITZ 1930. Quantitative Organic Microanalysis. Philadelphia.

RIPPEL, A. 1931. Neue Forschungen über die Gesetzmässigkeit des Pflanzenwachstums mit besonderer Berücksichtigung der Ernährungsprobleme. Die Ernährung der Pflanze *27* (11—12): 251—253.

SCHMITZ-DUMONT, W. 1894. Über den Nährstoffbedarf ein- und zweijähriger Kiefern. Thar. Forstl. Jahrb. *44:* 205—217.

SPILLMAN, W. J. and LANG, EMIL 1924. The Law of Diminishing Returns. Yonkers, N. Y.

—— 1933. Use of the Exponential Yield Curve in Fertilizer Experiments. U. S. Dept. of Agri. Technical Bul. 348: 1—66.

STAHL, E. 1900. Der Sinn der Mykorhizenbildung. Eine vergleichend-biologische Studie. Jahrb f. wiss. Bot. *34:* 539—668.

STATENS METEOROLOGISK-HYDROGRAFISKA ANSTALT. Sweden. 1930. Årsbok.

TAMM, OLOF and MALMSTRÖM, CARL 1926. The Experimental Forests of Kulbäcksliden and Svartberget in North Sweden. I. Geology. II. Vegetation. Skogsförsöksanstaltens Exkursionsledare XI.

TIRÉN, LARS 1934. Några iakttagelser över den naturliga föryngringens uppkomst på Kulbäckslidens försökspark. (Zusammenfassung: Einige Beobachtungen über die Entstehung der natürlichen Verjüngung in dem Versuchswald Kulbäcksliden.) Svenska Skogsvårdsföreningens Tidskrift *32* *(I—II):* 251—274.

TYNER, EDWARD H. 1935. The Feeding Power of Plants for the Potassium in Feldspar, Exchangeable Form, and Dilute Solution. Soil Science *39* (6): 405—422.

VAGELER, P. and ALTEN, F. 1933. Die Bodenuntersuchung und Bodenbeurteilung nach physikalisch-chemischen Gesichtspunkten. Die Ernährung der Pflanze *29* (7): 121—132.

WALLACE, H. A. and SNEDECOR, GEORGE W. 1931. Correlation and Machine Calculation. Iowa State College Publication *30:* No. 4, (Revised edition). Ames, Ia.

WEBER, R. 1891. Lehrbuch der Forsteinrichtung mit bes. Berücksichtigung der Zuwachsgesetze der Waldbäume. Berlin.

WILLCOX, OSWIN, W. 1930. Principles of Agrobiology, or The Laws of Plant Growth in Relation to Crop Production. New York.

SAMMANFATTNING

STUDIER ÖVER BARRTRÄDSPLANTANS UTVECKLING I RÅHUMUS.

III. Tallplantans (Pinus silvestris L.) utveckling i krukkulturer i olika jordar och under olika bestrålningsintensiteter.

Författaren av denna avhandling studerade vid Statens skogsförsöksanstalt från augusti 1929 till senhösten 1930 tack vare ett stipendium från National Research Council Fellowship. En del av undersökningarna fortsattes sedermera vid Harvard Forest, Petersham, Mass., U. S. A., Harvard-universitetets undersöknings- och studieskog. Hösten 1935 återkom författaren till skogsförsöksanstalten för manuskriptets slutliga utarbetande. Då en väsentlig del av undersökningen har utförts vid försöksanstalten och behandlar en fråga av stort intresse för vår skogsskötsel, har avhandlingen införts i anstaltens meddelanden. Ett större tryckningsbidrag har lämnats av Harvard University, Cambridge, Mass., U. S. A. Efterföljande korta sammanfattning avser att göra den svenska, med engelska språket icke förtrogne läsaren bekant med de huvudsakliga resultaten av de gjorda, i många avseenden synnerligen ingående undersökningarna. Den som vill närmare studera frågan, hänvisas till huvudavhandlingen.

Undersökningarna på försöksanstalten gingo ut på att samtidigt studera markens, i detta fall humustäckets och ljusets inflytande på tallplantans första utveckling. Försöken utfördes i samma växthus som användes av mig vid de år 1927 publicerade försöken (HESSELMAN 1927). Tallplantorna uppdrogos i krukor, innehållande en tredjedel humus och två tredjedelar sand. Fyra olika slag av humus användes, nämligen:

1) Lucker, god råhumus från ett växtligt, björkblandat gran-tallbestånd å Brända holmen, Degerö Stormyr, Kulbäckslidens försökspark.

2) Dålig råhumus från ett c:a 250-årigt lavbehängt granbestånd å Storliden, Kulbäckslidens försökspark.

3) Humus från en mycket hårt bränd fläck å en avverkningsyta å Storliden.

4) Nitrificerande jord från ett hygge nära Glindran, Björkviks sn, Södermanland.

Dessutom uppdrogos plantor i sand utan humusinblandning samt i sand med en blandning av humus från Björkvik ($^5/_6$) och humus från Storliden ($^1/_6$).

För att åstadkomma olika belysningsintensiteter användes tre spjälburar, där spjälorna voro orienterade i söder och norr. Spjälornas bredd och inbördes avstånd voro så avpassade, att det i växthuset infallande ljuset skulle minskas till $\frac{1}{2}$, $\frac{1}{4}$ och $^1/_{16}$ i respektive spjälburar (se fig. 1, sid. 594). Genom termoelektriska apparater mättes den infallande strålningen i växthuset och i de olika ljusburarna. De använda apparaterna registrerade den totala infallande strålningen, sålunda icke blott det för det mänskliga ögat förnimbara ljuset. Beräknat i procent av strålningen i det fria voro strålningsintensiteterna i växthuset och i spjälburarna följande (mätningar $^1/_6$—$^3/_9$ 1935) med lektor AURÉNS apparat och enligt anstaltens egna undersökningar, se tab. 2.

Växthuset	Spjälburarna		
	½	¼	1/16
55 %	24,8 %	12,2 %	6,0 %

Den till synes enkla anordningen var i många avseenden tillfredsställande. Endast i buren 1/16 var den infallande strålningskvantiteten avsevärt större än som beräknats. Mellanrummen mellan spjälorna läto solstrålarna tidvis falla direkt in på plantorna alldeles som ett överskuggande skogsbestånd i fria naturen. Genom elektriskt drivna fläktar utjämnades temperaturskillnaderna, så att differenserna blevo utan betydelse för försöket, se tab. 4.

Försöken igångsattes i maj månad, plantorna skördades i september. Såsom mått på utvecklingen användes plantornas torrvikt.

De viktigaste resultaten kunna sammanfattas på följande sätt.

1) Vikten av plantor, som uppdragits i sand blandad med råhumus utmärkt av hög kvävemobilisering, tilltar direkt proportionellt mot ökningen i strålningsintensiteten upp till 55 % av fullt solljus (högre intensiteter ej prövade). Vikten av plantor, som uppdragits i sämre jord, tilltar med växande strålningsintensitet men närmar sig ett övre gränsvärde, som ligger lägre, ju lägre kvävemobiliseringen är, se tab. 5 och fig. 5.

2) Med avtagande strålningsintensitet avtager plantornas torrsubstanshalt. Ju fattigare jorden är, desto högre är torrsubstanshalten hos de i jorden uppdragna plantorna. Förändringar i torrsubstanshalten förorsakade av olika kvävetillförsel vid en bestämd strålningsintensitet är större vid höga än vid låga intensiteter. Torrsubstanshalten hos skott av plantor, som uppdragits i humus med god kvävemobilisering, ändras litet med växande strålningsintensitet, förutsatt att intensiteten är större än 10 % av fullt solljus, i sämre jord vid strålningsintensiteter däremot först över 20 %, se fig. 6.

3) Rotsystemets utveckling influeras mycket av strålningsintensiteten. Plantor uppdragna vid 6 % av fullt solljus utveckla ej några sidorötter. Vid 12 % utveckla några plantor sidorötter, andra däremot ej. Vid dessa strålningsintensiteter inverkar markens beskaffenhet föga på rotutvecklingen, endast huvudrotens längd påverkas. Är strålningsintensiteten omkring 25 % av solljuset, framträder markens inflytande och vid 55 % är detta inflytande starkt, se fig. 7.

4) Förhållandet mellan skott och rot påverkas både av strålningsintensiteten och av markens bördighet. Rotsystemets svaga utveckling vid strålningsintensiteter lägre än 20 % är tydligen att tillskriva skottets extensiva utveckling. Marken är emellertid ej utan inflytande vid dessa bestrålningsstyrkor. Vid högre intensiteter är markens inflytande större, bestrålningens mindre. Förhållandet mellan rot och skott blir vid dessa högre intensiteter mer eller mindre konstant vid växlande bestrålning, ehuru markens inflytande tydligen framträder. I bättre jord är skottet i förhållande till roten kraftigare utvecklat än i fattigare, se fig. 8.

För att närmare studera de frågor, som dessa undersökningar gåvo anledning till, anordnades i Petersham, Harvard Forest, en serie nya försök. I dessa användes i stället för humus sand, som vattnades med näringslösningar av noga känd sammansättning. De olika belysningsintensiteterna åstadkommos genom användandet av mässingsnät av olika täthet. Som kvävekälla användes ammoniumnitrat i olika koncentrationer, se fig. 9.

Upp till en koncentration av 175 à 200 mg kväve per liter ökas plantornas torrvikt, stiger därefter koncentrationen, inträder till en början ingen ökning, varefter en sänkning av plantornas torrvikt inträder allt eftersom koncentrationen tilltager. Kvävets inverkan bestämmes av strålningsintensiteten. Experimenten visa att mellan logaritmen för kvävetillförseln och logaritmen för plantans torrvikt finnes ett lineärt samband. Mellan logaritmen för strålningsintensiteten och plantans torrvikt finns likaledes ett lineärt samband under vissa näringsbetingelser, när vid strålningsmätningen den totala strålningsenergien mätes. Mellan näringslösningens kvävehalt och plantans inre kvävehalt råder vid lägre kvävekoncentrationer hos näringslösningen ett lineärt samband. Experimenten visa dessutom, att en inre kvävehalt av omkring tre procent utgör optimum för ernående av högsta torrvikt hos ettåriga tallplantor, se fig. 11, 12, 13 och 14.

Dessa under relativt enkla näringsbetingelser funna, lagbundna samband mellan kvävetillförsel och plantutveckling kunna användas som grundlag vid diskussionen av plantutvecklingen i sand-humuskulturerna. Kvävetillförseln i dessa kulturer är resultatet av en mikrobiologisk process, och de metoder, som hittills använts för att bedöma resultaten av denna, nämligen lagringsproven, ge endast approximativa värden. Förhållandena i sand-humus-kulturerna äro dessutom i flera hänseenden mycket mer komplicerade än i de relativt enkla näringslösningarna. Användes som mått för tillgängligt kväve den i lagringsproven av sand-humus funna kvävemobiliseringen, finner man ej samma enkla relation mellan plantvikt och kvävetillförsel som i försöken med näringslösningar. Plantorna i god råhumus äro i förhållande till kvävetillförseln mycket bättre än i humusformer med svagare kvävemobilisering. Man kunde då misstänka, att något annat ämne fattades i dessa senare råhumusformer, vilket verkade nedsättande på plantornas utveckling. För att undersöka denna fråga analyserades plantornas halter av kväve, kali och fosforsyra. Som jämförelse tjänade tyska undersökningar över ett- och tvååriga tallplantor från plantskolor. Förhållandet mellan kväve, fosfor och kali var i dessa

N : P : K
1 : 0,12 : 0,33

Hos tallplantorna i sand-humus-kulturerna visade sig följande relationer,

	22 % bestrålning	50 % bestrålning	27 % bestrålning[1]
	N : P	N : P	N : K
God råhumus...	2,88 % : 0,346 %	2,90 % : 0,294 %	3,28 % : 1,53 %
	1 : 0,12	1 : 0,10	1 : 0,47
Bränd råhumus.	2,08 % : 0,356 %	2,38 % : 0,340 %	2,28 % : 1,12 %
	1 : 0,17	1 : 0,14	1 : 0,49
Dålig råhumus..	1,13 % : 0,343 %	1,14 % : 0,316 %	0,97 % : 0,97 %
	1 : 0,13	1 : 0,28	1 : 1

Av dessa analyser framgår, att hos plantor uppdragna i humus med låga kvävemobiliseringkoefficienter upptagning av fosfor och kali är proportionsvis större än av kväve. Det är tydligt att plantornas tillväxt ej bestämmes av fosfor och kali men av det kväve, som tillfördes plantorna.

De relativt enkla förhållanden, som visat sig förefinnas mellan lösningarnas kvävehalt och plantornas inre kvävehalt samt mellan plantornas torrvikt och bestrålningsintensiteten, när man drar upp plantorna i sand med näringslösningar, återfinner man ej i sand-humuskulturerna. Förhållandena äro mer komplicerade.

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[1] Under skärm av ett vattenskikt.

Vissa lagbundenheter påminnande om dem hos plantorna i sand med näringslösning återfinner man dock. Sålunda råder mellan logaritmen för torrvikten och logaritmen för kvävehalten ett lineärt samband inom försök med samma sand-humusblandning men ej för samtliga försök inneslutande olika humusformer. Resultaten ordna sig nämligen i två grupper. Den första gruppen innehåller plantor, som uppdragits i jord med svag kvävemobilisering — sand och sand med dålig råhumus. Den andra gruppen omfattar plantor, uppdragna i substrat med god kvävemobilisering. I den första gruppen är stegringen i torrvikt stor i förhållande till ganska små ändringar i inre kvävehalt, i den andra gruppen är stegringen mindre stark. (Jfr. fig. 18.).

Hos plantorna i sand-humuskulturerna varierar kvävehalten vid olika bestrålningsintensiteter. Med tilltagande bestrålning tilltar kvävehalten något olika hos plantorna i olika sand-humuskulturer. Härigenom skilja sig dessa plantor från dem i sand-närsalt-kulturerna, där kvävehalten är densamma i olika bestrålningsintensiteter, när plantorna uppdragas i samma sand-närsalt-koncentration. Genom att rötterna hos dessa plantor omspolas av lösningar av fria ioner, regleras den inre kvävehalten av den yttre lösningens koncentration.

I naturlig jord och i sand-humuskulturerna konkurrera plantorna om näringen med mikroorganismerna i marken, en del av näringen är absorberad av organiska eller oorganiska ämnen. Under sådana förhållanden influerar bestrålningsintensiteten på näringsupptagningen genom att påverka plantrötternas utveckling. Även förhållandet mellan rötterna och de mykorrhizabildande svamparna påverkas av bestrålningen.

Undersökningarna belysa sålunda på ett intressant sätt kvävets och bestrålningens inverkan på plantutvecklingen. Vid låga bestrålningsintensiteter bestämmes plantutvecklingen enbart av bestrålningen. Växer bestrålningen kan kvävet bli den begränsande faktorn, om kvävemobiliseringen är svag eller kvävetillgången låg. Vid vissa bestrålningsintensiteter kan en ökning av tillgängligt kväve ersätta en brist i belysningen. Alltefter som kvävetillgången ökas, kan en ökning av bestrålningen utnyttjas. Bestrålningsintensiteten kan ökas tills kvävetillgången blir den begränsande faktorn. Plantutvecklingen bestämmes sålunda av ett samspel mellan bestrålningen och kvävetillgången, se fig. 20. Men härvid inverkar även bestrålningens inverkan på rotutvecklingen, se fig. 21 och 22. Först vid en viss bestrålningsintensitet, som för tallen kan uppskattas till 20 % av fullt solljus eller till fem—sju kilogramkalorier per cm^2 under månaderna juni—augusti, utvecklas ett väl balanserat rotsystem. Ett dylikt rotsystem är nödvändigt för plantans utveckling, även om alla andra faktorer äro gynnsamma.

De utförda försöken bekräfta sålunda den vid försöksanstaltens tidigare undersökningar framhållna betydelsen av kvävemobiliseringen för de unga plantornas utveckling. Utan kvävemobilisering i humustäcket blir plantutvecklingen svag, även om ljustillgången är god. En god kvävemobilisering kan å andra sidan ej utnyttjas, om ej belysningen når en viss intensitet. Vid vissa belysningsgrader kan god kvävetillgång ersätta en viss ljusbrist. Hur detta samspel mellan ljus och kvävemobilisering påverkar föryngringen i svenska skogsbestånd kommer att närmare behandlas i ett par snart utkommande avhandlingar i Meddelanden.

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