Macro Element Nutrition of Pine, Spruce, and Birch Seedlings in Nutrient Solutions

Inverkan av varierad makronäringstillförsel på tall-, gran- och björkplantor i näringslösningar

by

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Preface

In the present paper a series of investigations from the years 1954—1960 is described. Pine *(Pinus silvestris,* L.), spruce *(Picea abies,* Karst.), and birch *(Betula verrucosa,* Ehrh.), the three dominating forest tree species in Sweden, have been grown under controlled light and temperature conditions in nutrient solutions with varied concentrations of the macro nutrients. The main purpose has been to study the leaf analysis method as a diagnostic instrument in these species and to compare their nutritional properties, and a surveying study was regarded desirable for later investigations. Most of the results have been published in three papers in Physiologia Plantarum (66, 68, 69), but the limited space there has permitted only brief discussions of the problems. Further more, it has not been possible in these papers to compare the results of the three species. It was, therefore, regarded of interest to publish the earlier data concerning macro nutrients together with recent ones in a more comprehensive paper where the results are treated in an uniform way.

To my teacher in the Department of Physiological Botany, University of Lund, Professor Hans Burström, and the former and present heads of the Department of Botany and Soils, Forest Research Institute, Professor Carl Malmström and Professor Carl Olof Tamm, I wish to express my sincere thanks for their never-failing interest and for all suggestions, impulses, and critical discussions they have given me.

I am also very much indebted to the staff of the Department of Botany and Soils for their help and encouragement. In addition I wish to mention especially those who with interest and care have carried out the technical and analytical work, namely Mrs. Britta Hultin, Miss Birgitta Kjellberg, Mrs. Sigrid Santesson, and Mrs. Britt Sigeman.

During the course of the investigation I have had the great advantage of discussions with many colleagues to whom I owe my sincere thanks. Among these I should like to express my appreciation to Mssrs. Bertil Matérn, Nils Molin, and Harald Nilsson at the Forest Research Institute for their interest and willingness to engage in stimulating debates.

The English has been corrected by Mrs. Gail Åkerman to whom I wish to express my sincere thanks.

Stockholm, February, 1962.

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TABLE OF CONTENTS

Chapter I. Introduction

The research on the nutrition of forest tree species has progressed parallelly with the corresponding research in agriculture and horticulture. Thus, the fertilization experiments with forest trees were early developed by the introduction of soil, litter, and plant analysis (4, 41, 147, 148, 186, 197). The necessity of various elements for a healthy development of forest tree seedlings was studied in pot culture experiments (*e.g.* 118) and the requirements of micro nutrients have been investigated since the thirties by many workers (56, 90, 91, 138, 151, 196). The data, however, have been obtained slowly in forestry and they are difficult to interpret, especially on account of the slow crop rotation and the heterogeneous and complicated soil structure. The fundamental questions about classification of soil fertility, the nutrient status of forest trees and stands, or nutrient requirements of various species cannot, therefore, generally be answered today with a satisfactory degree of accuracy. Nevertheless, there is a great amount of literature available on forest tree nutrition, as is seen from bibliographies and reviews (*e.g.* 78, 86, 184, 195), and during the last decades the interest has been more and more focused on the problems mentioned above.

It may be stated that it is of primary importance to be able to determine the nutrient status of plants, that is their internal nutrient situation in relation to a defined status, if quantitative nutrient conditions are studied, for instance, the effect of a fertilization or the nutrient requirements of different species. Concerning these problems only very few conclusive data are available for forest tree species. By using data with indirect value of evidence it is in some cases possible to make certain deductions. It has, for instance, been noticed that birch invades clear-cut areas and other comparably nitrogen-rich locals (58, 59, 60, 170, 175, 180). On raw humus soils with low pH, high carbon/nitrogen ratio, and slow nitrogen turnover or on otherwise poor soils the conifers and especially pine easily become dominant (58, 101, 199). This indicates that birch is comparatively more and pine less nitrogen-requiring. This conclusion is also confirmed by the practical experience that pine is the most suitable tree species on poor sites. However, in this way it is not possible to arrive at any far-reaching or certain conclusions.

Some workers have determined the nutrient uptake of different forest tree species in nurseries *(e.g.* 98) or in stands of varying age *(e.g.* 134, 135, 142). The purpose of these investigations varies but it ought to be pointed out here that these data cannot be used to determine nutrient requirements, since the nutrient status of the seedlings or trees is not known. It is probable in these studies that the status of the different nutrient elements may vary from deficiency to luxury and possibly even toxic levels. This is, in fact, also indicated by the percentage values, and means that the potentially highest possible growth rate on the site, also when considering the nutrient factors only, is probably not reached and that the actual growth rate in relation to the highest possible one may vary in the different species. This is, of course, of great importance for the nutrient amounts absorbed and for the nutrient requirements of the species, absolutely or in relation to each other.

In the diagnosis of the nutrient status of forest trees the foliar analysis method has been regarded as promising. The concept of foliar diagnosis ("diagnostique foliaire") was introduced by Lagatu and Maume in 1924 (80) who studied the nutritional properties of the vine. These workers emphasized in a series of papers (1924—1933, *cf.* 48) the importance of well-defined sampling and the consideration of the interrelations between the main nutrients (nitrogen, phosphorus, and potassium). Thus, they used the quotients between the contents instead of the percentages as such in their interpretation of the results. The methods of Lagatu and Maume were adopted by especially Thomas and co-workers (1929—1944, *cf.* 48). The interactions between different nutrients have later been studied by several workers and especially the interactions between the positive ions ("ion antagonism") are well-known phenomena (26, 92). Leyton (84, 85, 86) has in his studies of the nutrition of various forest tree species discussed the use of the quotients N/P, N/K, or K/P for diagnostic purposes.

The usefulness of the foliar analysis has been demonstrated in agricultural plants especially by Lundegårdh (92, 93, 94). Lundegårdh found the nutrient contents in the green matter of "supreme importance" for the growth and development of plants. Though his investigations in the beginning were purely theoretical he was later of the opinion that the leaf analysis method was utilizable for diagnosis of the nutrient supply from the soil and for practical estimation of fertilization requirements. The basis was laid in investigations on the ion absorption (92, 93) and Lundegårdh stated that the concentrations in the nutrient medium influence growth only to the extent that the nutrients are taken up and transported to the green parts. At first, however, Lundegårdh introduced the method of "Triple Analysis" (analysis of subsoil, surface soil, and plant material) but later he stated that "analysis of the leaf alone is generally adequate".

In forest tree species Mitchell (109, 111) and Mitchell and Chandler (112) carried out the first more comprehensive studies based on the analysis of plant parts and they found a strong correlation between supply, internal nutrient concentration, and growth. They emphasized the importance of the actual element percentage in the leaves, in relation to an experimentally determined optimum content, for the magnitude of the growth response to fertilization. Their main problem was to classify the nutrient quality of forest sites. Tamm (171, 174) maintained that it is difficult to estimate the nutrient status of the forest soils on the basis of foliar analysis on account of the complicated relations between various factors in the soil. The relations between external and internal nutrient concentrations depend undoubtedly on many factors that may be varying in a forest stand, for instance the light intensity (45 109), the development of mycorrhiza (104), and the water relations (144). The real importance of these factors is known only to a very little extent. Tamm (171, 175) was of the opinion that the foliar analysis method offers a possible and convenient way of estimating the nutrient status of a stand or a single tree and that it is best utilized for diagnosis of nutrient deficiencies. He found it probable that ranges of nutrient content exist within which growth is clearly reduced owing to deficiencies and that these are valid under a fairly wide variation of natural conditions. Tamm (175) mentioned some preliminary "deficiency levels" of percentages of nitrogen, phosphorus, and potassium in leaves of pine, spruce, and birch obtained from unfertilized plots in experiments where fertilization was found to give growth responses.

Leyton (85) regarded the foliar analysis as an usable guide "not only to the nature and extent of particular mineral deficiencies limiting tree growth but also to the interpretation of field observations" if the sampling is satisfactorily carried out (83, 87, 110, 112, 172, 174). Leyton (85) pointed out, however, as Tamm (171, 174), the difficulties in forecasting the growth response after a fertilization on account of the complex interactions with other factors. Leyton (85, 86), Tamm (171, 174, 175) and others have also emphasized the fact that the lack of well-defined and fundamental data limits the possibility of interpreting the analytical values from forest tree species. This limitation in our knowledge is all the more conspicuous as the results in one of the most detailed studies on forest tree species available (111) have not been confirmed in most other investigations.

The foliar analysis method is comparative (*cf.* 112) and its usefulness depends on the knowledge about the meaning of the analytical values.

Available data about forest trees come from many species, are often conflicting, and cover as a rule only few elements or levels of the elements. It is, therefore, not possible today to settle, whether the interactions noticed between the nutrient status of the trees and other factors (*e.g.* 72) depend on a varying physiological meaning of the internal nutrient concentrations or if the internal concentrations have a relatively constant meaning but correspond to a varying growth on account of, for instance, secondary effects of fertilizers. Thus, at the present state of knowledge about forest tree nutrition one of the most outstanding problems is how the nutrient status of trees may be defined. The primary problem of the present investigation is, therefore, the question of whether there is a physiological background for the use of leaf analysis as a diagnostic method in the studied species and if so which percentages may be regarded as optimum and which indicate deficiency under controlled conditions.

In such a study several methods are utilizable (6, 12, 48, 61). The author has chosen to start with a fundamental study of the influences of varied supply of one element at a time under conditions where a strict control of nutrient supply, light, and temperature is possible. Therefore, seedlings were grown from seeds in nutrient solutions in a constant room with artificial light. This method has the advantage that the growth conditions and especially the nutrient supply may be well defined since all nutrients supplied by the solutions are practically completely available to the seedlings. Further more, it is easily possible to vary the nutrient status of the seedlings within a very broad range with this method. On the other hand, the direct applicability of the laboratory results in the field is uncertain. The investigation, therefore, is planned to be completed with fertilization experiments in forest nurseries to attain a wider validity of the results and to get more detailed data. These field experiments have been in progress for some years but it is still too early to draw more extensive conclusions. In the present paper only the laboratory experiments are presented.

The temperature and light conditions were chosen to permit a rapid and healthy development of the seedlings. The composition of the nutrient solutions is based on the prospect that the element variation is made at otherwise optimum or nearly optimum nutrition under the actual growth conditions. The experiments, therefore, were started with a series of preliminary studies of the solution effects. These studies led to the *control solutions* that were supposed to have compositions that are close to optimum for the respective species under the actual conditions. The length of the growth period was determined for each species on the basis of two conditions, namely, that the seedlings at harvest would be large enough to permit safe chemical analyses to a satisfactory extent and that they then were still in rapid growth to avoid an increase of the internal element percentages on account of decreasing growth rate.

The experiments were planned and treated to give information also about other problems of interest. Thus, a series of growth measurements have been carried out to study the formative effects of the nutrient factors on the seedlings. This is of interest in connection with, among other things, the relations between fertilization and seedling quality in forest nurseries (*cf.* 1, 10, 17, 18, 19, 120, 127). Deficiency symptoms have been recorded to study the possibility of distinguishing between different causes of deficiency by means of the visual symptoms directly or by leaf analysis. The chemical analyses have been carried out on leaves as well as on stems and roots to permit studies on, among other things, the significance of analytical results from different seedling parts and the total nutrient uptake. Leaves and roots have been further analyzed for as many as possible of the macro nutrients to yield a more comprehensive estimate of the nutrient status of the seedlings and a study of the interactions between the elements at varied supply of one of them.

Of a very great interest is to study whether there are specific differences between the species in their nutritional properties. This study is regarded as a second main purpose of the investigation. The species, however, are very different in many characteristics and they react probably differently to the climatic conditions. Yet, if there are substantial differences between the species with regard to their nutritional properties this ought to be revealed in the analytical results.

Some experimental series are not the same as published before (66, 68, 69). The earlier sulphur series comprised no supra-optimum supplies and have, therefore, been repeated. At the same time the sulphur analysis method has been refined to a greater accuracy. The earlier potassium series with birch gave results that on repetition have not been confirmed. Among other things the deficiency symptoms are not in agreement with the earlier ones. The potassium series with birch is, therefore, repeated as a whole and the new series is presented here.

Some experiments have not been published before. It was evident at an early stage of the investigation that there is a change in some characteristics with time. Thus, for instance, the deficiency symptoms were not developed immediately but appeared after some time what indicates a change in the internal nutrient status. Experiments, therefore, have been carried out with controls and low supplies of nitrogen and potassium and with harvest after different growth periods to study the time course of growth, chemical composition, and nutrient uptake of the seedlings. Further more, a preliminary experiment with birch in flowing water cultures at varied pH and with nitrate and ammonium as alternative nitrogen sources is regarded worthy of mention. Some experiments with varied total concentration in the solutions and the same proportions between the elements are also presented.

Chapter II. Technique

A. Treatment of Seeds and Seedlings

Seeds. It has not been possible to get genetically controlled seeds for the experiments, but seeds have been chosen to give a rather uniform material from which the seedlings were selected. Thus, birch seeds were collected on one tree at Bogesund near Stockholm and pine and spruce seeds come from stands in central Sweden. By using a large number of seeds when starting each experiment it has been possible to make a strict selection of seedlings for plantation in the nutrient solutions. During the first half of the growth periods the number of seedlings have been further decreased by removing the largest and smallest seedlings. At harvest a material of acceptable uniformity has been obtained. In Table 1 some data about the conifer seeds are compiled. These seeds are relatively large, whereas the birch seeds are so tiny that their nutrient contents are negligible.

Seed Treatment and Germination. For the first birch experiments the seeds were germinated on wet filter paper in Petri dishes. Later all seeds were germinated in an apparatus according to Jacobsen (*cf.* 3), where a more

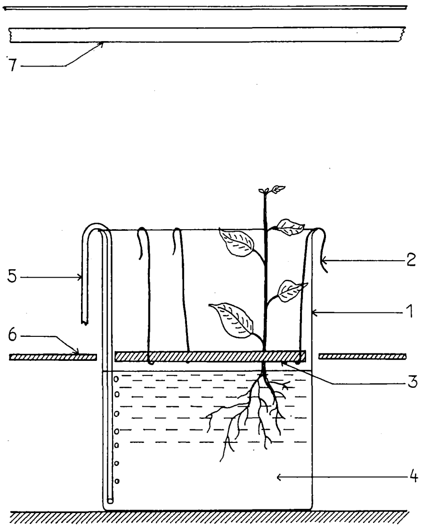


Figure 1. Principle sketch of the growth method. 1. One-litre beaker of pyrex glass. 2. Plastic-coated copper threads. 3. Black, nontransparent plate of perspex. 4. Nutrient solution. 5. Tube for aeration of the nutrient solution. 6. Masonite plate. 7. Fluorescent tube with reflector.

Table 1. Weight and nutrient contents of pine and spruce seeds

Seed	Weight of 1 000 seeds, g	Contents, % of dry weight					Contents, μg per seed				
		N	P	K	Ca	Mg	N	P	K	Ca	Mg
Pine	4.19	5.56	1.02	0.88	0.034	0.36	230	43	37	1.4	15
Spruce	4.99	3.30	0.72	0.92	0.016	0.32	160	36	45	0.8	16

uniform germination occurs. Soaking of the seeds was usually carried out only in connection with germination in Petri dishes. To avoid diseases all pine and spruce seeds were treated with tetramethyl thiuram disulphide, which has been shown to give good results when germinating soft wood seeds (*cf.* 116). The germination was carried out at 25—30°C for seven to ten days.

Plantation in Nutrient Solutions. After germination 10—20 mm long seedlings were selected. At this stage the pine and spruce seedlings had not shed the seed coats. The seedlings were placed in one-litre pyrex glass beakers containing the nutrient solution. For fixation of the seedlings plates of 5 mm thick, black, nontransparent perspex were used. Holes, 3—5 mm in diameter, were bored in each plate and in these holes the seedlings were fixed with cotton-wool pellets. The plates were hung up in the vessels with plastic-coated copper threads (Figures 1 and 2) in the beginning in contact with the nutrient solution. When the seedlings were big enough the plates

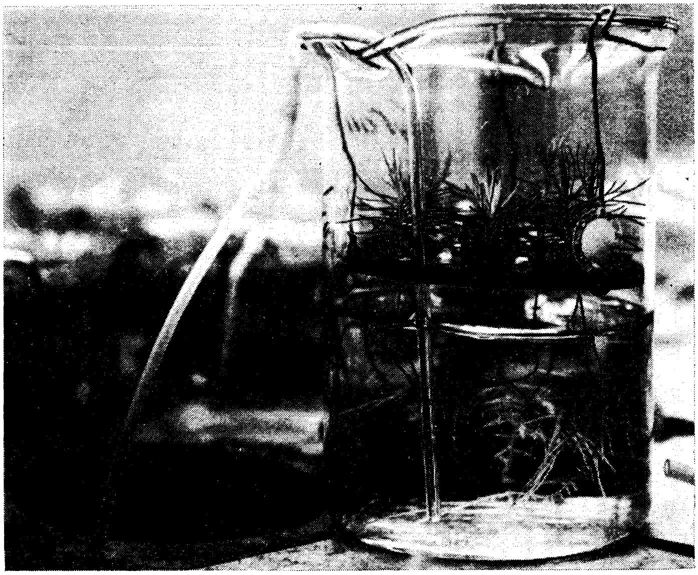


Figure 2. A control vessel with about two-month-old spruce seedlings. The vessel is lifted up from its position.

were raised to a level 5—10 mm above the surface of the nutrient solution. At the same time the wet cotton-wool pellets were exchanged. During the period when the plates were in contact with the nutrient solution and the period immediate thereafter the vessels were covered with transparent celluloid or polyethylene.

Thinning and Number of Seedlings. In each vessel 13—16 seedlings were planted. During the first period some seedlings have often died from various causes. The seedlings were thinned to the same number during the first half of the whole growth period. In some vessels a greater number of seedlings died than was calculated and in these cases only a few seedlings have remained at the end of the experiments. The results from these vessels are not fully comparable with the others on account of uncontrolled selection and this will be mentioned in each case. At the end of the experiments usually 4 birch, 9 spruce, and 12 pine seedlings have remained. In the last experiments with pine, the time and sulphur series, 9 seedlings remained at the harvest, because it was found difficult to maintain a higher number intact in the vessels.

Growth Conditions. The vessels were placed in a room with controlled light and temperature conditions. At the same level as the perspex plates within the vessels masonite plates were placed on the outside (Figures 1 and 2). In this way the roots and nutrient solutions could be satisfactorily darkened and generally green algae did not appear to any considerable extent. As light source fluorescent tubes with a colour temperature of 3000°K were used. The light intensity was about 3000 lux at the brim level of the vessels. The light period was 18 hours and the dark period 6 hours long.

The light intensity is low and has probably been a growth-limiting factor for all three species. Maximum growth is, thus, of course not used here to denote the highest possible growth of the seedlings but the highest growth that, under the prevailing climatic conditions, can be obtained at varied nutrient supply. Low light intensity is also reported to affect the nutrient uptake in pine seedlings (*cf.* 45). Baker (2) was of the opinion that the shade tolerance of trees varies with the nutrient quality of the site. It is known since Garner and Allard (44) that the relative lengths of light and dark periods are of great importance for the vegetative as well as the reproductive development of plants. In the experiments external conditions were desired that permitted the seedlings to grow to a sufficient size and to be in rapid growth at harvest. Suitable conditions were reached for spruce and birch with the first photoperiod applied and this was not altered. Under this condition pine had a tendency to form buds after about 130 days in the controls but within this time it did not reach the same size as that attainable by spruce and birch (see Figure 24, p. 44). Experiments with a shorter light period to reach a more continuous growth with pine (14 hours according to Downs and Borthwick, 35) showed that the growth rate became very low under the otherwise actual conditions. It seemed, therefore, better to apply the same photoperiod to all three species. By means of a careful planning of the analytical work it has been possible to get rather complete analyses also of pine.

The temperature has been 20°C for pine and spruce and 25°C for birch ± 0.5°C during the light period. Also during the dark period the temperature was controlled, but it was not always possible to reach the intended 12°C ± 1 but periodically it was up to 16°C.

The experiments were started with birch that showed excellent growth at a temperature of 25° C. In preliminary experiments with pine and spruce it was found that these species had a comparably poor growth at this temperature and that they grew much better at 20° C, which is in agreement with earlier results (*cf.* 32, 158). Stålfelt (158) has shown that 25° C is a critical temperature for pine and spruce at low light intensities (10 per cent of day light) on account of rapid inhibition of assimilation with increasing temperature above 25° C. The temperature was held low during the dark period to diminish respiration losses in the dry matter. It has been shown that thermoperiodism is of great importance to the growth of many plants also for other reasons (*cf.* 77, 194).

Length of Growth Period. The growth period in the nutrient solutions was in the element series about 75 days for birch, 160 days for spruce, and 95 days for pine. Harvesting was always carried out 2—3 days after the last change of the nutrient solutions.

B. Nutrient Solutions

The nutrient solutions were changed once a week and had a volume of one-half litre. All chemicals used in the experiments were of analytical grade and the water was distilled once in a pyrex glass distiller.

Composition of the Nutrient Solutions. As a basis for the variations in supply of the different elements a control nutrient solution for each species was tested in preliminary experiments. The control solutions have been the common component in all series of varied element concentrations that are thought to yield the maximum growth or nearly so. The compositions of the control solutions are found in Tables 2 and 3, and the different variations of the supplements are found in tables below (Tables 7—12) and at the end of the paper (Tables I—IV).

Basic Solutions. The basic solutions were planned to make the mixing of the final solutions with all variants as simple as possible with minimum risks for mistakes. The concentrations in the basic solutions were chosen to give the control concentrations when diluted 1 :100, that is when 5 ml is given per vessel. The nutrient elements were supplied with sources that contain only

Table 2. Basic solutions. Dilution 1:100 gives control concentrations. + indicates varied, × not varied compounds within respective series

Compound	g/litre			Used in series						
	Pine	Spruce	Birch	Control	N	P	K	Ca	Mg	S
1. NH_4NO_3	14.3	14.3	40.0	×	+	×	×	×	×	×
2. $NaH_2PO_4, 2H_2O$	10.1	5.05	50.4		×	+	×			
3. KCl	9.5	9.5	33.5*		×	×	+			
4. KH_2PO_4	8.8	4.4	43.9	×				×	×	×
KCl	4.6	7.1	9.8*							
5. $CaCl_2, 6H_2O$	21.9	21.9	65.7	×	×	×	×	+	×	×
6. $MgSO_4, 7H_2O$	15.4	15.4	49.2	×	×	×	×	×		
7. $MgCl_2, 6H_2O$	14.5	14.5	40.6						+	×
8. $Na_2SO_4, 10H_2O$	20.8	20.8	64.4						×	+
9. $FeCl_3, 6H_2O$	0.50	0.50	1.4	×	×	×	×	×	×	×
$MnCl_2, 4H_2O$	0.06	0.06	0.18							
H_3BO_3	0.10	0.10	0.29							
$ZnCl_2$	0.004	0.004	0.012							
$CuCl_2, 2H_2O$	0.005	0.005	0.015							
$Na_2MoO_4, 2H_2O$	0.0007	0.0007	0.0022							

* The potassium supply in the sulphur series and in the control of the potassium series of birch was decreased. The KCl concentrations were in these cases: 3. 24.0 and 4. 0 g/litre.

the elements Na, Cl, H, or O besides the nutrient. In certain series potassium phosphate instead of sodium phosphate was used because less potassium chloride was then needed to give the accurate potassium concentration. Except the studied elements also the micro nutrients Fe, Mn, B, Zn, Cu, and Mo were supplied. The basic solutions are presented in Table 2.

Nutrient Solutions Immediately after Plantation. Preliminary experiments showed that many seedlings died immediately after plantation. This difficulty was overcome by means of various measures and by using diluted solutions during the first weeks, namely 1 : 4 during the first week and 1 : 2 during the second for pine and birch and 1 : 4 during the first two weeks and 1 : 2 during the third for spruce. The dilutions were made with control solutions but with the varied element excluded. During these periods the vessels were covered and the perspex plates were in contact with the nutrient solutions as described above (p. 13).

Aeration. With exception for the first weeks of each experiment the nutrient solutions were continuously aerated with press air filtered through cotton-wool and water.

Hydrogen Ion Concentration. The pH in the fresh solutions was for birch

Table 3. Concentrations of the elements in the control solutions

Element	ppm			Element	ppm		
	Pine	Spruce	Birch		Pine	Spruce	Birch
N	50	50	140	Fe	0.93	0.93	2.8
P	20	10	100	Mn	0.17	0.17	0.5
K	50	50	175*	B	0.17	0.17	0.5
Ca	40	40	120	Zn	0.02	0.02	0.06
Mg	15	15	48	Cu	0.02	0.02	0.06
S	20	20	64	Mo	0.003	0.003	0.009

* The potassium supply in the sulphur series and in the control of the potassium series of birch was decreased to 126 ppm.

4—4.5 and for pine and spruce 4—5. During the course of the week between the change of solutions, the pH decreased somewhat. Only in some treatments of birch did the pH go below 4 during the last weeks.

Injuries or growth reductions at very high or low pH values have been reported several times, but it is also known that the effects of pH are dependent on the nutrition (133, 137). For forest tree seedlings pH 4—6 has been reported as suitable (*e.g.* 30, 82, 167, 168, 169). Good growth has also been recorded at very low pH (down to 3.2) in humus by Süchting (164), which he attributed to a good nutrient status of the humus.

Several preliminary experiments with various pH levels in the nutrient solutions were made. These experiments showed that the pH range of 4—5 permits good growth of all three species. The pH control in these experiments was, however, not satisfactory. Therefore, experiments have been started with continuously changed solutions to study the pH effects (*cf.* 137). One of the preliminary series with birch seems worthy of mention in this connection, even if it certainly comprises too few seedlings to justify any far-reaching conclusions.

Experiments with Birch at Varied pH in Flowing Nutrient Solutions

Technique. The seedlings were grown under the same climatic conditions as in the main experiments. From high-standing 10 litre flasks the solutions were divided into 4 tubes ending in capillary tubes for regulation of the flow. The solution was then led to cultural tubes, drained by a tubulation at a level of 50 ml. In each of these tubes one seedling was planted and thus 4 seedlings were supplied from each 10 litre flask. Before plantation in the flowing solutions the seedlings were grown for 14 days in diluted ordinary solutions as described for the main experiments (p. 12—16). After an additional 36 days the seedlings were harvested.

Two types of nitrogen sources were used (ammonium sulphate and sodium nitrate) and 9 different pH levels (each half pH unit from 3.5 to 7.5) was used for each nitrogen source. The pH of the solutions was adjusted by using phosphoric acid as the phosphorus source and then by adding sodium hydroxide under stirring and continuous pH measurement until the desired pH was

Table 4. Growth and analytical data at various pH levels and with two different nitrogen sources in flowing nutrient solutions. The values are means of 4 (pH 3.5—6.0) or 2 (pH 6.5—7.5) seedlings. Birch

pH	N-source	Total dry weight mg/seedling	Per cent of dry weight leaves			
			N	P	K	Ca
3.5	Nitrate	500	4.88	0.56	2.96	0.24
4.0	„	1 020	4.31	0.50	3.61	0.36
4.5	„	950	4.36	0.45	3.19	0.47
5.0	„	780	4.55	0.51	2.91	0.45
5.5	„	1 040	4.44	0.52	3.22	0.51
6.0	„	490	4.38	0.56	3.08	0.52
6.5	„	750	4.24	0.46	2.40	0.26
7.0	„	700	4.00	0.49	2.27	0.29
7.5	„	670	4.14	0.45	2.21	0.34
3.5	Ammonium	1 320	4.39	0.53	2.27	0.19
4.0	„	1 080	4.80	0.59	2.33	0.26
4.5	„	1 320	4.25	0.75	2.61	0.28
5.0	„	1 200	4.17	0.72	2.15	0.32
5.5	„	1 360	4.51	0.88	2.15	0.32
6.0	„	1 180	4.39	1.00	2.24	0.36
6.5	„	1 100	4.41	0.77	2.09	0.15
7.0	„	1 010	4.83	0.74	1.86	0.14
7.5	„	980	4.26	0.72	1.86	0.17

reached. The same proportions between the elements as in the control for birch of the main experiments (Table 3) were used in the solutions except for calcium at high pH and for phosphorus. The phosphorus portion was doubled to get a better pH stability. The absolute amounts of the elements were ¼ (½ for phosphorus) of the amounts in the control of the main experiments. At pH 6.5 or higher calcium was not supplied from the 10 litre flasks because precipitates then stopped the flow through the capillary tubes. Instead calcium was supplied as solid sulphate or tertiary phosphate directly in the culture tubes. The latter compound led very soon to strong calcium deficiency symptoms and these seedlings are, therefore, omitted. Calcium sulphate functioned better and caused certainly quite low calcium contents in the leaves but not as low as those corresponding to deficiency symptoms or clearly reduced growth in the main experiments (Table 4, *cf.* Table 26, p. 81). In all solutions versene-diol (kindly placed at my disposal by the Dow Chemical Company) was supplied at a rate of 0.06 g per 10 litre as a chelating agent (*cf.* 28).

The pH was held constant within the limits ± 0.3 pH units from the predetermined level as measured on the out-flowing solution. If this limit was reached in some treatment, the flow was increased in the whole experiment by using shorter capillary tubes. The change of capillary tubes was made 21 days after the plantation in flowing solutions. The flow was first 50 ml then 100 ml per hour and culture tube (the solution was changed once and twice an hour respectively).

Results and Conclusions. Seedling dry weights and analytical results are given in Table 4. Even if the results are uncertain in the details there are reasons to believe that pH is of little importance for growth at least between 4 and 5.5 and that better growth is reached with NH_4^+ than with NO_3^-, which is in agreement with results reported for other forest tree species (*e.g.* 161). The nutrient contents in the leaves are, however, relatively high and it is not known to what extent this affects the results. The results indicate that the pH range used in the main experiments may be regarded as suitable for birch.

Total Salt, Sodium, and Chlorine Concentrations. When the supplies of the nutrient elements were varied in the nutrient solutions the total salt concentration, the sodium and chlorine supplies have also varied. In some solutions only very small amounts of sodium were added (as molybdate, see Table 2). In the present experiments signs of sodium deficiency have, however, never been noticed. Chlorine was always supplied in relatively great amounts.

Beneficial effects of sodium have been reported for some plants (*e.g.* 36, 81, 188). Swan (161) found, on the other hand, no significant effect of sodium on the growth of Picea, Pinus, and Tsuga species in sand cultures. Chlorine has been reported as beneficial by some workers (*e.g.* 37, 88, 99, 156, 188). It seems probable that the low and intermediate supplies of sodium and chlorine in the present experiments are of no general importance for the results. In connection with potassium deficiency the sodium supply may have been of importance in accordance with the findings of, *e.g.*, Dorph-Peterson and Steenbjerg (34).

Since many workers have found more or less specific effects of plants by salts (*cf.* 6, 13, 61, 153) it is of importance to take the possibility of secondary effects in the experiments by these factors into account, especially in connection with high supplies. It is obvious, however, that it is not possible in the present investigation to distinguish between the different effects of a varied salt. The only thing that may be judged is whether secondary effects may possibly be present in some treatments by using the growth results from all experiments. This test is made in Figures 3—5.

The rings represent the experiments with varied total salt concentration but constant element proportions and the dots represent all the series with varied element supply. The dots and rings represent means of the results from two vessels, except in the case of the rings for birch where duplicates are lacking. Relative seedling dry weight (per cent of maximum) is plotted against total salt concentration (m.eq/litre) in Figure 3, against sodium concentration (log ppm Na) in Figure 4, and against chlorine concentration (log ppm Cl) in Figure 5. In the diagrams broken "ceiling lines" are drawn between the points of highest growth. From the intercepts between the "ceiling lines" and the level of 90 per cent of maximum growth thin lines are drawn vertically to show the limits for no or very small growth effects.

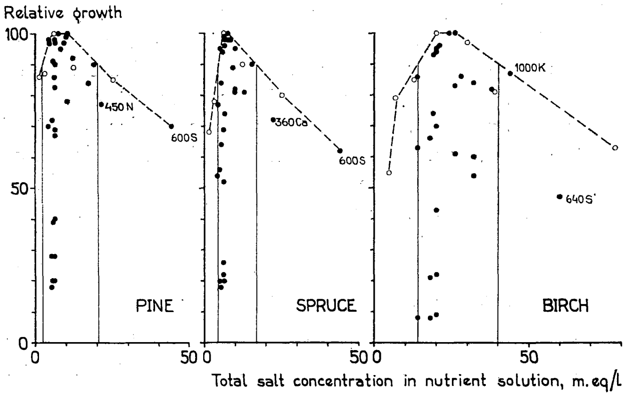


Fig. 3.

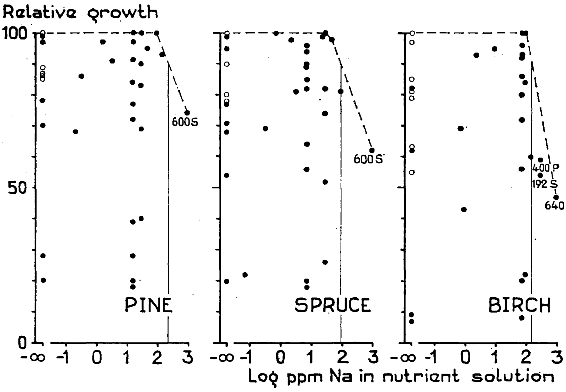


Fig. 4.

Figures 3—5. Possible effects on seedling dry weights (per cent of maximum) of *total salt concentration* (Figure 3), *sodium concentration* (Figure 4), or *chlorine concentration* (Figure 5) in the nutrient solutions. Rings represent the experiments with various total salt concentrations but the same proportions between the elements as in the controls. Dots represent all treatments within the elements series.

It is seen from the diagrams in Figures 3—5 that the total salt, sodium, or chlorine concentrations are generally of small importance for the conclusions in the present paper because very few dots are situated outside the thin lines. At certain high supplies (indicated in the diagrams) growth reductions are noticed and the reasons for this will be further discussed below (p. 50—56).

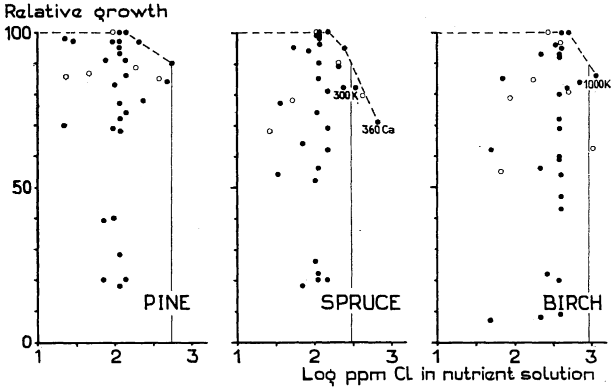


Fig. 5.

C. Mycorrhiza

Since the forest tree species studied generally form mycorrhiza in nature it is of importance to mention that the seedlings lack mycorrhiza in the present experiments. It is, however, found that the seedlings grow very rapidly in the solutions.

Several workers have claimed that mycorrhiza is of importance for the development of forest trees, especially under nutrient deficiency (*cf.* 15, 19, 52, 104). Whether this is the case in nutrient solutions is not known. It is doubtless that the mycorrhiza fungi can transport mineral elements from the root medium to the seedlings, as is shown by Melin and Nilsson (105—107). It is thought that the relatively large surface of a mycorrhiza is more efficient for the nutrient uptake than a root. In a nutrient solution where the contact between the roots and the nutrient medium is very close it is doubtful whether such an increase of the surface would be of decisive importance for the nutrition. If so, this can only affect the relations between the external and internal concentrations of the nutrients and the uptake mechanism. In the present paper the main problem is the relation between internal content and growth, and it does not seem very probable that this relation is affected by the mycorrhiza. Yet, it is possible that the fungi influence growth in other ways about which little is known.

D. Sampling and Growth Measurements

At harvest the roots were washed with distilled water and pressed between filter paper to remove excess water. The seedlings were divided in shoots and roots (pine and spruce) or in leaf-blades, stems + leaf-stalks, and roots (birch). Stem lengths were determined individually but root lengths for all roots together in each vessel. The 2—4 longest root branches were omitted because they could vary tremendously, at least in pine and spruce. Fresh weights were determined as rapidly as possible. After air or vacuum (at about 50° C) drying the pine and spruce shoots were divided into leaves and stems. The dry weights were determined per vessel after a second vacuum drying.

E. Analytical Methods

The samples were ground or cut and vacuum-dried again before weighing for the chemical analyses. From each vessel a single analysis was made of each element, but this was repeated in cases when the values of the duplicates were more divergent than usual. The errors in the analytical values are generally below 3 per cent but may be higher in some cases of very low percentages. Differences between duplicate values are, however, mainly depending upon the experimental errors.

Digestion of the Samples. The weighed samples were digested by boiling in Kjeldahl flasks according to three different methods depending on the analysis required. For nitrogen analyses 1.1—1.5 ml sulphuric acid and 0.5 g catalyst consisting of potassium, cupric, and mercuric sulphates were added to the samples before boiling. For phosphorus, potassium, calcium, and magnesium the samples were boiled with 15—25 ml nitric acid and 5—10 ml perchloric acid. The solutions were then divided for the various analyses. For sulphur 3 ml nitric acid and 1 ml perchloric acid were used.

Nitrogen. The ammonia was distilled and collected in 0.01 M hydrochloric acid in an apparatus according to Parnas and Wagner. The excess hydrochloric acid was then titrated with sodium hydroxide with a mixture of methyl red and methylene blue as indicator.

Phosphorus. An aliquot was pipetted from the solution intended for the P, K, Ca, and Mg analyses and evaporated with nitric acid and sulphuric acid to obtain all phosphorus in the ortho-form. Dilute hydrochloric acid was added and the solution was neutralized with sodium carbonate. Phosphorus was then determined colorimetrically (Beckman spectrophotometer B) according to Scheel (146).

Potassium was determined flame-photometrically in a propane or gasol/air flame (Jena metal interference filter 768a).

Calcium was first precipitated as oxalate and centrifuged. The precipitate was then dissolved in hydrochloric acid and calcium was determined flame-photometrically in an acetylene/air flame (Jena metal interference filter 616a).

Magnesium was determined flame-photometrically in an acetylene/oxygen flame at the line 2852 ÅU according to Knutson (76).

Table 5. Percentile standard errors in growth and analytical values calculated with analysis of variance by using logarithmic values

Standard error in		± ε %		
		Pine	Spruce	Birch
Seedling fresh weight		15.8	6.2	12.1
Seedling dry weight		11.4	7.4	16.3
Leaf dry weight		11.5	8.0	17.0
Root dry weight		13.9	10.2	17.4
Stem length		2.1	6.2	7.2
Contents in leaves	N	4.2	7.9	5.7
	P	9.5	8.8	6.4
	K	5.7	6.9	5.0
	Ca	8.2	13.0	20.0
	Mg	9.1	12.8	8.0
	S	11.9	5.6	17.0
Contents in roots	N	10.8	7.3	5.7
	P	6.5	8.2	9.3
	K	8.5	11.1	14.6
	Ca	9.4	10.7	14.9
	Mg	8.5	17.4	11.6
	S	8.8	7.3	21.3

Sulphur was determined according to Gustafsson (51) with some modifications. An aliquot was evaporated with a great excess of barium chloride to avoid losses of sulphuric acid. Sulphur was reduced to hydrogen sulphide with a solution of hydrochloric acid, acetic acid, and hypophosphite, distilled in nitrogen atmosphere and collected in a solution of zinc and sodium acetates. The hydrogen sulphide was reacted with ferric-ammonium chloride and p-amino dimethyl aniline to methylene blue that was measured colorimetrically (Beckman spectrophotometer B).

F. Statistics

All experiments were made in duplicate in two blocks with each treatment placed at random. In the harvest time series three control vessels were used for each harvest occasion. During the course of the experiments the vessels were moved by exchanging block places or positions within the blocks. Percentile standard errors have been calculated with analysis of variance on the whole material by using logarithmic values. These errors are found in Table 5. The values are estimations of the experimental errors in the averages between two determinations.

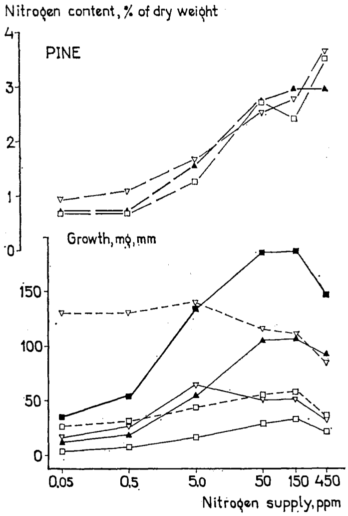


Fig. 6.

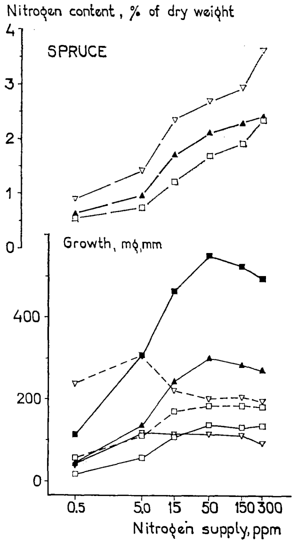


Fig. 7.

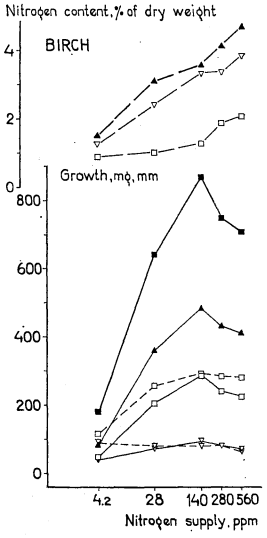


Fig. 8.

Figures 6—8. Growth and analytical results at varied *nitrogen* concentration in nutrient solutions (logarithmic scale).

■ Whole seedlings
▲ Leaves
□ Stems
▽ Roots
———————— Dry weight, mg
– – – – – – – Length, mm
——— ——— ——— Content, per cent of dry weight

Chapter III. Experimental Results

In Tables I—IV at the end of the paper the more important experimental results are given individually for each vessel.

A. Nitrogen Series

Growth. The seedling dry weight reaches the highest values at a nitrogen supply of 150, 50, and 140 ppm in pine, spruce, and birch respectively (Figures 6—8). These supplements correspond to the controls in spruce and birch, whereas the controls in pine (at 50 ppm nitrogen) have a dry weight of about 98 per cent of the maximum. On the sub-optimum side strong growth reductions are found and the lowest supplies have produced about 20 per cent of the highest seedling dry weight in all three species. The seedling dry weights are also clearly reduced by high nitrogen supplies and especially pine has reacted strongly and only four seedlings have survived in one of the vessels with the highest supply.

In all three species the dry weights of leaves and stems have reached a maximum at the same supply as the seedling dry weights and in birch also the root weight. In pine and spruce the root weights are highest at a lower supply (5 ppm, Figures 6 and 7). The root dry weights vary, on the whole, less with the nitrogen supply than the shoot dry weights in all three species.

The stem lengths vary less than the stem dry weights, especially in birch (Figures 6—8) but the maximum appears at the same supply as the root or seedling dry weight maximum. The root lengths, on the other hand, are in all three species high at low supplies and decrease then on the whole with increasing nitrogen supply.

Table 6. Length of pine leaves at varied nitrogen and phosphorus supplies in a preliminary experiment. Ten leaves per seedling have been measured

Nitrogen supply, ppm	Leaf length, mm	Phosphorus supply, ppm	Leaf length, mm
0.05	9	0.02	26
0.5	27	0.2	45
5.0	54	2.0	80
50	80	20	80
150	78	60	74
450	75	180	58

Lengths of the leaves are generally not measured in the experiments, because manipulations with the samples have been avoided with regard to the

Table 7. Phosphorus, potassium, calcium, and magnesium contents in leaves and roots at varied nitrogen supply

N supply, ppm	Contents, per cent of dry weight							
	Leaves				Roots			
	P	K	Ca	Mg	P	K	Ca	Mg
PINE								
0.05	0.16	0.97	0.38	0.18	0.68	1.32	0.22	0.14
0.5	0.18	0.87	0.36	0.18	0.70	1.36	0.18	0.12
5.0	0.20	0.92	0.30	0.16	0.68	1.70	0.12	0.12
50	0.23	0.92	0.26	0.13	0.72	2.12	0.10	0.10
150	0.26	1.06	0.28	0.16	0.72	1.83	0.10	0.10
450	0.25	1.01	0.26	0.16	0.65	1.30	0.08	0.10
SPRUCE								
0.5	0.28	0.78	0.37	0.12	0.42	0.98	0.52	0.13
5.0	0.24	0.74	0.30	0.11	0.53	1.64	0.22	0.12
15	0.24	0.94	0.26	0.13	0.52	1.75	0.22	0.10
50	0.23	0.92	0.19	0.11	0.41	1.06	0.22	0.08
150	0.25	0.96	0.20	0.12	0.46	1.32	0.13	0.02
300	0.26	1.02	0.24	0.13	0.52	1.36	0.16	0.04
BIRCH								
4.2	0.43	2.09	0.65	0.47	1.65	4.11	0.24	0.32
28	0.34	2.90	0.36	0.34	1.36	3.08	0.17	0.12
140	0.39	2.38	0.30	0.34	1.24	2.24	0.16	0.10
280	0.40	2.70	0.33	0.37	1.29	2.71	0.12	0.14
560	0.48	2.94	0.40	0.37	1.34	2.52	0.18	0.14

chemical analyses. In some preliminary experiments such measurements were made in pine seedlings and the results seem worth mentioning, because the length of pine leaves varies greatly with the nutrient status. The results shown in Table 6 are, however, not fully comparable to the other growth results, because in the actual experiments only the nitrogen and phosphorus supplies were the same as in the present experiments and, further more, the pH in the solutions was higher (about 6). It is seen from Table 6 that the leaf length is strongly influenced by the nitrogen supply and that the maximum length appears at 50—150 ppm nitrogen, that is at the same supply as the seedling dry weight maximum.

Internal Nitrogen Concentrations. With increasing nitrogen supply the internal nitrogen concentrations as per cent of dry weight increase in leaves, stems, as well as roots generally over the whole ranges investigated (Figures 6—8). In pine, however, the nitrogen concentration is constant in leaves and stems between the two lowest supplies and in the leaves also between the two highest, when, on the other hand, the concentrations in stems and roots increase rapidly. The nitrogen concentrations are usually lowest in the stems in all three species and highest in the roots of pine and spruce and in the leaves of birch. In pine these differences are small.

Internal Concentrations of Other Elements. At low nitrogen supplies the calcium and magnesium concentrations are higher than at high supplies in leaves as well as roots (Table 7). The tendency, however, is less marked in pine than in spruce and birch seedlings. In birch a similar tendency is found for phosphorus and potassium, especially in the roots, and also for phosphorus in spruce. In pine, on the other hand, the phosphorus concentration increases with the nitrogen supply and is highest in the roots at optimum nitrogen supply as is also the potassium concentration.

Deficiency and Toxicity Symptoms. Evident deficiency symptoms have appeared in the leaves at the lowest (birch) or the two lowest (pine and spruce) nitrogen supplies. The symptoms consist of chlorosis of the leaves, especially the youngest, whereas older leaves fade and die. These symptoms are similar in all three species but in birch leaves violet spots were also noticed on the undersides. With increasing nitrogen supply the leaf colour was continuously changed to dark green, but at the supplies 5, 15, and 28 ppm nitrogen for pine, spruce, and birch respectively characteristic symptoms may be regarded as not present even if the leaf colour still was lighter than at higher supplies.

At the highest supplies clear symptoms of some toxicity were noticed in spruce and especially pine. The symptoms consist of fading and brown leaf tips. Tendencies of this type of symptoms were also seen in the pine seedlings at the next highest supply even if these have produced maximum growth.

B. Phosphorus Series

Growth. The highest seedling dry weights correspond to 20, 1, and 100 ppm phosphorus in the nutrient solutions for pine, spruce, and birch respectively (Figures 9—11). The dry weights, however, are high within wide ranges of supply in all three species. Thus, the seedling dry weight is above 92 per cent of the highest in pine at all supplies from 2 ppm and higher, above 98 per cent from 1 ppm in spruce, and in birch 94 per cent also at the supply 3 ppm. In pine and spruce the control phosphorus concentrations (20 and 10 ppm) are clearly within the optimum ranges and in the birch (as also in the pine) series the control has produced the highest seedling dry weight. The lowest supplies have led to strong growth reductions in pine and spruce. The dry weight of the birch seedlings is certainly reduced

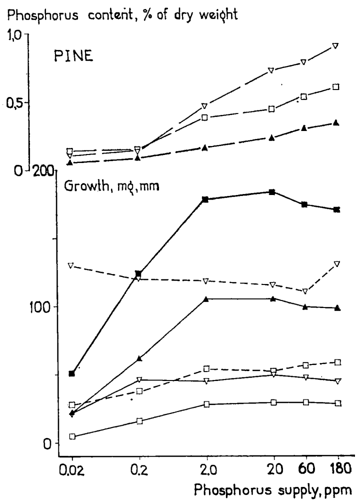


Fig. 9.

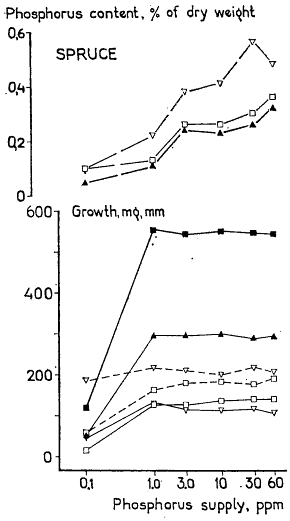


Fig. 10.

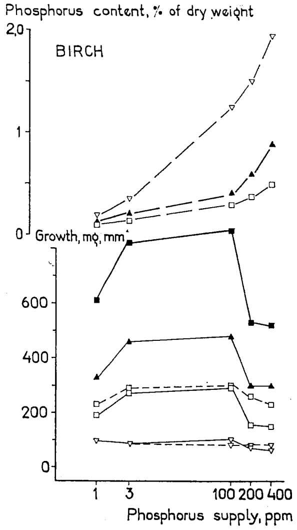


Fig. 11.

Figures 9—11. Growth and analytical results at varied *phosphorus* concentration in nutrient solutions (logarithmic scale).

■ Whole seedlings
▲ Leaves
□ Stems
▽ Roots
——————— Dry weight, mg
– – – – – – – Length, mm
—— —— —— Content, per cent of dry weight

Table 8. Nitrogen, potassium, calcium, and magnesium contents in leaves and roots at varied phosphorus supply

P supply, ppm	Contents, per cent of dry weight							
	Leaves				Roots			
	N	K	Ca	Mg	N	K	Ca	Mg
PINE								
0.02	2.54	1.06	0.27	0.14	1.66	1.14	0.08	0.08
0.2	2.62	1.11	0.32	0.14	1.97	1.21	0.12	0.08
2.0	2.57	1.05	0.30	0.14	2.91	1.82	0.08	0.09
20	2.76	0.92	0.26	0.13	2.52	2.12	0.10	0.10
60	2.78	1.02	0.26	0.14	2.97	1.96	0.06	0.12
180	2.74	1.08	0.28	0.12	2.51	1.58	0.10	0.11
SPRUCE								
0.1	2.46	1.19	0.34	0.21	1.98	0.89	0.22	0.03
1.0	1.74	0.74	0.21	0.13	2.24	1.26	0.14	0.07
3.0	1.94	0.81	0.24	0.12	2.58	1.10	0.14	0.06
10	2.12	0.92	0.19	0.11	2.71	1.06	0.22	0.08
30	2.02	0.85	0.22	0.12	2.93	1.24	0.14	0.06
60	2.24	1.34	0.20	0.12	2.86	1.60	0.13	0.13
BIRCH								
1.0	3.02	2.37	0.31	0.41	2.42	3.16	0.13	0.18
3.0	3.72	2.76	0.39	0.46	3.13	2.45	0.10	0.15
100	3.60	2.38	0.30	0.34	3.32	2.24	0.16	0.10
200	4.02	3.10	0.42	0.46	3.12	2.72	0.16	0.14
400	4.01	2.92	0.39	0.36	3.18	3.28	0.17	0.16

at the lowest supply but not very strongly. At high supplies there is no clear supra-optimum effect in spruce and in pine this effect is clear but it does not amount to 10 per cent growth reduction. In birch, on the other hand, the two highest supplies have both caused a very strong reduction of the seedling dry weight.

The leaf and stem dry weights vary in a similar way as the seedling dry weight, whereas the root dry weight reaches maximum or shows a less markedly growth reduction at lower supplies.

The stem lengths vary less than the stem dry weights, whereas the root lengths show a comparably small variation with varied phosphorus supply. In pine and birch the maximum length is found at the lowest supply.

The length of the pine leaves is strongly affected by the phosphorus supply (Table 6), but it must be remembered that these values are not fully comparable to the other growth data (*cf.* p. 26).

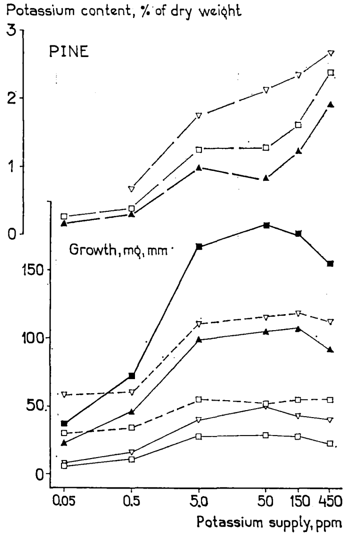


Fig. 12.

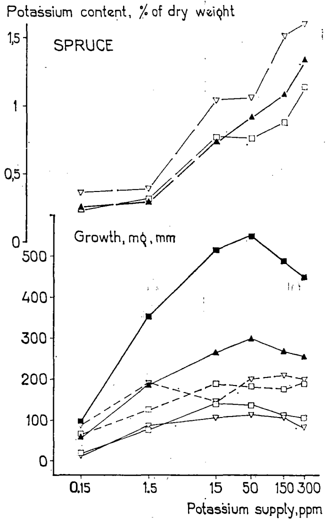


Fig. 13.

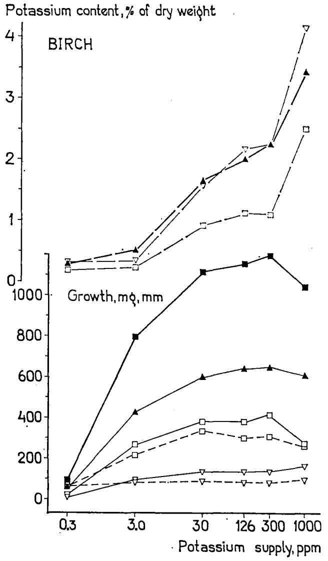


Fig. 14.

Figures 12—14. Growth and analytical results at varied *potassium* concentration in nutrient solutions (logarithmic scale).

■ Whole seedlings
▲ Leaves
☐ Stems
▽ Roots
——— Dry weight, mg
– – – – Length, mm
— — — Content, per cent of dry weight

Internal Phosphorus Concentrations. With logarithmically increasing phosphorus supply the internal phosphorus concentrations increase on the whole slowly within the sub-optimum range and also at high supplies in pine and spruce (Figures 9—11). In spruce within the optimum range there is not a continuous increase of the internal concentrations but even a decrease in the leaves between 3 and 10 ppm. This pattern depends mainly on the value at the supply 3 ppm and cannot, therefore, be regarded as fully certain. There is, however, a similar tendency also in pine and birch, but the experimental data do not cover the actual range so well as in the spruce series. The phosphorus concentration is highest in the roots and lowest in the leaves (pine and spruce) or stems (birch).

Internal Concentrations of Other Elements. With varied phosphorus supply there is a comparably small and irregular variation in the concentrations of nitrogen, potassium, calcium, and magnesium in leaves and roots (Table 8).

Deficiency Symptoms. Visual deficiency symptoms have appeared in the leaves of all three species at the lowest supply of phosphorus. The symptoms consist of a dark green colour that in the spruce and especially the birch leaves is combined with an anthocyanin colouring. In spruce there is also a chlorosis in the tips of the youngest leaves that is not noticed in the other species.

Toxicity symptoms have not appeared within the phosphorus series, not even in birch where high supplies are connected with a strong growth reduction.

C. Potassium Series

Growth. The highest seedling dry weights are reached at 50 ppm potassium in the nutrient solutions for pine and spruce and at 300 ppm for birch (Figures 12—14). These supplies correspond to the controls of pine and spruce, whereas the birch control (126 ppm potassium) has produced 96 per cent of the highest seedling dry weight. The supply ranges producing good growth are wide in all three species. Thus, 91 and 97 per cent of maximum growth are found in pine at 5 and 150 ppm respectively, 94 per cent in spruce at 15 ppm, and 93 per cent in birch at 30 ppm. The supply ranges on the sub-optimum side are well covered in all three species. Thus, the lowest supplies correspond to seedling dry weights of about 20 per cent of the maximum in pine and spruce and 8 per cent in birch. In all three species clear supra-optimum dosages are also reached and the highest supply in the birch series has caused the death of some seedlings (1 and 2 in the two vessels).

Table 9. Nitrogen, phosphorus, calcium, and magnesium contents in leaves and roots at varied potassium supply

K supply, ppm	Contents, per cent of dry weight							
	Leaves				Roots			
	N	P	Ca	Mg	N	P	Ca	Mg
PINE								
0.05	3.89	0.43	0.22	0.25	—	0.70	0.11	—
0.5	3.54	0.35	0.24	0.22	4.06	0.67	0.07	0.07
5.0	2.94	0.28	0.26	0.12	3.42	0.73	0.08	0.10
50	2.76	0.23	0.26	0.13	2.52	0.72	0.10	0.10
150	2.81	0.28	0.26	0.14	2.67	0.74	0.10	0.10
450	2.76	0.30	0.27	0.14	3.02	0.69	0.10	0.10
SPRUCE								
0.15	2.07	0.32	0.29	0.21	3.03	0.62	0.20	0.10
1.5	2.19	0.26	0.27	0.16	2.78	0.40	0.13	0.08
15	2.24	0.24	0.22	0.12	2.40	0.42	0.12	0.10
50	2.12	0.23	0.19	0.11	2.71	0.41	0.22	0.08
150	2.30	0.26	0.25	0.14	2.53	0.44	0.16	0.13
300	2.20	0.23	0.20	0.12	2.86	0.46	0.13	0.13
BIRCH								
0.3	3.40	1.36	0.90	1.24	3.14	2.16	0.28	0.52
3.0	3.44	0.85	0.42	0.58	3.01	0.98	0.10	0.23
30	3.79	0.52	0.39	0.44	3.21	0.91	0.10	0.12
126	3.52	0.48	0.35	0.40	2.68	1.02	0.10	0.12
300	3.38	0.40	0.30	0.32	2.60	0.85	0.10	0.10
1 000	3.32	0.44	0.30	0.32	2.70	1.22	0.08	0.14

The different seedling parts reach maximum dry weights at about the same supplies as those corresponding to maximum seedling dry weight. This is, thus, valid also for the roots which reach the maximum at high rather than at low supplies in contrast to what was found in the nitrogen and phosphorus series.

As in earlier series, the stem lengths vary less than the stem weights. The root lengths, on the other hand, are comparatively much influenced by potassium deficiency, especially in pine, and reach the maximum at relatively high supplies as also the root weights.

Internal Potassium Concentrations. With logarithmically increasing potassium concentration in the nutrient solutions the internal potassium percentage increases slowly at low supplies and rapidly at high (Figures 12—14). In the passage from sub-optimum to optimum supplies the concentration increase is comparatively slow and in the pine leaves there is even a decrease. This tendency is more pronounced in stems and roots than in the leaves of spruce and birch.

The potassium concentration is in pine and spruce highest in the roots. The lowest concentrations are found in the leaves of pine and in the stems of birch. In birch there are small differences between the concentrations in leaves and roots and in spruce between leaves and stems at least at sub-optimum supplies.

Internal Concentrations of Other Elements. In potassium deficiency there is a common tendency to high concentrations of other elements (Table 9). Very striking are the high calcium and magnesium concentrations in the birch leaves and roots at low supplies, but these tendencies are less obvious or lacking in pine and spruce.

Deficiency and Toxicity Symptoms. Evident deficiency symptoms have appeared in all three species at the two lowest supplies. The potassium deficiency symptoms of the pine and spruce seedlings consist of chlorosis in the younger leaves, especially in the leaf tips which later fade and become brown. In pine the fading leaf tips is the dominating symptom. In birch the older leaves are dark green, whereas the younger have chlorotic margins. The leaf-blade is buckled and in the chlorotic parts brown spots of dead tissues are developed.

Symptoms of toxic effects of high potassium supplies have been noticed in birch at the supply of 1000 ppm. The leaves are pale and tips and margins fade. Some seedlings have died as mentioned above.

D. Calcium Series

Growth. In all three species the controls have produced the highest seedling dry weights within the calcium series (40 ppm calcium in pine and spruce and 120 ppm in birch, Figures 15—17). The pine seedlings, however, have grown practically as well at the supplies 0.12 and 4 ppm as also the spruce seedlings at 12 and 120 ppm. The seedling dry weight maximum of birch is more pronounced than that of pine and spruce. In birch the lowest calcium supply has caused a very strong growth reduction but not in pine and spruce where it corresponds to 70 respectively 54 per cent of the highest seedling dry weight. On the supra-optimum side strong effects are noticed in all three species and in the pine and spruce series the highest supply has caused the death of many seedlings (of both species all seedlings died in one of the vessels, whereas 6 and 8 seedlings have survived in the duplicate vessels). The six seedlings of pine have a comparably high dry weight, but

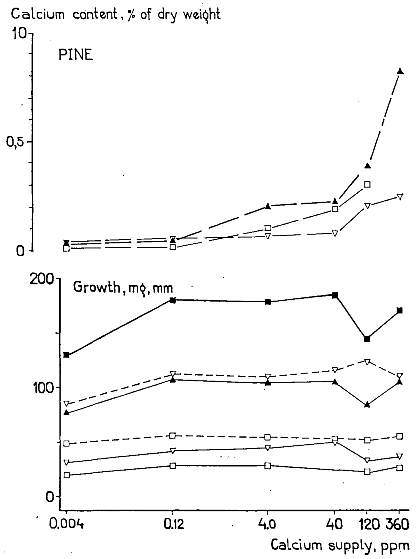


Fig. 15.

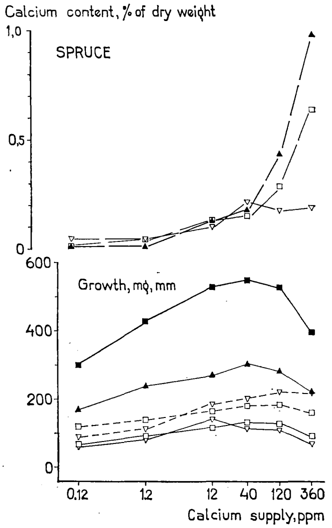


Fig. 16.

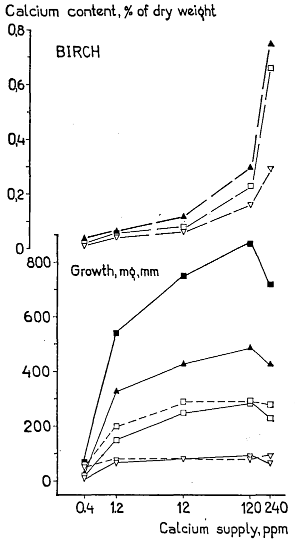


Fig. 17.

Figures 15—17. Growth and analytical results at varied *calcium* concentration in nutrient solutions (logarithmic scale).

■ Whole seedlings
▲ Leaves
□ Stems
▽ Roots
———— Dry weight, mg
– – – – – – – Length, mm
—— —— —— Content, per cent of dry weight

Table 10. Nitrogen, phosphorus, potassium, and magnesium contents in leaves and roots at varied calcium supply

Ca supply, ppm	Contents, per cent of dry weight							
	Leaves				Roots			
	N	P	K	Mg	N	P	K	Mg
				PINE				
0.004	2.80	0.26	1.16	0.17	2.44	—	1.82	0.18
0.12	2.78	0.26	1.17	0.16	2.76	—	2.06	0.17
4.0	2.68	0.28	1.14	0.14	3.04	0.78	1.94	0.16
40	2.76	0.23	0.92	0.13	2.52	0.72	2.12	0.10
120	2.72	0.28	1.24	0.12	3.00	0.86	1.90	0.13
360	2.73	0.26	1.06	0.13	1.52	0.75	2.25	0.11
				SPRUCE				
0.12	2.30	0.26	1.08	0.12	2.43	0.41	0.74	0.10
1.2	2.06	0.22	0.87	0.10	2.46	0.37	0.77	0.11
12	2.06	0.26	0.98	0.12	3.00	0.50	1.37	0.10
40	2.12	0.23	0.92	0.11	2.71	0.41	1.06	0.08
120	2.08	0.22	0.86	0.11	2.66	0.46	1.37	0.08
360	1.92	0.21	1.03	0.09	2.90	0.41	1.29	0.06
				BIRCH				
0.4	—	—	—	—	—	—	2.37	0.34
1.2	3.27	0.40	2.02	0.51	3.48	1.32	2.49	0.16
12	3.90	0.51	2.63	0.44	3.60	1.50	2.62	0.14
120	3.60	0.39	2.38	0.34	3.32	1.24	2.24	0.10
240	3.20	0.32	2.58	0.32	3.37	1.25	2.48	0.13

they cannot be regarded as fully representative because their survival may depend on an especially good start of these seedlings.

The dry weights of leaves, stems, and roots vary in the calcium series in a similar way as the seedling dry weights. The root weight variation is, thus, of the same type as in the potassium series but different to that of the nitrogen and phosphorus series.

The stem lengths vary again less than the stem weights, but the root lengths are relatively strongly reduced in calcium deficiency and reach the maximum at very high supplies.

Internal Calcium Concentrations. With logarithmically increasing supply the calcium concentrations increase generally more and more rapidly and very steeply in leaves and stems within the supra-optimum range (Figures 15—17). At low supplies the differences between the concentrations in the organs are relatively small but at higher supplies the leaves have the highest and the roots the lowest concentrations.

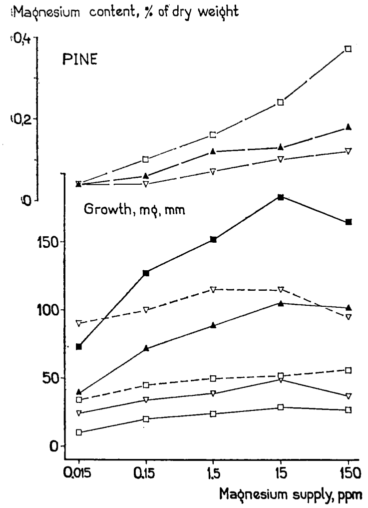


Fig. 18.

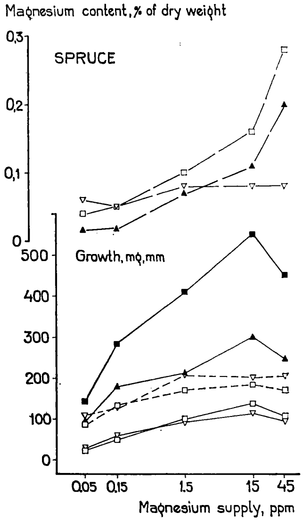


Fig. 19.

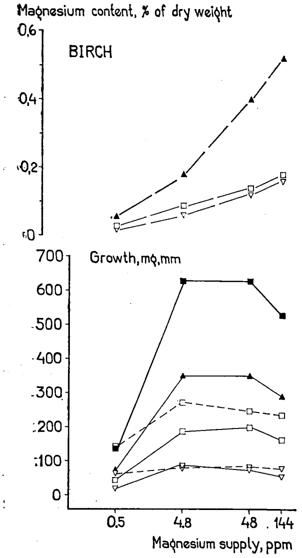


Fig. 20.

Figures 18—20. Growth and analytical results at varied *magnesium* concentration in nutrient solutions (logarithmic scale).

■ Whole seedlings
▲ Leaves
☐ Stems
▽ Roots
———————— Dry weight, mg
– – – – – – – Length, mm
—— —— —— Content, per cent of dry weight

Internal Concentrations of Other Elements. The concentrations of nitrogen, phosphorus, and potassium are influenced only to a small degree by the calcium supply (Table 10). The magnesium concentrations are somewhat high at low calcium supply in the pine and birch seedlings but little affected in spruce.

Deficiency and Toxicity Symptoms. Deficiency symptoms were noticed in the leaves at the two (pine and spruce) or three (birch) lowest supplies. Thus, the symptoms have appeared also at levels corresponding to good growth, especially in pine and birch. In pine and spruce the young leaves are chlorotic and faded at the tips. In pine the brown leaf tips dominate the symptom picture. It is characteristic also in birch that the leaf tips die, resulting in more rounded leaves than is normal. The leaf margins are white and the leaf-blades are buckled. Calcium deficiency causes also dying meristems in shoots as well as roots of the birch seedlings. This phenomenon is very marked also in the roots of pine and spruce. The dieback of the meristems causes an intensified branching.

Toxicity symptoms have appeared in pine at the two highest and in spruce at the highest supply of calcium. At the highest supply many pine and spruce seedlings died as mentioned above. The symptoms consist of fading and brown leaf tips. No similar symptoms have been recorded in the birch seedlings.

E. Magnesium Series

Growth. The highest seedling dry weights are found in the controls of pine and spruce (15 ppm magnesium) and in birch about the same seedling dry weight is found at the concentrations 4.8 and 48 ppm magnesium in the solutions (Figures 18—20). The 48 ppm represents the birch control. The maxima of pine and spruce are quite pronounced and there are evident sub-optimum as well as supra-optimum effects in all three species.

The different seedling parts show a dry weight variation that is very similar to that of the total seedling dry weight.

The stem and root lengths vary less than the corresponding dry weights in all three species.

Internal Magnesium Concentrations. On the whole the internal magnesium concentrations increase more and more rapidly with logarithmically increasing magnesium supply (Figures 18—20). As was found in the potassium series there is, however, also here a tendency in pine and spruce to a less marked increase in the internal magnesium concentrations in the passage from sub--optimum to optimum supplies. The magnesium concentration is highest in the stems of pine and spruce in contrast to what is found for the other macro

Table 11. Nitrogen, phosphorus, potassium, and calcium contents in leaves and roots at varied magnesium supply

Mg supply, ppm	Contents, per cent of dry weight							
	Leaves				Roots			
	N	P	K	Ca	N	P	K	Ca
PINE								
0.015	2.54	0.32	1.34	0.57	3.31	0.78	1.86	0.20
0.15	2.58	0.29	1.14	0.48	2.52	0.73	2.18	0.14
1.5	2.74	0.31	1.12	0.36	—	0.86	1.91	0.12
15	2.76	0.23	0.92	0.26	2.52	0.72	2.12	0.10
150	2.70	0.31	0.98	0.24	2.96	0.84	2.57	0.12
SPRUCE								
0.05	1.78	0.32	1.91	0.28	2.87	0.64	1.12	0.33
0.15	1.72	0.28	1.40	0.26	2.30	0.49	1.06	0.20
1.5	2.19	0.26	1.06	0.28	2.48	0.48	1.26	0.14
15	2.12	0.23	0.92	0.19	2.71	0.41	1.06	0.22
45	1.97	0.22	0.98	0.21	2.68	0.46	1.09	0.12
BIRCH								
0.5	3.30	0.50	3.98	0.45	—	—	3.08	0.18
4.8	4.14	0.52	3.57	0.38	2.94	0.91	2.92	0.26
48	3.82	0.42	2.86	0.30	3.44	0.87	2.34	0.14
144	3.94	0.44	2.92	0.28	3.24	0.82	2.26	0.10

elements. In pine the concentration is lowest in the roots, which is also the case in spruce at high supplies. The birch seedlings have throughout the highest magnesium concentrations in the leaves and lowest in the roots.

Internal Concentrations of Other Elements. In magnesium deficiency there is a tendency to low nitrogen concentrations in the leaves of all three species (Table 11). The same tendency is seen in the birch roots but rather the contrary in the pine and spruce roots. On the other hand, in magnesium deficiency high concentrations of phosphorus are found in the spruce and birch seedlings and of potassium and calcium in the leaves of all three species and in the birch roots.

Deficiency Symptoms. Visual symptoms have appeared in the leaves at the two lowest (pine and spruce) or the lowest supply (birch). In the pine and spruce leaves the symptoms consist of chlorotic leaf tips with a sharp border against the green bases. With increasing deficiency the yellow part increases and the tips fade. The birch leaves have yellow margins and areas between the veins. Brown spots appear in the yellow parts.

Toxicity symptoms have not appeared in the magnesium series.

Table 12. Nitrogen, phosphorus, potassium, calcium, and magnesium contents in leaves and roots at varied sulphur supply

S supply, ppm	Contents, per cent of dry weight									
	Leaves					Roots				
	N	P	K	Ca	Mg	N	P	K	Ca	Mg
PINE										
0	3.12	—	0.96	0.26	0.18	2.58	—	0.66	0.10	0.21
0.2	2.64	—	0.84	0.31	0.11	2.16	—	1.32	0.08	0.20
2.0	3.06	—	1.04	0.32	0.10	2.66	—	2.11	0.09	0.12
20	3.12	—	1.06	0.32	0.12	2.80	—	1.70	0.08	0.13
60	2.96	—	1.05	0.26	0.11	2.57	—	1.69	0.07	0.14
600	2.86	—	0.92	0.24	0.19	2.78	—	1.34	0.06	0.12
SPRUCE										
0	1.80	0.22	—	0.43	0.12	1.78	0.60	1.16	0.19	0.10
0.2	2.08	0.24	0.72	0.31	0.14	2.16	0.62	1.42	0.14	0.10
2.0	2.31	0.26	0.84	0.26	0.10	2.70	0.48	1.59	0.14	0.09
20	2.18	0.28	1.07	0.24	0.13	2.70	0.56	1.44	0.20	0.07
60	2.22	0.28	1.12	0.24	0.13	2.82	0.47	1.44	0.14	0.08
600	2.40	0.30	—	0.20	0.10	2.94	0.50	1.40	0.16	0.08
BIRCH										
0	2.50	0.58	1.70	—	—	2.44	1.26	2.62	0.20	0.19
0.64	3.02	0.52	2.22	0.39	0.42	2.60	0.86	2.22	0.20	0.14
6.4	3.79	0.49	2.49	0.38	0.40	3.05	0.83	2.86	0.12	0.14
64	3.58	0.40	2.66	0.32	0.36	3.11	0.88	2.38	0.11	0.09
192	3.88	0.42	2.65	0.36	0.40	2.79	1.09	2.52	0.18	0.13
640	3.36	0.54	3.45	0.39	0.36	2.70	1.25	2.40	0.22	0.10

F. Sulphur Series

Growth. In all three species the control sulphur supply (20 ppm in pine and spruce and 64 ppm in birch) corresponds to the highest seedling dry weights (Figures 21—23). The pine seedlings show, however, good growth already at 0.2 and 2 ppm and practically the same growth at 60 ppm as in the control. In the spruce and birch series the seedling dry weight maxima are more pronounced, but in spruce also the supply of 2 ppm and in birch 6.4 ppm has produced high seedling dry weights. In all three species there are very clear sub-optimum and supra-optimum effects. The lowest supply of sulphur means no addition of sulphur to the solutions and the corresponding seedling dry weights are about 20 per cent of the maximum in pine and spruce and 9 per cent in birch. At the highest supplies the growth is clearly reduced and toxicity symptoms were noticed in all three species. However, no seedlings have died.

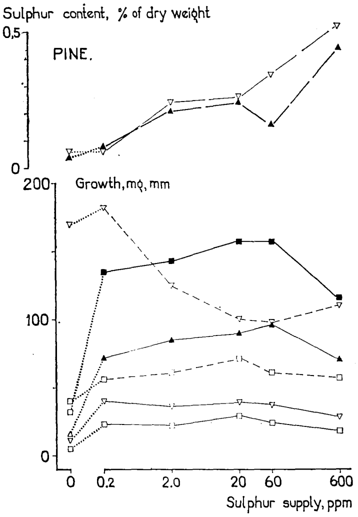


Fig. 21.

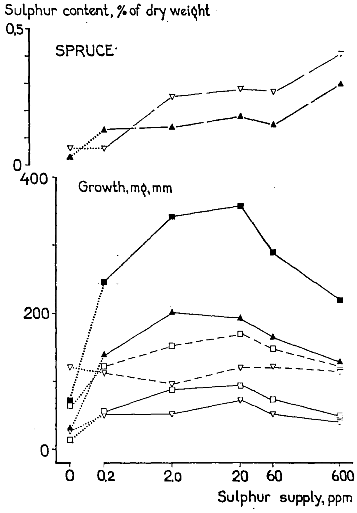


Fig. 22.

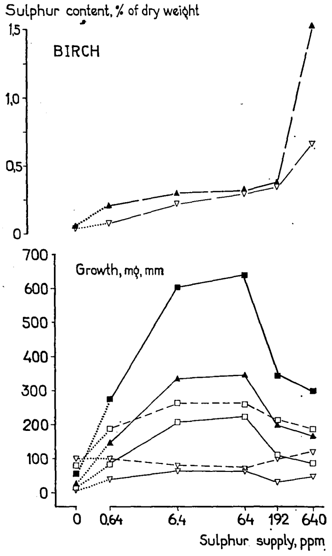


Fig. 23.

Figures 21—23. Growth and analytical results at varied *sulphur* concentration in nutrient solutions (logarithmic scale).

■ Whole seedlings
▲ Leaves
□ Stems
▽ Roots
——————— Dry weight, mg
– – – – – – – Length, mm
—— —— —— Content, per cent of dry weight

The leaf and stem dry weights vary, on the whole, in a similar way as the seedling dry weights. The root dry weights show less pronounced variations and reach maximum at 0.2 ppm in pine. The pattern is similar to what was found in the nitrogen and phosphorus series.

The stem lengths vary as for the other elements less than the stem weights. The roots are long at low sulphur supplies, which is most evident in pine and the minimum lengths correspond to high seedling dry weights in all three species.

Internal Sulphur Concentrations. With logarithmically increasing sulphur supply the internal sulphur concentrations increase most obviously within the supra-optimum range but also at low supplies (Figures 21—23). Within the optimum range the internal concentration increase is small or lacking. In connection with the passage of the optimum there is even a decrease in the pine leaves and the spruce leaves and roots. The stems are not analyzed because the samples are generally too small to permit certain analysis. The sulphur concentration is generally somewhat higher in the roots than in the leaves of pine and spruce, whereas the opposite relation is found in birch.

Internal Concentrations of Other Elements. The nitrogen concentrations are low in the spruce and birch leaves at low sulphur supplies and the same tendency is found in the roots (Table 12). This effect is not seen in pine. Also the potassium concentrations are low at low sulphur supplies, which is most obvious in the pine and spruce roots and the spruce and birch leaves. The phosphorus, calcium, and magnesium concentrations vary little with the sulphur supply. In some cases however, high values are found at low supplies.

Deficiency and Toxicity Symptoms. Symptoms of sulphur deficiency were noticed in pine and spruce leaves at the two lowest supplies and in birch leaves at the two lowest. In all three species the youngest leaves are chlorotic. The colour is generally evenly distributed on the leaves but older yellow birch leaves have often green margins.

Toxicity symptoms have appeared in all three species at the highest supply. The symptoms consist of brown leaf tips and were most pronounced in spruce.

G. Series with Varied Total Salt Concentrations but the Same Element Proportions

Growth. The seedling dry weights reach the highest values in the controls of all three species and lower as well as higher total salt concentrations have caused reduced growth (Table 13). This is most pronounced in birch where ¼ and 4 times the control concentrations have produced only 55 and 63 per cent, respectively of the control seedling dry weight. These values for birch are, however, uncertain since duplicate treatments are lacking. The corresponding growth values in spruce are 68 and 80 per cent and in pine 88 per cent.

Table 13. Seedling dry weight and nutrient content in leaves and roots at varied total concentration of the nutrient solution but constant proportions between the elements. The control concentrations are put equal to 1

Relative concentration	Dry weight, mg/seedling	Contents, per cent of dry weight									
		Leaves					Roots				
		N	P	K	Ca	Mg	N	P	K	Ca	Mg
PINE											
1/4	157	2.70	0.26	1.00	0.26	0.14	2.07	0.54	2.27	0.12	0.10
1/2	160	2.88	0.30	1.11	0.26	0.14	2.72	0.70	2.23	0.08	0.10
1	178	2.76	0.23	0.92	0.26	0.13	2.52	0.72	2.12	0.10	0.10
2	162	2.82	0.33	1.22	0.30	0.18	2.79	0.97	2.43	0.13	0.12
4	156	2.82	0.32	1.30	0.32	0.22	2.50	0.89	2.80	0.09	0.09
SPRUCE											
1/4	372	1.85	0.22	0.93	0.20	0.11	1.94	0.39	1.52	0.26	0.09
1/2	429	1.92	0.24	0.85	0.19	0.11	2.92	0.47	1.42	0.24	0.06
1	548	2.12	0.23	0.93	0.19	0.11	2.71	0.41	1.06	0.22	0.08
2	495	2.21	0.23	0.98	0.31	0.16	2.93	0.50	1.62	0.26	0.07
4	440	2.00	0.25	1.25	0.42	0.21	2.97	0.60	1.87	0.34	0.06
BIRCH*											
1/4	455	3.84	0.35	2.67	0.24	0.34	2.80	0.51	3.12	0.04	0.16
1/3	647	3.94	0.42	2.67	0.26	0.34	2.82	0.72	2.60	0.06	0.19
2/3	695	3.91	0.42	2.68	0.35	0.39	2.88	1.04	2.54	0.16	0.13
1	822	3.82	0.36	2.62	0.28	0.42	3.40	0.94	2.34	0.15	0.12
3/2	794	3.93	0.33	2.43	0.23	0.45	3.24	1.04	3.11	0.15	0.13
2	666	4.16	0.45	2.99	0.40	0.47	2.87	2.05	2.62	0.22	0.14
4	515	4.30	0.59	3.42	0.62	0.51	3.00	1.53	4.83	0.13	0.26

* The birch experiment lacks duplicate treatments.

Internal Element Concentrations. The element concentrations in leaves and roots generally vary little with the total salt concentration in the nutrient solutions (Table 13). The strongest effects are found at high supplies in birch. In the leaves the potassium, calcium, and magnesium concentrations are most strongly influenced but in the roots the phosphorus and potassium concentrations.

Evident visual symptoms of deficiency or toxicity have not been noticed within these series.

H. Harvest Time Series

Growth Rate. The varied factors in the harvest time series are described in Table 14. With increasing length of the growth period the average rate of dry matter production for the whole growth period increases as long as

Table 14. The varied factors within the harvest time series

Varied factors	Pine	Spruce	Birch
Length of growth periods, days			
Harvest occasion 1	59	94	49
2	72	122	63
3	94	164	76
4	115	185	91
Supplies, ppm			
Nitrogen, Control	50	50	140
Low N	5	5	14
Potassium, Control	50	50	126
Low K	0.75	0.75	1.26

the experiments have been followed (Figure 24, Table 15). This is especially obvious at control supplies but generally also at low supplies of nitrogen or potassium. At low potassium supply the spruce seedlings were comparatively small on the last harvest occasion, and there is in spruce a general tendency to decreasing growth rate between 164 and 185 days of growth in comparison to the preceding period (Figure 26).

Table 15. Average rates of dry matter production and length of stems and roots after different growth periods

Growth period, days	mg dry matter produced per day and seedling			Length of stems, mm			Length of roots, mm		
	Control	Low N	Low K	Control	Low N	Low K	Control	Low N	Low K
PINE									
59	0.8	0.8	0.5	33	32	20	57	60	50
72	1.1	1.1	0.7	41	38	25	73	80	55
94	1.5	1.4	0.7	55	40	30	90	120	60
115	2.4	1.8	1.0	59	48	44	130	158	72
SPRUCE									
94	1.1	1.1	0.8	87	81	68	63	60	55
122	1.8	1.6	1.1	100	88	74	73	100	60
164	3.7	2.3	1.6	188	113	84	167	265	130
185	4.0	2.5	1.5	184	117	87	193	265	135
BIRCH									
49	1.6	2.1	1.1	98	107	87	48	55	38
63	4.5	4.2	3.4	190	168	138	60	82	45
76	9.6	6.5	4.5	265	225	160	73	90	52
91	14.8	8.8	5.4	341	280	177	78	100	68

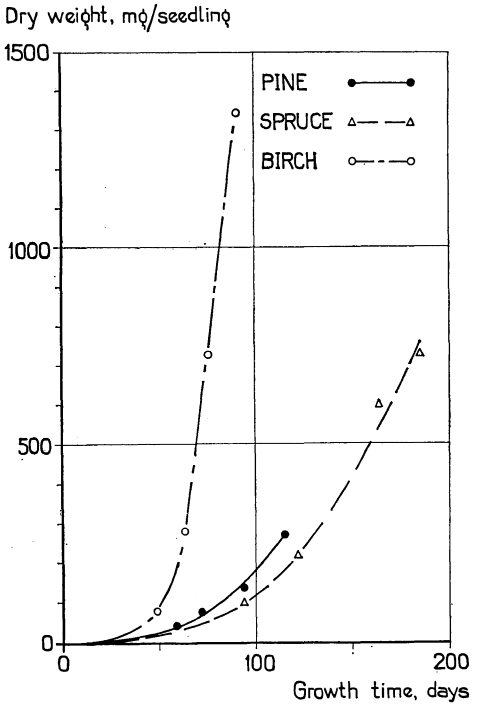


Figure 24. Change of control seedling dry weight with increasing growth time.

The average growth rate for a certain length of the growth period has been much greater for birch than for pine and spruce. At 90—95 days of growth the birch seedlings have a dry weight that is about 10 times greater in the controls than that of pine and spruce (Figure 24, Table 15). The pine seedlings have grown somewhat more rapidly than the spruce seedlings. At low supplies of nitrogen and potassium the differences in growth rates are not so great.

At low nitrogen supply a comparatively good growth is found in all species during the first periods and in birch even a greater growth rate than in the controls during the first 49 days (Table 15). The pine and spruce seedlings treated with low nitrogen supply have up to 94 days grown with about the same growth rate as the control seedlings. The low potassium supply that is at a relatively lower level than the low nitrogen supply has caused growth reductions in all three species already during the first period.

Growth of the Different Seedling Parts. With increasing length of the growth period the dry weights of the different seedling parts do not always increase at the same rate (Figures 25—27). In all three species the leaf fraction of the total dry weight decreases with increasing length of the growth period. The root fraction, on the contrary, increases in pine and

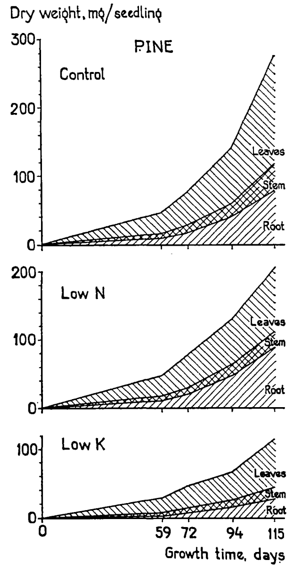


Fig. 25.

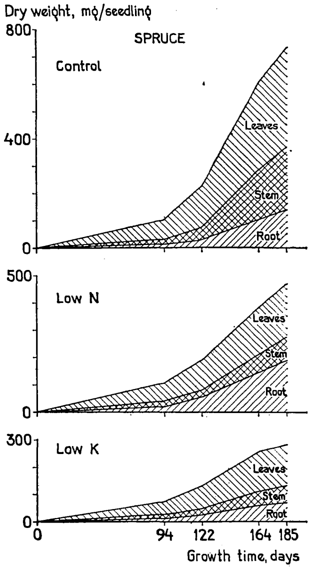


Fig. 26.

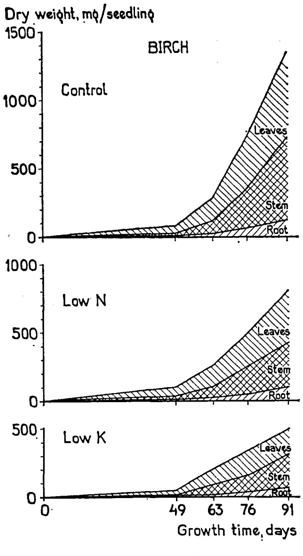


Fig. 27.

Figures 25—27. Dry weight of root, root + stem, and whole seedlings at *varied lengths of growth period* and at control, low nitrogen, and low potassium supply.

spruce, especially at low nitrogen supply, and is nearly constant in birch. The stem fraction increases strongly in birch and also in spruce.

The lengths of the stems and roots increase with the length of the growth period (Table 15) but much less then the corresponding dry weights.

Table 16. Nitrogen and potassium contents in leaves, stems, and roots at various lengths of the growth period

Growth period, days	Nitrogen content, % of dry weight						Potassium content, % of dry weight					
	Control			Low N			Control			Low K		
	Leaves	Stems	Roots	Leaves	Stems	Roots	Leaves	Stems	Roots	Leaves	Stems	Roots
PINE												
59	3.17	2.91	2.68	2.95	2.07	2.39	1.33	1.53	2.37	0.58	0.61	0.68
72	3.12	2.53	2.45	2.52	1.68	1.74	1.27	1.38	2.00	0.48	0.59	0.62
94	3.06	2.42	2.42	1.57	1.37	1.59	1.05	1.14	1.70	0.36	0.44	0.44
115	3.01	2.85	2.69	1.56	1.66	1.35	0.90	0.96	1.37	0.39	0.40	0.44
SPRUCE												
94	2.29	1.98	2.97	1.80	1.38	2.25	1.14	1.35	1.69	0.36	0.43	0.50
122	2.15	1.74	2.56	1.47	1.08	1.63	0.94	1.11	1.53	0.30	0.33	0.38
164	2.22	1.79	2.75	1.12	0.80	1.38	0.86	1.02	1.37	0.26	0.34	0.35
185	2.25	1.47	2.91	1.20	0.81	1.20	0.86	0.77	1.07	0.26	0.24	0.27
BIRCH												
49	4.52.	2.43	3.31	4.16	1.96	3.03	2.13	2.51	3.85	0.94	0.91	0.76
63	4.18	1.75	3.26	3.68	1.40	2.50	2.35	2.07	3.94	0.61	0.30	0.52
76	3.61	1.66	3.03	2.77	1.26	2.23	2.05	1.19	2.58	0.40	0.20	0.40
91	3.42	1.45	3.31	2.42	0.99	1.88	2.04	1.11	2.05	0.32	0.16	0.28

Internal Nutrient Concentrations. With increasing length of the growth period there is a general tendency to decreasing internal nutrient concentrations (Tables 16 and 17). This is especially obvious for nitrogen and potassium in birch at low supplies of these elements (Table 16). In the controls the nitrogen concentrations are little affected in the pine seedlings, whereas the potassium concentration decreases continuously in all three organs. On the whole, the same relations are also found in the control seedlings of spruce, but in birch the nitrogen concentration in the leaves and stems decreases more markedly. The phosphorus, calcium, and magnesium concentrations vary little in the control leaves except for birch where increased calcium concentrations are noticed contrary to the general tendency of decreasing percentages (Table 17).

At low nitrogen supply the nitrogen concentration in the leaves of all three species is in the beginning only somewhat lower than in the controls (Table 16). With increasing length of the growth period the concentration decreases, at first rapidly and then more slowly and becomes in pine and spruce constant or increases somewhat. This tendency is also seen in stems and roots. At low potassium supply the potassium concentration is in all organs essentially lower than in the controls already on the first harvest occasion and

Table 17. Phosphorus, calcium, and magnesium contents as per cent of dry weight in control leaves at various lengths of the growth period

Harvest	Pine			Spruce			Birch		
	P	Ca	Mg	P	Ca	Mg	P	Ca	Mg
1	0.26	0.28	0.21	0.29	0.20	0.13	0.56	0.27	0.50
2	0.24	0.23	0.18	0.25	0.16	0.12	0.46	0.22	0.44
3	0.23	0.27	0.15	0.20	0.19	0.10	0.45	0.29	0.40
4	0.21	0.32	0.20	0.20	0.18	0.13	0.56	0.46	0.44

then generally decreases continuously with increasing length of the growth period.

Deficiency symptoms. The low nitrogen supply has not caused quite characteristic symptoms of nitrogen deficiency more than in spruce on the third and fourth harvest occasions. Also in pine and birch, however, the leaves were on the last two occasions light green. At the low potassium supply, on the other hand, specific symptoms appeared in spruce already on the second harvest occasion and in birch on the third. These symptoms developed with time and were very marked in spruce on the third and fourth occasions and in birch on the fourth occasion. Pine never had symptoms of potassium deficiency. The symptoms that have been observed were of the same type as have been described above for nitrogen and potassium.

Chapter IV. Influences of the Solutions

A. Relations between Nutrient Supply and Dry Matter Production

1. *Optimum Solutions*

The Concentrations of the Optimum Solutions. One of the prerequisite conditions for the investigation was that one element is varied under otherwise optimum or nearly optimum nutrition. One of the first steps, therefore, was to determine suitable growth conditions and optimum solutions adapted for these conditions in preliminary experiments, which led to the growth periods, number of seedlings per vessel, climatic conditions, and control nutrient solutions (see Table 3, p. 17) that have been used in all later experiments. For the dry matter production the control solutions were supposed to contain optimum amounts of all elements. The experiments have shown that the control solutions in fact have produced maximum or nearly maximum seedling dry weight not only in all series with varied element concentration but also in the series with varied total concentration

Table 18. Some seedling characteristics of the controls grown at different occasions

Experimental series	Growth period	Number of days	Dry weight, mg/seedling	Growth rate mg/day	Content in leaves, per cent of dry weight					
					N	P	K	Ca	Mg	S
Pine, N, P, K, Ca, Mg	Aug.—Oct. 1957	97	183	1.9	2.76	0.23	0.92	0.26	0.13	0.28
„ S	June—Sept. 1959	99	157	1.6	3.12	—	1.06	0.32	0.12	0.24
„ Time	Febr.—May 1960	94	141	1.5	3.06	0.23	1.05	0.27	0.15	—
Spruce, N, P, K, Ca, Mg	June—Nov. 1956	160	549	3.4	2.12	0.23	0.92	0.19	0.11	0.18
„ S	July—Dec. 1959	155	358	2.3	2.18	0.28	1.07	0.24	0.13	0.18
„ Time	Jan.—June 1960	164	606	3.7	2.22	0.20	0.86	0.19	0.10	—
Birch, N, P, Ca	Aug.—Oct. 1955	72	867	12.0	3.60	0.39	2.38	0.30	0.34	0.24
„ K	June—Sept. 1960	80	1 149	14.4	3.52	0.48	2.00	0.35	0.40	—
„ Mg	Apr.—June 1954	73	626	8.6	3.82	0.42	2.86	0.30	0.40	—
„ S	Oct.—Dec. 1959	73	636	8.7	3.58	0.40	2.66	0.32	0.36	0.32
„ Time	Apr.—June 1960	76	730	9.6	3.61	0.45	2.05	0.29	0.40	—
„ Total conc.	Febr.—Apr. 1954	72	822	11.4	3.82	0.36	2.62	0.28	0.42	—

and the same proportions between the elements (Figures 6—23 and Table 13). Only in three series did the control seedlings have a lower dry weight than the maximum, namely in the nitrogen series with pine (98 per cent of maximum seedling dry weight), the phosphorus series with spruce (99 per cent), and the potassium series with birch (96 per cent). It may be concluded that the concentrations of the control solutions approach the optimum fairly well and that, consequently, *the effects that are found at varied supply of an element have not been influenced by otherwise extreme macro nutrient supplies.* Yet, it is possible that the most suitable composition of the solution when an element is supplied at a low rate is not the same for the other elements as in the controls. It seems, however, probable that the growth at low supply of an element is determined by this to such a degree that a change of the concentrations of the other elements cannot generally increase the growth but rather decrease it. When it comes to the micro nutrients no effects have been noticed in any of the experiments indicating that extreme micro element concentrations have been present.

Properties of the Control Seedlings on Different Growth Occasions. The experiments have been carried out during the course of several years and the results have been obtained from experiments at different seasons. In Table 18 some data that describe the properties of the control seedlings on different growth occasions are found. It is seen that the seedling dry weights and average growth rates vary within quite wide limits. The element concentrations of the leaves, on the other hand, vary only to a small degree. The greatest variation is found in the potassium concentration of the birch leaves.

There is no variation with the season that is valid in all three species. The age of the seeds does not seem to be decisive more than possibly in pine. Thus, it is not possible to obtain a conclusive causality in the variability, but it is obvious that in birch the high growth rate causes that small variations in, for instance, the length of the lag phase will be important for the final size of the seedlings. The low growth rate of the spruce controls in the sulphur series cannot be explained on this basis, but it is seen that the growth rates are comparatively low also in the sulphur series with pine and birch grown at the same time. It may be concluded that the internal nutrient concentrations have a high degree of reproducibility but that the dry weight of the control seedlings at harvest varies during the course of the investigation. This variation in growth, however, will be of little importance for the conclusions if, within each series, relative growth values are used in the interpretation of the results.

The Time Course of the Relation between Nutrient Supply and Growth. As is seen from the time series a low nitrogen supply produces in the beginning a seedling dry weight that is as great as that obtained with the control supply (Table 15, p. 43). Later on, the growth rate decreases at a low supply in relation to that at a high. Thus, there is a tendency that the concentrations of the optimum solution lie within a lower interval during the early stages than during the later. This change in the optimum concentrations with the growth time is according to, for instance, Rippel (143) of minor importance when the growth cycle is determinated, but in the present investigation it is of decisive importance because the seedlings were harvested when still in rapid growth and because they lack a definitive end stage. This will be further discussed below (p. 71—73).

2. *Sub-Optimum Solutions*

From the element series it is seen that the supplies lower than the control supply have usually produced a lower dry weight than the controls. It is obvious from the time series, however, that this relative growth inhibition is a function of time and that the difference in growth rate between seedlings at low and at control supply increases with time. A similar change as in the optimum concentrations discussed above appears thus also at low supplies, and it may be concluded that *there is a general change in the supply/growth relation with time reflected by an increase in the concentration requirement for maintaining a constant relative growth level.*

3. *Supra-Optimum Solutions*

Growth reductions on account of high supplies have been noticed in most element series and in the series with varied total concentrations. In the phosphorus series with pine and spruce this growth reduction is less than 10 per cent of the highest seedling dry weight and in the spruce series no supra-optimum supplies can be established. As the cause of the growth decreases is not necessarily the high supplies of the *nutrient elements,* it is of importance to discuss the possibility of secondary effects of the high supplies of the salts. A first judgement (see p. 19—20 and Figures 3—5) indicates that secondary effects are generally of low importance for the experimental results but that the conditions at the highest supplies in many cases are critical. In Table 19 some data about the supplies leading to clear growth reductions have been gathered. The values that are critical according to Figures 3—5 are printed in italics and the limit values corresponding to 90 per cent of maximum growth in the diagrams are also given in the table.

Total Salt Concentration. From Figure 3 (p. 20) it is seen that 90—100—90 per cent of maximum growth is reached when the total salt concentration is about 2.5—20 m.eq/litre for pine, 4—17 for spruce, and 14—40 for birch. These concentrations correspond to osmotic pressures of about the following magnitudes: 0.1—0.7 atmospheres for pine, 0.2—0.6 for spruce, and 0.5—1.5 for birch. It is obvious according to the conclusions about the supply/growth relation above (p. 50) that these values are valid only under the conditions of the present experiments and not values of a wider physiological meaning. It is also remarkable that the growth rate of the birch seedlings in flowing water cultures (see p. 17—19, Table 4) is essentially higher than in the main experiments in spite of a concentration in the solutions of only about ¼ of that in the controls. *The osmotic pressures and salt concentrations that have produced maximum growth in the experiments are, therefore, not optimum in themselves but the optimum factor is the nutrient supply that corresponds to these salt concentrations.* It is here, as in many earlier reported experiments, probable that the seedlings have a wide range in their adaptation to the salt concentrations if the nutrient supply is held within adequate limits. However, the question is whether high salt concentrations may be of importance for the growth reductions at high supplies within the present experiments.

Hoagland (62) found that 0.32—0.85 atmospheres produced the highest growth of barley in water cultures. In sand cultures the values were on the average higher (0.48—1.45 atmospheres). In most plants 2—2.5 atmospheres have been regarded as the upper limit for good growth (*cf.* 62, 63, 89). In sand cultures Wadleigh *et al.* (189) found 0.5 atmospheres as optimum for maize and similar results were obtained by Hayward and Spur (55) for flax in sand cultures and Gauch and Wadleigh (47) for beans in water cultures. However, many reports about good growth at high osmotic pressures are also found in the literature, for instance, Reed and Haas (139) for Citrus species in sand cultures (optimum about 1.2 atmospheres) and Hayward and Long (53, 54) for tomato (1.5 atmospheres better than 0.5) and peach (good growth up to about 2 atmospheres) in sand cultures. High optimum values are also reported by, for instance, Tottingham (187), Shive (149, 150) and McCall (102).

In the present investigation comparatively high salt concentrations and osmotic pressures have been present in some cases within the element series (Table 19). In all three species this is found at the highest sulphur supply but in pine also at the highest nitrogen and calcium supply, in spruce at the highest calcium supply, and in birch at the highest potassium supply. *In these cases, therefore, it cannot be excluded that high total salt concentrations may be of importance for the growth reductions.*

Sodium. In the present investigation certain nutrient elements have been varied as sodium salts, namely phosphorus and sulphur, and in some cases high sodium concentrations have been present in the solutions (Table 19).

Table 19. Data about the supra optimum nutrient solutions and the corresponding relative seedling dry weights (per cent of maximum) and percentages of respective macro elements in the leaves (per cent of dry weight). The upper limit values found in Figures 3—5 corresponding to 90 per cent of maximum seedling dry weight are also given. Values critical as supra-optimum are in italics

Element	Concentration in nutrient solution				Element percentage in leaves	Relative growth
	Element, ppm	Total salt, m.eq./litre	Na, ppm	Cl, ppm		
PINE						
Limit values		20	220	550		
Nitrogen	450	*21*	15	116	3.0	77
Phosphorus	60	8	45	116	0.30	95
	180	12	134	116	0.34	92
Potassium	450	17	15	479	1.91	84
Calcium	120	10	0	235	0.41	78
	360	*22*	0	*660*	0.82	93
Magnesium	150	19	29	540	0.18	90
Sulphur	600	*44*	*869*	138	0.44	74
SPRUCE						
Limit values		17	90	300		
Nitrogen	150	10	7	116	2.3	95
	300	16	7	116	2.4	90
Potassium	150	9	7	207	1.1	89
	300	13	7	*343*	1.3	82
Calcium	120	10	0	247	0.50	95
	360	*22*	0	*672*	0.99	72
Magnesium	45	10	29	239	0.20	82
Sulphur	60	10	87	150	0.15	81
	600	*44*	*869*	150	0.30	62
BIRCH						
Limit values		40	140	900		
Nitrogen	280	28	74	370	4.2	86
	560	38	74	370	4.7	82
Phosphorus	200	26	*149*	370	0.62	61
	400	32	*297*	370	0.91	60
Potassium	1 000	*44*	74	*1 126*	3.4	87
Calcium	240	26	0	463	0.75	83
Magnesium	144	32	92	685	0.52	84
Sulphur	192	32	*276*	402	0.38	54
	640	*60*	*920*	402	1.5	47

In the pine and spruce experiments the sodium concentrations may be regarded as critical only in connection with the highest sulphur supply (Figure 4, p. 20) when the total salt concentration is high too. In birch the sodium concentration appears to be high at the two highest supplies in the phosphorus as well as the sulphur series. In none of these cases are the internal concentrations of other nutrient elements influenced to any considerable degree (Table 8, p. 29, and Table 12, p. 39). Nor have earlier experiments shown that sodium has strong antagonistic effects (26). Magistad *et al.* (97) found in their material that the sodium concentration was not the main factor but that the high osmotic pressure caused injuries to the plants. Hoagland and Snyder (64), on the other hand, found that sodium concentrations of more than 100 ppm led to injuries of strawberry in water cultures. The limit values found here (Table 19) are with the exception of spruce essentially higher than this value. Injuries by high sodium levels have also been reported by, for instance, Jones *et al.* (75) and Martin and Jones (100). Evident growth reductions are not found in the present experiments when the sodium concentration in the solution is lower than 220 ppm in pine, 140 ppm in birch, and 90 ppm in spruce (Table 19). These limit values cannot, however, be settled as limits for sodium effects but may depend on other factors. *It seems not unlikely, on the other hand, that the high sodium concentrations at the highest sulphur supply may be of importance for the growth reductions noticed in all three species and in birch possibly also at the highest phosphorus supply and the next highest sulphur supply.*

Chlorine. High chlorine concentrations are present in some treatments when the nutrient elements are supplied as chlorides, namely at the highest calcium supply in pine, the highest potassium and calcium supplies in spruce, and the highest potassium supply in birch (Table 19). Toxic effects of high chlorine concentrations in the nutrient medium have often been reported (23) and conifer seedlings have been regarded as sensitive to chlorine-containing fertilizers (74, 119, 122, 129). *The very high chlorine concentrations in the nutrient solutions in the mentioned cases cannot be excluded as an important factor for the growth reductions.*

Nitrate. In the nitrogen series growth reductions are found in all three species at high supplies and the spruce and especially the pine seedlings showed symptoms of toxic effects. Critical total salt concentrations are present only at the highest supply in the pine series and high sodium or chlorine concentrations are not actual in these cases. The total salt concentration, however, is not extremely high in the pine series and has probably not caused the toxic effects.

In the experiments with flowing water cultures (p. 17—19) the birch seedlings have grown better with ammonium than with nitrate nitrogen. Similar results have been recorded in forest nurseries with spruce (*cf.* 72) and this has later been confirmed for spruce as well as pine in several not yet published experiments. Many workers have reported data that agree with these observations (123, 124). Swan (161) found in Pinus banksiana grown in sand cultures very great differences in growth between ammonium and nitrate fertilized seedlings and intermediate growth when both sources were used. Tendencies in the same direction were also noticed in Picea and Tsuga species. These results indicate that the toxic effects noticed here may depend on high nitrate concentrations in the solutions and that the pine seedlings may be especially sensitive to nitrate.

To test whether nitrate is accumulated in the tissues at high nitrogen supplies and whether this may be the cause of the toxic effects, a qualitative analysis (diphenyl amine) was carried out on the leaf and root samples. If a strong colour change was noticed also a quantitative estimation of the nitrate amount was made (reduction with Dewarda's metal and determination as ammonia). Such estimations were motivated in only a few cases, namely in birch leaves at the two highest supplies (0.10 and 0.22 per cent nitrogen of the dry weight as nitrate), in the birch roots at the three highest supplies (0.05, 0.10, and 0.22 per cent), and in the spruce roots at the two highest supplies (0.04 and 0.08 per cent). In pine no nitrate amounts were recorded. The results are not fully conclusive since the analyses were carried out with dried materials. The greatest toxicity, however, was noticed in pine and, therefore, there is nothing that indicates that an internal accumulation of nitrate has caused the toxicity.

At present no conclusive data have been presented that makes it possible to decide the reasons for the differences in the ammonium and nitrate effects or for the toxic effects noticed here. The internal nitrogen concentrations are not extremely high (Table 19, Figures 6—8, p. 24) and essentially higher values have often been reported in healthy seedlings with good growth. Many factors may be of importance (*cf.* 157) and further experiments are needed to reveal the causality. However, it is possible to state that *high nitrate concentrations in the nutrient solutions have probably caused growth reductions and toxic symptoms in the present experiments.*

Nutrient Concentrations in the Leaves. So far, the possibilities of secondary effects of the nutrient salts have been discussed. The uptake and internal concentrations of the nutrient elements themselves may, of course, also be of decisive importance for the growth reductions at high supplies. It is seen from Table 19 that high internal nutrient concentrations are reached in many cases. The sensitivity of the seedlings to high internal nutrient concentrations is not known, but it seems possible to arrive at certain conclusions by comparisons with data from the literature.

In the nitrogen series the growth reductions correspond to rather moderate percentages of nitrogen in the leaves. Mitchell (111) found for Pinus strobus 3.5 + per cent in the shoots as toxic and this value is confirmed by, for instance, Bensend (10) and Fowells and Krauss (43) for some other pine species. In spruce very good growth has been recorded at nitrogen contents in current leaves of nursery seedlings above 2.5 per cent of the dry weight (*cf.* 72). From the flowing water cultures with birch seedlings it is seen that very good growth is produced at contents up to 4.8 per cent nitrogen in the leaves when ammonium sulphate is used as the nitrogen source (Table 4, p. 18). There are, thus, no reasons to believe that high internal nitrogen concentrations cause the growth reductions at high supplies in the nitrogen series.

At high phosphorus supplies neither the growth reduction nor the internal phosphorus content reach high values in the pine and spruce seedlings. In birch, however, the growth reduction is quite remarkable at the two highest supplies, but the phosphorus contents in the leaves are not very high when compared with values given by Tamm (176) from a phosphorus-potassium poor area supplied with a high amount of a phosphorus fertilizer (0.55—1.14 per cent phosphorus in the birch leaves). Yet, in Tamm's material a small growth reduction was in fact recorded in connection with the highest phosphorus contents in the birch leaves. At the same time, however, the potassium deficiency symptoms were stronger, indicating a secondarily caused greater potassium deficiency on the phosphorus fertilization. It seems probable that in the present study high internal phosphorus concentrations have not caused the growth reductions, at least not alone.

The growth reductions at high potassium supplies are connected with high potassium contents at least in pine and especially in birch. The highest contents recorded by Tamm (175) in current leaves of pine is about 1 per cent and of spruce about 1.2 per cent (Appendix II) and the highest value in birch leaves is about 1 per cent (Table VI; see also Tamm, 172, 176). Swan (161) found no growth reductions in Picea glauca and P. mariana at contents in the shoots up to 1.6—1.7 per cent potassium. The highest values found by Swan for Pinus banksiana is 1.2 per cent. Thus, it is possible that the growth reductions found at high potassium supplies in the pine and birch series are caused to a great extent by a high potassium uptake. This does not seem probable in the case of spruce.

Increasing and high calcium supplies certainly cause a rapid increase in the internal calcium concentrations (Figures 15—17, p. 34) but the highest values recorded (Table 19) are not very high in relation to what are common levels in the field (*cf.* 67, 70, 71, 169, 172, 174, 175, 176). Chapman (30) found in sand cultures that Pinus echinata seedlings cannot survive in culture media having a soluble-calcium content of approximately 500 ppm or more. Chapman's nutrient solutions, however, seem to have had quite high total salt concentrations and the seedlings were not analyzed. The cause of the calcium effects, therefore, cannot be revealed in this case. It is possible that the seedlings are sensitive to high internal calcium concentrations when grown in cultures, but it does not seem probable that this is the whole reason for the toxic effects in the present experiments.

When it comes to magnesium and sulphur, available and conclusive data for forest tree species are almost lacking for comparisons. It seems, however, usually not very probable that the internal concentrations of these elements are decisive for the growth reductions at high supplies, possibly with exception for the highest sulphur supply in the birch series (Table 19).

Conclusions. It is seen that generally it is not possible to determine the cause of the growth reductions at high supplies. By the elimination of different possibilities it seems probable that secondary effects of the nutrient salts at high supplies are of great importance and it cannot be claimed with certainty that high internal concentrations of the nutrient elements are of greater importance. On the other hand, it must be remembered that there is a general tendency to decreasing internal concentrations with time in the experiments (Tables 16 and 17, p. 46 and 47) and the internal concentrations may have been higher and possibly toxic during the earlier stages. This trend, however, is also valid for other factors. Further more, the presence of two or more values near the critical level of the discussed factors may be of greater importance than each of the factors alone. The growth reductions may also be caused by an unsuitable balance between the nutrients within the seedlings or in the nutrient solutions when some factor is close to a critical value. It may, in any case, be concluded that *the effects of high supplies must be interpreted with great caution and definite supra-optimum internal element concentrations cannot be determined in the material.* Yet, the internal percentages may be regarded to reflect the supra-optimum conditions of the solutions.

B. Relations between Supply and Uptake of the Varied Elements

When investigating the importance of the nutrition for the development and reactions of plants the study of the nutrient uptake is fundamental. The purpose here is not to illustrate the uptake mechanisms but to attempt to answer some questions, concerning the influence of the nutrient solutions on the nutrient uptake, which are of importance for the understanding and interpretation of the results and which motivate a thorough discussion even if many conclusions will seem quite self-evident.

During the first weeks solutions with lower concentrations have been used because the seedlings were injured by higher concentrations. At the same time the varied element was excluded except in the controls. It is obvious, however, that the growth rate also in the controls was very low during these weeks and that the nutrient uptake within this period may be neglected without greater approximations. In the following the nutrient supplies are calculated from the third week for pine and birch and from the fourth for spruce.

Usually the nutrient supply from the seeds is very low in relation to the total nutrient uptake and may be neglected. In the case of birch the seeds are very small and contain no considerable amount of nutrients. At the lowest supplies the total nutrient content in the pine and spruce seedlings is, however, often of the same magnitude as the seed content (Table 1, p. 13), and this will, therefore, be of great importance for the estimation of nutrient amounts absorbed from the solutions. Therefore, in Tables 20—25 the nutrient amounts of the seeds have, as far as they can be calculated, been subtracted from the content of the seedlings under the assumption that the seed nutrients have been fully utilized by the seedlings.

In some cases it has not been possible to analyze all parts of the seedlings, because the samples have been too small or because the analysis has failed without the possibility of repeating it. These cases are very few. In the sulphur series the stems have not been analyzed. The control stems have been utilized for other analyses than sulphur and in other cases the stems are too small for analyses. Therefore, the time-consuming sulphur analyses were not considered motivated in the cases where such could be carried out on stems.

1. The Time Course of the Nutrient Uptake

In Table 20 the uptake in the experiments with varied length of the growth period is shown together with the concentration of the solution, the total amount supplied, and the degree of utilization of the supply (amount element taken up as per cent of amount element supplied per vessel). The utilization per cent is given both as averages for the different whole growth periods and as averages between the first and last harvest.

It is seen from Table 20 that the nutrient absorption increases very rapidly in the control seedlings with increasing length of the growth period and that the uptake is accelerated with time except for the spruce seedlings during the period 164—185 days. At low supplies of nitrogen or potassium the uptake of respective element increases too, but less markedly than in the controls. In the case of nitrogen the seedlings have taken up nearly as much at low supply as at control supply until the first harvest occasion, but on

Table 20. Nitrogen and potassium uptake after varyingly long growth periods and at control and low supplies of the elements. The utilization of the supply (uptake per vessel as per cent of supply per vessel) is given both as an average for the whole growth period and as averages for the periods between the first and the fourth harvest occasions. The nutrient amounts in the seeds are subtracted from the uptake values

Growth time, days	Nitrogen						Potassium					
	Supply		Uptake, mg per		Utilization, per cent		Supply		Uptake, mg per		Utilization, per cent	
	ppm	mg/vessel	Vessel	Seedling			ppm	mg/vessel	Vessel	Seedling		
PINE												
59	50	175	10.5	1.2	6	28	50	175	6.1	0.7	3	9
72	50	225	18.0	2.0	8		50	225	9.8	1.1	4	
94	50	300	33.3	3.7	11		50	300	15.5	1.8	5	
115	50	375	69.7	7.8	19		50	375	25.6	2.9	7	
59	5	17.5	9.4	1.1	54	80	0.75	2.6	1.3	0.14	50	87
72	5	22.5	13.8	1.6	61		0.75	3.4	2.0	0.22	59	
94	5	30.0	16.2	1.8	54		0.75	4.5	2.1	0.23	47	
115	5	37.5	25.3	2.8	67		0.75	5.6	3.9	0.43	70	
SPRUCE												
94	50	275	20.4	2.2	7	34	50	275	11.5	1.3	4	14
122	50	375	41.9	4.6	11		50	375	21.2	2.4	6	
164	50	525	117.7	13.0	22		50	525	53.9	6.0	10	
185	50	600	139.5	15.5	23		50	600	57.3	6.4	10	
94	5	27.5	15.9	1.7	58	93	0.75	4.1	2.3	0.26	56	82
122	5	37.5	23.4	2.6	62		0.75	5.6	3.4	0.38	61	
164	5	52.5	38.8	4.3	74		0.75	7.9	5.5	0.62	70	
185	5	60.0	46.3	5.1	77		0.75	9.0	6.3	0.70	70	
BIRCH												
49	140	350	12.2	3.0	3	23	126	315	7.5	1.9	2	21
63	140	490	34.2	9.3	7		126	441	24.7	6.7	6	
76	140	630	81.8	20.4	13		126	567	51.5	12.9	9	
91	140	770	136.2	34.0	18		126	693	87.6	21.9	13	
49	14	35	14.4	3.6	41	102	1.3	3.2	2.0	0.5	62	86
63	14	49	30.3	7.6	62		1.3	4.4	4.2	1.0	95	
76	14	63	41.6	10.4	66		1.3	5.7	4.6	1.2	81	
91	14	77	57.1	14.3	74		1.3	6.9	5.2	1.3	75	

the fourth occasion they have only about one third of the control content. The potassium uptake is already on the first occasion essentially lower at low supplies than in the controls. On the fourth occasion the difference is somewhat greater in pine and spruce and much greater in birch.

It may be concluded that *a low, but not extremely low, nitrogen supply means a low nitrogen uptake in relation to the uptake at a higher supply* *first after a rather long period and then the difference increases with time. A comparatively lower potassium supply means a more rapid decrease in the potassium uptake in relation to the uptake at control supply.*

These relations are connected with the utilization of the supply (Table 20). During the first growth period about 5 per cent of the control nitrogen supply has been utilized. During the subsequent periods the utilization per cent increases to about 25—35 per cent. At low nitrogen supply an essentially higher fraction has been absorbed already from the beginning (about 40—60 per cent) and it increases then to about 80—100 per cent between the first and fourth harvest occasion. Thus, it is seen that *the seedlings for a time have been able to maintain nearly as high a nitrogen uptake at low supply as at high by utilizing a greater fraction of the supplied amount.* Also the dry matter production is about the same in the two cases in the beginning (Table 15, p. 43). *When the degree of utilization of the nitrogen supply exceeds about 60 per cent the uptake and dry matter production, however, is clearly influenced* (Tables 20 and 15).

The degree of potassium utilization at low supply is in all three species about the same as that found for nitrogen. Since the low potassium supply is lower than the low nitrogen supply absolutely as well as in relation to the control supplies the potassium absorption will be lower already from the beginning as is the dry matter production (Table 15, p. 43). In the controls the pine and spruce seedlings utilize the potassium supply to a lesser degree than the nitrogen supply, especially during the later periods, and, consequently, the potassium uptake will be comparatively lower. This is less marked in birch but since, contrary to what is the case in the pine and spruce series, the control supply of potassium is lower than that of nitrogen the potassium uptake is lower than the nitrogen uptake also in birch. Because a utilization of potassium to 50—60 per cent has led to a greater decrease in uptake and dry matter production than the corresponding utilization of nitrogen and because potassium on the whole is less utilized than nitrogen in the controls it seems as if *potassium cannot be utilized to the same degree as nitrogen with unaffected uptake and growth rate.* It is to be remembered, however, that nitrogen is supplied as both positive and negative ions. However, it has long been the opinion that different elements and salts are utilized to a varying degree by plants (*cf.* 93, 144).

2. *Rate of Uptake*

From the harvest time series certain data about the uptake rate of nitrogen and potassium may be obtained. In Table 21 both the absolute uptake rate per day and seedling and the uptake rate in relation to the average seedling

Table 21. **Rates of nitrogen and potassium uptake and these rates in relation to the average seedling dry weight for respective periods at different stages of seedling development and at control and low supply of nitrogen and potassium. The average rates between the first and fourth harvest occasions are also given. The nutrient amounts in the seeds are subtracted from the uptake values**

Growth period, days	Uptake rate, µg per day and seedling								Uptake rate per mg seedling dry weight							
	Nitrogen				Potassium				Nitrogen				Potassium			
	Control		Low N		Control		Low K		Control		Low N		Control		Low K	
PINE																
0—59	20		19		12		2.4		0.87		0.79		0.52		0.14	
59—72	62	111	38	32	31	38	6.2	5.4	1.00	0.88	0.59	0.32	0.50	0.35	0.16	0.12
72—94	77		9		32		0.5		0.71		0.09		0.29		0.09	
94—115	195		48		52		9.5		0.94		0.28		0.25		0.10	
SPRUCE																
0—94	23		18		14		2.8		0.44		0.34		0.26		0.074	
94—122	86	135	32	37	39	48	4.3	4.6	0.52	0.39	0.22	0.15	0.24	0.16	0.041	0.028
122—164	200		40		86		5.7		0.48		0.14		0.21		0.029	
164—185	119		38		19		3.8		0.18		0.09		0.03		0.014	
BIRCH																
0—49	61		73		39		10		1.54		1.40		0.99		0.36	
49—63	450	737	286	254	343	473	36	19	2.49	1.68	1.54	0.84	1.90	1.14	0.267	0.11
63—76	854		215		477		15		1.69		0.57		0.94		0.054	
76—91	907		260		600		7		0.87		0.40		0.58		0.017	

dry weight for the various periods are given. It is obvious that the differences between the uptake values on two subsequent harvest occasions may contain the sum of the experimental errors and give an incorrect picture of the true relations. Therefore, the average values corresponding to the three latest periods (between the first and fourth harvest occasions) are also given in the table.

At control supply the uptake rate increases very rapidly with time for nitrogen as well as potassium in all three species. This, however, is not valid for spruce during the last growth period. It is not probable that the decrease in uptake rate after about 160 days depends solely on experimental errors because it appears in all treatments. Further more, the uptake rate of nitrogen in relation to the dry weight of the control seedlings is practically constant during the first three periods, just as in pine, whereafter it decreases to a very low value. It seems, therefore, as if the spruce seedlings after about 160 days reach a stage under the present growth conditions when the general activity decreases. The primary reason does not seem to be the decrease in uptake rate since the nutrient status of the seedlings is not influenced during the period (Tables 16 and 17, p. 46 and 47). A similar rhythmic decrease in activity may also be of importance for the pine seedlings during the period 72—94 days, when a comparatively low uptake rate is seen for nitrogen as well as potassium at low supplies.

The uptake rate in relation to the seedling dry weight is changed only to a small degree with time in the controls if the first period is compared with the three later ones. For potassium a clear decrease, however, is seen in pine and spruce. At low nitrogen or potassium supplies the uptake rate decreases with time. In the birch seedlings it is found that the uptake rate in relation to the seedling dry weight reaches a maximum in the controls during the period 49—63 days. This tendency is also found at low nitrogen supply. This does not seem to be a question of a decrease in activity after 63 days similar to that recorded in spruce after 160 days, because the growth rate in birch increases all the time (Figure 24, p. 44). The relation may depend on either the fact that the supplied amount of nutrients is increasingly unsufficient or that the uptake capacity of the seedlings in relation to their dry weight decreases. It is seen from Table 20 that the nutrient solutions are never utilized to a very high degree in the controls and the internal concentrations of the other elements are not changed with time in such a way that they may be regarded as inhibitory (Table 17, p. 47). Thus, it seems as if the uptake capacity of the birch seedlings does not increase at the same pace as their dry weight what probably mainly depends on an increasing dry matter deposition in the stems.

When it comes to potassium all three species show with increasing growth time a decreasing uptake rate in relation to the seedling dry weight in the controls. Similar observations have been made on other species. Thus, for instance, Lundegårdh (93) and Burström (27) found that potassium in wheat seedlings was absorbed to a greater extent during the earlier stages of development than during the later ones. Burström (26, 27) reported in oats, however, a constant potassium uptake during the whole development and maintains that it is a question of specific differences between the two species.

It is seen that *the uptake rate of nitrogen and potassium practically throughout increases with time and that this depends mainly on the increasing seedling size and not on an increased uptake capacity per dry weight unit.* Instead the uptake capacity of potassium decreases with time, at least in pine and spruce.

At low supply the uptake rate in relation to seedling dry weight decreases on the whole continuously for both nitrogen and potassium. This depends undoubtedly on an insufficient supply of the elements rather than on a decreasing uptake capacity of the seedlings.

Table 22. Element uptake and utilization of supply (upptake per vessel as per cent of supply per vessel) at varied supply of the elements. The nutrient amounts supplied by the seeds are subtracted from the uptake values

Element	PINE					SPRUCE					BIRCH				
	Supply		Uptake, mg per		Utiliz., per cent	Supply		Uptake, mg per		Utiliz., per cent	Supply		Uptake, mg per		Utiliz., per cent
	ppm	mg/vessel	Vessel	Seedling		ppm	mg/vessel	Vessel	Seedling		ppm	mg/vessel	Vessel	Seedling	
N	0.05	0.30	0.50	0.04	100	0.5	5.0	6.1	0.68	100	4.2	18.9	9.0	2.25	48
	0.5	3.0	3.1	0.25	100	5.0	50	29	3.21	58	28	126	59	14.8	47
	5.0	30	22	1.87	73	15	150	74	8.27	49	140	630	98	24.6	16
	50	300	58	4.67	19	50	500	104	11.5	21	280	1 260	110	27.4	9
	150	900	64	5.09	7	150	1 500	109	12.1	7	560	2 520	107	26.8	4
	450	2 700	35	4.41	1	300	3 000	109	12.8	4					
P	0.02	0.12	0.03	0.002	25	0.1	1.0	0.51	0.056	51	1.0	4.5	2.8	0.71	62
	0.2	1.2	1.2	0.10	100	1.0	10	6.3	0.74	63	3.0	13.5	7.0	1.8	52
	2.0	12	5.8	0.45	48	3.0	30	13	1.5	43	100	450	16	3.9	4
	20	120	8.5	0.68	7	10	100	14	1.5	14	200	900	14	3.5	12
	60	360	7.9	0.76	2	30	300	16	1.8	5	400	1 800	19	4.9	1
	180	1 080	10.5	0.87	1	60	600	18	2.0	3					
K	0.05	0.30	0.24*	0.02*	> 80	0.15	1.5	1.7	0.22	100	0.3	1.5	1.1	0.24	73
	0.5	3.0	2.8	0.24	93	1.5	15	11	1.2	73	3.0	15	9.3	2.6	62
	5.0	30	24	2.0	60	15	150	37	4.1	25	30	150	61	15	41
	50	300	30	2.4	10	50	500	46	5.1	9	126	570	79	20	14
	150	900	31	2.8	3	150	1 500	50	5.5	3	300	1 500	75	21	5
	450	2 700	37	3.4	1	300	3 000	54	6.0	2	1 000	5 000	85	34	2
Ca	0.004	0.024	0.46	0.04	100	0.12	1.2	0.60	0.07	50	0.4	1.8	0.08	0.02	4
	0.12	0.72	1.0	0.08	100	1.2	12	1.1	0.12	9	1.2	5.4	1.2	0.30	22
	4.0	24	3.8	0.30	16	12	120	5.3	0.59	4	12	54	3.0	0.75	6
	40	240	4.9	0.39	2	40	400	9.3	1.0	2	120	540	9.2	2.3	2
	120	720	5.8	0.50	0.8	120	1 200	18	2.0	1.5	240	1 030	20	4.9	2
	360	2 160	4.5**	0.74**	> 0.2	360	3 600	24	3.0	0.7					
Mg	0.015	0.09	0.19	0.01	100	0.05	0.5	0.20	0.02	40	0.5	2.2	0.18	0.06	8
	0.15	0.90	0.8	0.06	89	0.15	1.5	0.67	0.07	45	4.8	22	3.4	0.86	15
	1.5	9.0	1.4	0.14	16	1.5	15	2.7	0.31	18	48	216	6.2	1.6	3
	15	90	2.9	0.23	3	15	150	5.7	0.62	4	144	648	7.7	1.9	1
	150	900	3.6	0.30	0.4	45	450	7.9	0.87	2					
S**	0	0	0.09	0.01	—	0	0	0.26	0.02	—	0	0	0.12	0.02	—
	0.2	1.2	0.63	0.07	52	0.2	2.0	1.9	0.21	95	0.64	2.9	1.4	0.34	48
	2.0	12	2.3	0.26	19	2.0	20	3.3	0.41	16	6.4	29	4.6	1.1	16
	20	120	2.7	0.30	2	20	200	4.9	0.54	2	64	290	5.1	1.3	2
	60	360	2.5	0.28	0.7	60	600	3.4	0.38	0.6	192	860	3.6	0.9	0.4
	600	3 600	4.1	0.46	0.1	600	6 000	5.0	0.55	0.1	640	2 900	12	2.9	0.4

* Content of shoots, roots not analyzed.

** Content of leaves + roots, stems not analyzed.

3. *Uptake at Varied Supply of the Elements*

In Table 22 the element uptake per vessel, per seedling, and the degree of the supply utilization are put in relation to the element supply in the series with varied element concentrations. With increasing supply the element uptake increases very rapidly within the sub-optimum range and then more and more slowly (see also Figures 28—30). Only in exceptional cases does the uptake decrease with increasing supply. In the nitrogen series with pine it is found that the seedlings have taken up less nitrogen at the highest than at the next highest supply (Table 22). This coincides with a low seedling dry weight and the appearance of toxicity symptoms. Also in the nitrogen series with birch a decrease in uptake is found between the two highest supplies but the decrease is less than in pine.

A marked decrease in the sulphur uptake with increasing supply is found in the sulphur series of all three species in the passage from optimum to supra-optimum supplies (Figures 28—30, Table 22). A similar tendency is also seen in the phosphorus series with birch. Thus, the uptake is relatively low at the next highest supply in these cases. This decrease coincides with a decrease of the seedling dry weight which, however, is less in pine than in the two other species. Also the internal sulphur concentration decreases in pine leaves and spruce leaves and roots (Figures 21—23, p. 40). In birch the decrease in uptake corresponds only to a decrease in dry weight (Figures 11 and 23, p. 28 and 40), but this dry weight decrease is great in both the sulphur and phosphorus series. At a further increase in supply the dry weight reaches low values in all three species, whereas the internal sulphur concentration increases so rapidly that the uptake reaches the highest value within the series. It is probable that this course of the supply/uptake relation is a question of toxic effects (*cf.* p. 50—56).

The increase in uptake is generally not proportional to the increase in supply. The utilization of the supply is essentially higher at low than at high supplies (Table 22). In many cases of the lowest supplies the total element content of the seedlings even exceeds the total amount given, in spite of the fact that the seed nutrient amounts are subtracted from the seedling content. The degree of utilization is then put equal to 100 in Table 22, since a greater utilization is impossible. The reason for the discrepancy may be impurities from the vessels, salts, or water but also errors in the analytical values or in the supplied amounts. The absolute values of the amounts of the elements are very small and an exact agreement between supply and uptake is hardly to be expected. It is also possible that nitrogen and sulphur are supplied by the air both through the solutions and roots and directly through the leaves (*cf.* 178). Nevertheless, it seems probable that the utilization of the low supplies often is very high and that it approaches 100 per cent of several elements. At the highest supplies the solutions are utilized to a very small extent by the seedlings and values of one per cent and lower are found in many cases (Table 22). This is not surprising since the growth of the seedlings is then often strongly reduced.

The different elements are utilized to a comparatively small degree at control supply. It is generally not possible to arrange the elements in a certain series of utilization of the optimum solutions, because there is a change with time in nutrient uptake, growth, as well as utilization. This makes a true estimation of the utilization/growth relations within the element series difficult. Certain very clear results may, however, be recognized. Thus, it is seen that the pine seedlings have grown very well at calcium supplies down to 0.12 ppm (Figure 15, p. 34) and at both high and low calcium utilization (Table 22) which is not the case with the spruce and birch seedlings. Good growth, on the other hand, is exclusively connected with a comparatively low utilization of magnesium and sulphur, but it must be remembered that the sulphur uptake is represented only by the content in leaves + roots.

At the same concentration of the elements in the nutrient solutions the elements are utilized to a decreasing degree according to the following series obtained from supply/utilization diagrams:

Pine: $N > K > P > Ca > Mg$

Spruce, birch: $N > K > P > Mg > Ca$

Sulphur cannot be included in these series since the total uptake is not determined. The degree of sulphur utilization, however, seems to be somewhat lower but of the same magnitude as of phosphorus.

It is seen that *the different elements are utilized to different degrees either when compared at the same (maximum) growth or at the same supply. It is also found that a higher supply is usually utilized to a lesser degree than a lower.* Within the deficiency range, however, tendencies are often found, especially in birch, to a low degree of utilization at the lowest supplies. The cause of this effect is probably in most cases a low utilization in the early stages and possibly a prolonged lag phase at very low supplies. In the case of birch the small seeds may account for a slow start when the supply is very low. In certain cases it is also possible that the deficiency leads to effects that obstruct the uptake. Thus, the roots are strongly affected in their tip growth in calcium deficiency, especially in birch, and here too the most marked example of a low utilization of a low supply is found (Table 22).

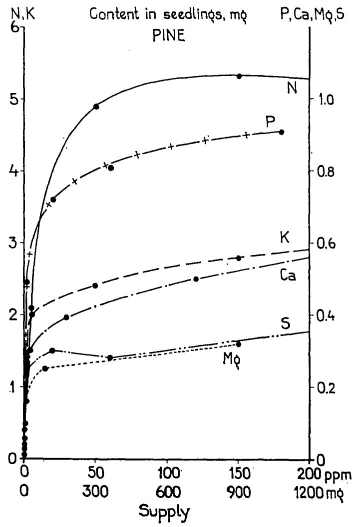


Fig. 28.

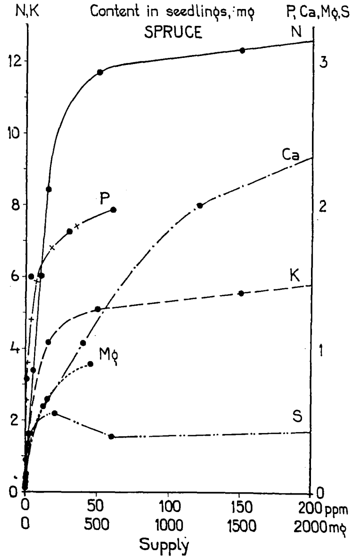


Fig. 29.

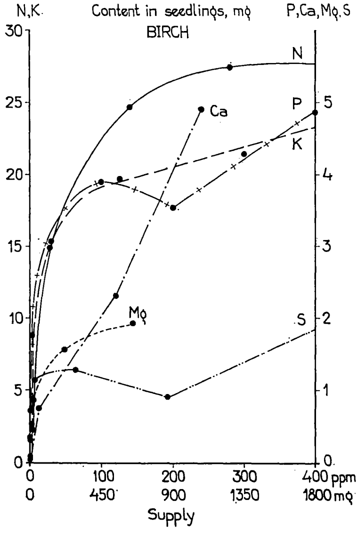


Fig. 30.

Figures 28—30. Nutrient contents (mg per seedling) at varied supply expressed as concentration (ppm) and as total supply (mg per vessel). The sulphur content refers to leaves + roots only.

Table 23. Element uptake in leaves + roots and utilization of supply for this uptake (uptake per vessel as per cent of supply per vessel) at varied concentration but constant proportions between the elements in the solutions. The control concentrations are put equal to 1

Relative concentration	Supply, mg per vessel					Uptake, mg per vessel					Uptake, mg per seedling					Utilization, per cent				
	N	P	K	Ca	Mg	N	P	K	Ca	Mg	N	P	K	Ca	Mg	N	P	K	Ca	Mg
PINE																				
1/4	75	30	75	60	22	38.0	5.6	32.6	3.2	1.9	3.3	0.49	2.0	0.28	0.17	51	19	43	5.3	8.4
1/2	150	60	150	120	45	50.1	7.5	25.8	3.6	2.3	3.8	0.57	2.0	0.27	0.17	30	13	17	3.0	5.1
1	300	120	300	240	90	51.8	7.5	25.2	4.0	2.3	4.1	0.60	2.0	0.32	0.19	17	6	8	1.7	2.6
2	600	240	600	480	180	36.0	6.3	19.6	3.3	2.1	3.8	0.71	3.1	0.34	0.22	6	3	3	0.7	1.2
4	1 200	480	1 200	960	360	42.6	7.6	27.0	4.0	2.8	3.6	0.63	2.2	0.33	0.25	4	2	2	0.4	0.8
SPRUCE																				
1/4	125	25	125	100	38	49.1	7.2	29.4	5.7	2.7	5.5	0.80	3.2	0.64	0.30	39	29	24	5.7	7.2
1/2	250	50	250	200	75	61.6	8.6	28.3	5.7	2.6	7.2	1.00	3.3	0.67	0.31	27	17	11	2.8	3.5
1	500	100	500	400	150	84.6	10.4	35.8	7.4	3.8	9.4	1.15	4.0	0.82	0.42	17	10	7	1.8	2.5
2	1 000	200	1 000	800	300	75.6	9.6	36.4	9.2	4.2	8.9	1.13	4.3	1.09	0.49	8	5	4	1.2	1.4
4	2 000	400	2 000	1 600	600	62.6	9.3	39.2	11.3	4.9	7.4	1.09	4.6	1.32	0.58	3	2	2	0.6	0.8
BIRCH*																				
1/4	158	112	219	135	54	48.7	4.9	36.1	2.8	4.1	12.2	1.23	9.0	0.70	1.04	31	4.4	16	2.1	7.6
1/3	210	150	292	180	72	66.2	8.1	46.6	4.0	5.6	16.5	2.02	11.6	1.02	1.40	32	5.4	16	2.2	7.8
2/3	420	300	584	360	144	69.8	9.8	49.7	5.9	6.5	17.4	2.45	12.4	1.17	2.17	17	3.3	8	1.6	4.5
1	630	450	875	540	216	84.0	10.2	57.6	5.8	8.3	21.0	2.55	14.4	1.45	2.07	13	2.3	7	1.1	3.8
3/2	945	675	1 312	810	324	82.6	9.5	51.4	4.7	8.7	20.7	2.38	12.9	1.17	2.17	9	1.4	4	0.6	2.7
2	1 260	900	1 750	1 080	432	72.6	13.2	53.9	6.8	7.6	18.1	3.31	13.4	1.69	1.90	6	1.5	3	0.6	1.8
4	2 520	1 800	3 500	2 160	864	56.5	10.6	51.1	7.4	6.4	14.1	2.64	12.8	1.85	1.59	2	0.6	1	0.3	0.7

* In the birch experiment duplicates are lacking.

4. Uptake at Varied Total Nutrient Supply but the Same Element Proportions

In these series the stems have not been analyzed and the total uptake cannot be calculated. If it is supposed, which seems justifiable, that the element transport to and from the stems is influenced to only a small extent by the varied supply, the relations will be about the same for the whole seedlings as for leaves + roots. In Table 23 the nutrient supply, the uptake in leaves + roots, and the utilization per cent calculated on these values are given. In these series the nutrient supply from the seeds lacks importance.

It is seen from Table 23 that the nutrient uptake per seedling is influenced to a comparatively small degree and that the effect is very obvious usually only at the lowest supplies. The uptake increases throughout, however, within the sub-optimum range but not always through the whole series. For nitrogen it is found that the controls have taken up most in all three species. This is also valid for phosphorus in spruce and potassium in birch, and the same tendency is seen for magnesium in birch. In pine the highest uptake of phosphorus, potassium, and calcium corresponds to the next highest supply. The decrease in uptake at the highest supplies depends probably on toxic effects caused mainly by high total salt, chlorine, and nitrate concentrations (*cf.* Figures 3—5, p. 20—21, and p. 50—56).

The nutrient supply is practically throughout decreasingly utilized with increasing supply. The comparatively low utilization of the lowest supply by the birch seedlings cannot be regarded as statistically certain since the series lacks duplicate treatments, but the same general tendency was found in the element series (Table 22). It is seen that the results in this and earlier discussed experiments give the same principal relations between supply and uptake.

5. Comparison between the Species

When the supply is approximatively optimum and, consequently, sufficient for the seedlings, the rate of uptake will be an expression of the capacity of the seedlings to absorb nutrients. It is found that *at the same length of the growth period the birch seedlings have a much greater nutrient uptake than pine, and spruce has the least.* This is shown in Table 21 (p. 60) for nitrogen and potassium, but it is also valid for the other elements since the internal concentrations throughout are highest in the birch seedlings and usually lowest in the spruce seedlings.

At low supplies the uptake capacity of the seedlings in the experiments is not decisive for the uptake rate but rather the insufficient supply in relation to the growth rate. Of importance is then the ability of the seedlings to utilize the supplied nutrient amounts. *After the same length of the growth period the birch seedlings have utilized nitrogen to a higher degree at low supply than the pine seedlings and pine somewhat more than spruce* (Table 20, p. 58). In the element series the birch seedlings have utilized low supplies generally less than pine and spruce (Table 22, p. 62), but it is seen from the time series that the utilization is higher at the end than at the beginning of the growth periods (Table 20). As has been pointed out, the birch seedlings are very small at the start and the nutrient supply from the seeds is very low. It seems, therefore, as if the slow start of the birch seedlings means a very low uptake in the beginning that is accentuated at low supplies. Consequently, the utilization per cent in birch is low estimated in the element series.

Thus, it may be stated that birch has a general tendency to a greater utilization and uptake of nutrients when the seedlings begin to grow in the solutions than pine and spruce and that spruce is less efficient than pine. However, it is also found that birch has the highest growth rate and spruce the lowest (Figure 24, p. 44) and that the uptake rate is dependent on the seedling size (Table 21, p. 60). Now the question arises as to whether the birch seedlings have a greater uptake rate and utilization only because of the higher growth rate or whether the birch seedlings have other properties that makes them superior to pine and spruce at the nutrient uptake. A fully conclusive answer on this question cannot be expected, since the investigation intervenes in a dynamic process. If the uptake rate is put in relation to the rate of dry or fresh weight production in the controls, it seems possible to get an idea of to what extent other factors may be of importance for the uptake rate in the three species. In Table 24 the uptake rate as per cent of the growth rate has been calculated from the control data in the time series. Similar values of comparison from the element series are found in Table 25. It is seen that the uptake rate in relation to the rate of dry matter production is practically constant with time in the pine and spruce seedlings but higher in pine than in spruce. In the birch seedlings the values are higher than in pine during the first two periods but decrease during the period 76—91 days to about the same level as for spruce. The corresponding values for the potassium uptake decrease with time in all three species but are on the average higher in the birch than in the pine and spruce seedlings and somewhat higher in pine than in spruce. Similar relations between the species are found in the element series and are also valid for other elements (Table 25).

The decreasing nitrogen uptake in relation to the rate of dry matter production in the birch seedlings is partly dependent on the fact that the stem fraction of the total dry weight increases with time. This is less marked in spruce and especially pine (Figures 25—27, p. 45). The internal concentrations of the elements in relation to the dry weight are low in the stems (Figure 8, p. 24, Table 16, p. 46). Thus, there is a morphological change in the seedlings with time that influences the uptake capacity when related to the dry weight. If the uptake rate instead is studied in relation to the rate

Table 24. Element uptake in relation to seedling dry or fresh weight in the controls of the harvest time series

PINE			SPRUCE			BIRCH		
Growth period	N	K	Growth period	N	K	Growth period	N	K
Amount element uptake as per cent of dry matter production								
0— 59	2.6	1.5	0— 94	2.1	1.2	0—49	3.8	2.4
59— 72	2.6	1.3	94—122	2.0	0.9	49—63	3.1	2.4
72— 94	2.7	1.1	122—164	2.2	0.9	63—76	2.5	1.4
94—115	3.1	0.8	164—185	1.9	0.3	76—91	2.2	1.5
Amount element uptake as per cent of fresh weight production								
0— 59	0.46	0.27	0— 94	0.50	0.28	0—49	0.62	0.38
59— 72	0.55	0.27	94—122	0.48	0.22	49—63	0.49	0.39
72— 94	0.53	0.20	122—164	0.66	0.28	63—76	0.66	0.37
94—115	0.95	0.26	164—185	0.83	0.13	76—91	0.71	0.47

of fresh weight increase of the seedlings, the effect of the morphological changes is diminished. The uptake rate in relation to the rate of fresh weight production is found in Tables 24 and 25 for the controls of the harvest time and element series respectively.

It is seen from the harvest time series that there is a tendency to increasing rate of nitrogen absorption in relation to the rate of fresh weight increase with time (Table 24). The potassium uptake/fresh weight relation is quite constant but shows a low value for spruce in the period 164—185 days, which probably is connected with the above-discussed decrease in activity (p. 60). It is also found that the differences between the species are small in the uptake/fresh weight relation but that there is still a tendency to a

Table 25. Element uptake in relation to seedling dry or fresh weight in the controls of the element series

Element	Amount element uptake as per cent of dry weight			Amount element uptake as per cent of fresh weight		
	Pine	Spruce	Birch	Pine	Spruce	Birch
N	2.5	2.1	2.8	0.54	0.55	0.58
P	0.37	0.28	0.46	0.079	0.073	0.094
K	1.3	0.93	1.7	0.26	0.24	0.36
Ca	0.21	0.19	0.27	0.043	0.049	0.054
Mg	0.13	0.12	0.25	0.027	0.030	0.048
S*	0.19	0.17	0.20	0.041	0.046	0.055

* Uptake in leaves + roots. Sulphur not analyzed in stems.

higher uptake capacity in the birch than in the conifer seedlings for most elements (Table 25). Pine and spruce are, on the other hand, in this connection practically equal.

Thus, it may be concluded that *the differences between the species in the rate of nutrient absorption mainly depend on differences in growth rate.* If growth is expressed on dry weight basis, morphological differences between the species causes that differences in uptake capacity are still obtained. When growth, however, is expressed on fresh weight basis the differences are diminished. It seems, therefore, as if the uptake capacity per unit "protoplasm" will be about the same in the three species.

It may be mentioned in this connection that climatic factors have often been shown to influence the nutrient uptake (*cf.* 144). The only difference between the species in such conditions is the temperature during the light period that has been 25° C for birch and 20° C for pine and spruce. According to Burström (26) Q_{10} (15—25° C) is about 1.5—1.7 for the potassium, calcium, and magnesium uptake. Wanner (193) arrived at similar results and reported that Q_{10} is higher for the negative ions and is influenced by the concentrations in the solutions. Thus, it is possible that the temperature difference may be of some importance for the difference in the uptake rate of the species. The temperature effect, however, is also present in the growth rate and it is seen that the difference between the species in uptake capacity is very small when expressed on basis of the fresh weight. The complicated influence of temperature in relation to other growth factors on the nutrient uptake and growth of the three studied species cannot be revealed here, but it can only be stated that the temperature conditions used here are the best among those tested and that growth in the experiments is very good in all three species in comparison to what is found in the field.

C. Influences of Element Variations on the Uptake of Other Elements

As far as possible all the investigated macro elements have been analytically determined in leaves and roots. The analytical results for the unvaried elements are found in Tables 7—12 (p. 26—39).

It is found that there are usually only small variations in the percentages of the unvaried elements. Certain well-known interactions (*cf.* 95, 144), however, may be recognized. Thus, for instance, there is often an interaction between the elements supplied as positive ions. This ion antagonism (*cf.* 26) is found of NH_4^+ on Ca and Mg and also on K in birch (Table 7), of K^+ on Ca and Mg, especially in birch (Table 9), of Ca^{++} on Mg in pine and spruce (Table 10), and of Mg^{++} on K and Ca (Table 11).

Further more, at low sulphur supplies the nitrogen contents in the leaves are low in spruce and birch, which tendency is also found in the roots (Table 12). Low contents of Kjeldahl nitrogen have been considered a consequence of decreased nitrate reduction in sulphur deficiency (*cf.* 40, 79).

The interactions between the elements recognized in the analytical data are usually not very strong. *The high or low contents of unvaried elements found may be regarded as a part of the picture at certain deficiencies* and are, therefore, of no decisive importance for the study of the relations between internal percentages of the varied elements and growth. The results indicate, on the other hand, that *it is motivated to take into account the internal percentages of more than one element for a safe diagnosis of the nutritional relations on the basis of leaf analysis.*

D. Some Remarks on the Functions of the Nutrient Solutions

The nutrient supply may be expressed either as concentration or as absolute, totally supplied amount. It is seen, however, that the seedlings utilize the supply often to a very high degree (Table 22, p. 62) and the solutions cannot always be regarded to have constant concentrations of the elements. The initial concentrations of the solutions are, however, an expression of the rates of supply (here used in the meaning: amount of nutrient supplied per time unit) and the ppm (mg/litre) value is equal to mg/two weeks because the solutions had a volume of one-half litre and were changed once a week.

Is is found in the time series that a low nitrogen supply in the beginning produces practically the same growth and nitrogen uptake as the control supply (Tables 15, 20, and 21, p. 43, 58, and 60). It is also found that the nitrogen concentration in the leaves is close to the estimated optimum range in both cases (*cf.* Tables 16 and 26, p. 46 and 81). At continued growth the low supply means in relation to the value of the controls a more and more reduced nitrogen uptake and dry matter production and an internal nitrogen status that is impaired down to a certain level. These relations are illustrated in the principle diagrams of Figure 31 by means of the nitrogen experiments with spruce. Similar pictures are obtained with the other species or with the potassium experiments and the principle seems to have a high validity also for other elements.

It is seen from Figure 31 that if the same absolute and total amount of nitrogen is given, a low rate of supply yields a higher dry weight than a high rate of supply, but the growth rate is then lower. At the same length of the growth period (solid curves) a higher rate of supply gives a higher dry weight than a lower one up to an optimum value that increases with the growth time. This maximum shift (heavy, long-short dashed line) has long

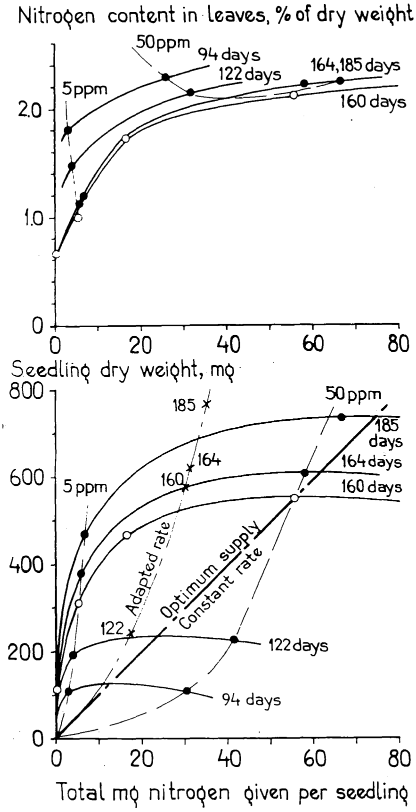


Figure 31. Principle diagram (nitrogen experiments with spruce) of the time variation of the nitrogen concentration in the leaves and the seedling dry weight *at varied totally supplied amount of nitrogen.*

●	Data from the time series
○	Data from the nitrogen series
————	Curves connecting points representing the same length of the growth period
— — —	Curves connecting points representing the same initial nitrogen concentration in the nutrient solutions
▬ ‑ ▬	Line of maximum shift at constant rate of supply
—— – ——	Curve of maximum shift at adapted rate of supply
×	Calculated points of maximum at different growth periods and at adapted rate of supply

been recognized (*e.g.* 108, 143) and means simply that larger seedlings require a higher rate of supply than smaller ones to maintain maximum growth rate. In the present material the maximum shift seems to be approximately linear in Figure 31. This is to be expected, since it is found that the uptake capacity of the seedlings per dry weight unit is approximatively constant (*cf.* p. 59—61, Table 21).

It may be concluded that the nutrient concentration, which in the element series is found to be optimum (50 ppm nitrogen for spruce, Figure 31), is too high in the beginning and too low in longer growth periods. At the time of harvest of the element series an unnecessarily great amount of nutrients has been supplied to get maximum growth. By using a lower supply rate in the beginning and by increasing it successively in relation to the increase of the growth rate of the seedlings an essentially lower total supply would be needed and a somewhat higher seedling dry weight would be the result. This is shown in Figure 31 with a thin, long-short dashed curve and with × marking estimated maximum points at different growth times.

These relations show that *the essential property of the solutions for the rate of nutrient uptake and growth is the nutrient amounts supplied per time unit, in relation to the growth rate, and not primarily the element concentration.* This seems to depend mainly on the condition that the nutrient status of the seedlings (the internal nutrient concentrations) is influenced by the relation between the growth rate and the rate of supply and that in this connection the internal nutrient status is the main factor determining the growth rate (see Figure 38, p. 79). The amount of element that is required to maintain a certain nutrient status and growth rate depends, among other things, on the capacity of the seedlings to utilize the nutrient supply. According to Olsen (132) plants can use practically all the supply without decreasing uptake rate if the proportions between the elements are constant. Not until a concentration of 0.003 m.eq/litre was reached did Olsen notice a decrease in the uptake rate. At changed proportions between the elements the uptake rate of the elements was influenced at higher concentrations. This would imply that if the nutrients were supplied in the same proportions as they are taken up, the plants would be able practically to deplete the solutions of their salts. This is not in agreement with the present results. Olsen's results as well as earlier (*cf.* 63) and the present ones indicate certainly the importance of the rate of supply over that of the concentration. However, it is seen from the time experiments that 5 and 50 ppm nitrogen have led to about the same uptake rate only as long as the lower supply is utilized less than to about 50—60 per cent (Tables 20 and 21, p. 58 and 60) and the corresponding value for potassium is lower (p. 59). This utilization, thus, is not as great as that Olsen found to be possible without reduction

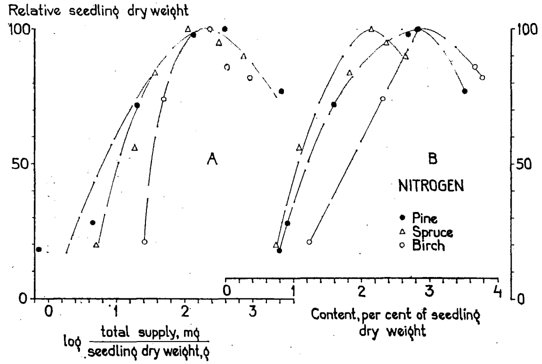


Fig. 32.

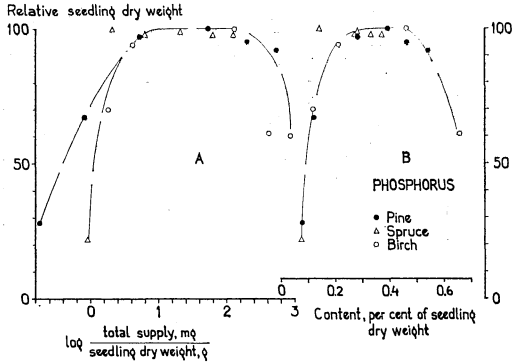


Fig. 33.

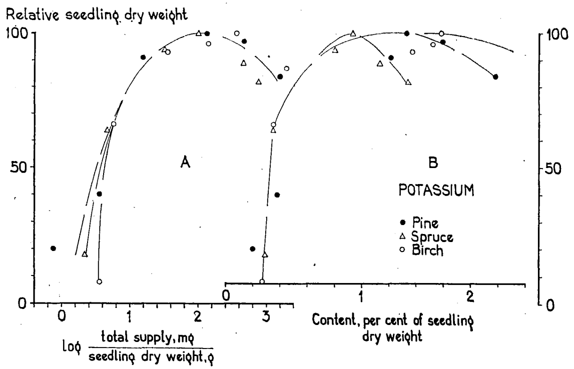


Fig. 34.

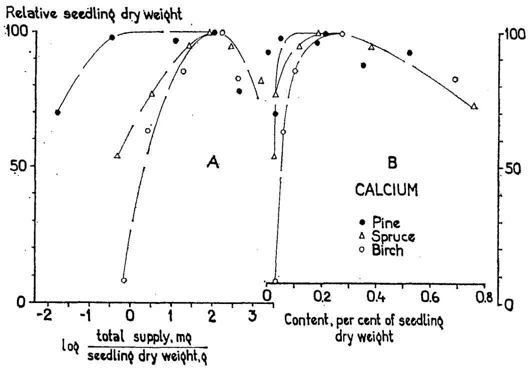


Fig. 35.

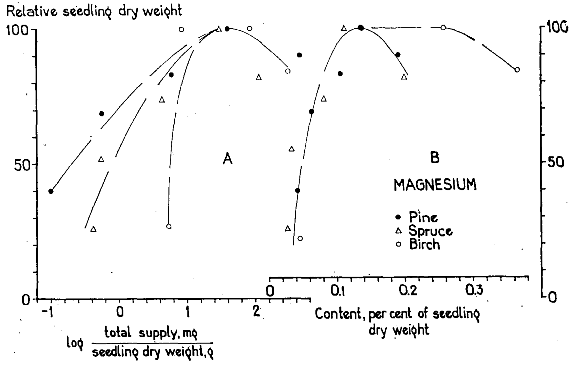


Fig. 36.

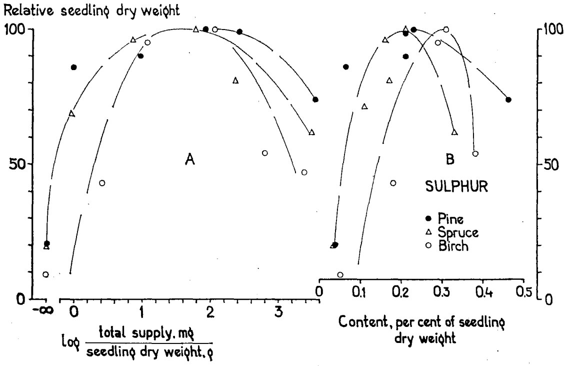


Fig. 37.

Figures 32—37. Nutrient requirements for reaching different relative seedling dry weights at constant (diagrams A) or adapted (diagrams B) rate of supply. In the case of sulphur the content refers to leaves + roots only.

of the uptake rate. Further more, it is found that to reach maximum or nearly maximum growth the different elements are utilized to a varying degree (p. 64).

The nutrient supply in experiments may be based on one of the following conditions: constant rate of supply, constant concentration, or adapted supply according to the uptake of the seedlings. In the present experiments the rate of supply is maintained constant, whereas the concentrations decrease during each week. If the concentrations should be held constant a continuous change or a great volume of solution would be necessary. The required nutrient amounts would then be very great. When the supply is adapted according to the uptake of the seedlings by using low concentrations in the beginning and then successively higher or by a continuous compensation of the amounts taken up, the supply requirement approaches the least possible that is the "internal requirement". By a constant rate of supply the nutrient requirement will be higher.

The requirements of nutrient supply for a certain relative dry matter production are found in Figures 32—37. In the diagrams the requirement at constant rate of supply $\left(\frac{\text{total amount of supply}}{\text{seedling dry weight}}\right)$ as well as the least possible requirement of supply (nutrient content as per cent of seedling dry weight) are given. It is seen from the diagrams that there are differences between the elements as well as the species. The elements may be arranged in the following series according to decreasing requirements:

At constant rate of supply (diagrams A):
Pine: $N > K > Mg > S,P > Ca$
Spruce, birch: $N > K,Ca > Mg > S,P$

At adapted rate of supply (diagrams B):
Pine: $N > K > P > Mg > Ca$
Spruce, birch: $N > K > P > Ca > Mg$

Sulphur cannot be placed in the latter series since the total sulphur content in the seedlings is not known, but the requirement seems to be about equal to that of phosphorus also in these series. *The requirements of different elements come in the same order for the three species with the exception of calcium for which element pine has a very low requirement.*

When the species are compared in their requirements of different elements *at constant rate of supply* it is seen that *the differences are small within the optimum region but that within the sub-optimum region the requirements of the birch seedlings practically throughout are the highest and that of the pine seedlings the lowest.* The requirement of potassium is, however, quite the same in the three species except at the lowest supplies.

The requirements *at adapted rate of supply* are practically equal in the species for phosphorus and within the sub-optimum range also for potassium and magnesium. However, it is seen that *the spruce seedlings have the lowest and the birch seedlings the highest requirement of nitrogen and there is a general tendency that the birch seedlings have higher requirements than the conifers.*

The requirements of nutrients are, of course, closely related to the properties at the nutrient uptake. It was shown above that the capacity of the control seedlings to take up nutrients in relation to the dry weight was greatest in the birch seedlings and smallest in the spruce seedlings whereas the differences between the species are small when the uptake is put in relation to the fresh weight (Tables 24 and 25, p. 69). This depends mainly on the differences between the species in their morphology. If the requirements at adapted rate of supply are calculated on the basis of the fresh weight (nutrient content as per cent of fresh weight) it will be seen that the curves of the three species throughout will be very close to each other, but still with a tendency to greater requirements of the birch seedlings within the sub-optimum region. Thus, *it seems as if the "protoplasmatic" nutrient requirements of the three species are about the same.*

The functions of the nutrient solutions in the present experiments may be summarized as follows:

1. The control solutions supply the seedlings with a nutrient amount that is sufficient for maximum growth under the present growth conditions but that is high in the beginning and low if longer growth periods are used. This depends on the fact that the nutrients are supplied at a constant rate and not at a rate that is adapted for the actual requirements of the seedlings per vessel at the different stages of development.

2. The sub-optimum solutions mean reduced nutrient uptake and growth first after a certain period, the length of which depends on the rate of supply and the element involved. Gradually an adaptation of the growth rate to the low supply is reached, which is seen from, for instance, the decreasing change in the internal nutrient concentrations with time.

3. The supra-optimum solutions contain for the seedlings toxic amounts of salts. The different effects of the salts cannot be clearly distinguished. When the seedlings become larger the toxicity seems to decrease.

4. There is, thus, a general trend in the relation between rate of supply and growth per vessel towards greater rates of supply (concentrations) with increasing growth time to reach a certain relative growth rate. Consequently, the solutions used here are specially adapted to the present experimental conditions.

Chapter V. The Significance of the Internal Element Concentrations

A. Relations between Element Concentration in the Leaves and Dry Matter Production

1. The Time Course of the Relation

From the results of the harvest time series is seen that the internal nutrient concentrations tend to decrease with increasing length of the growth period (Table 16, p. 46, Figure 31, p. 72). There are indications, however, that the optimum concentrations in the leaves are changed only to a small extent with time. It is found, for instance, that the low nitrogen supply has produced a very good relative growth in the beginning (Table 15, p. 43, Figures 25—27, p. 45) and the nitrogen content of the leaves is then also close to the optimum level found in the element series (Table 26, p. 81). In the birch seedlings it is seen that the low nitrogen supply on the first harvest occasion corresponds even to a higher dry weight than the control supply and that the nitrogen concentration in the leaves also agrees better with the optimum content found in the element series than that of the control leaves.

These results support the opinion that the nutrient content of the green matter is the decisive factor for the effects of the nutrients on plants (*cf.* 94), but indicate also that a low supply leads to another and better nutrient status of the seedlings in the beginning of the growth period than later on. This means that the dry weight found at harvest does not correspond fully to the nutrient status measured at the same time but that the estimated nutrient status will be too high or the seedling dry weight too low in their mutual relation. The ability of the seedlings to utilize their better nutrient status during the earlier stages is, however, slight since their possible growth rate then is low. Later on, when the growth ability increases, the change in the internal concentration decreases. It may, therefore, be quite generally concluded that the effect of the time change in the internal concentrations on the growth values measured at harvest is less than it appears from the magnitude of the change in the concentrations. This is schematically illustrated in the principle diagram of Figure 38 that is founded on the nitrogen experiments with spruce.

It is seen from Figure 38 that a certain rate of supply leads to decreasing concentrations in the leaves with increasing growth time (thin, dashed curves) and that this effect is stronger at low than at high concentrations of the solutions. It is also seen that the decrease is greatest in the beginning.

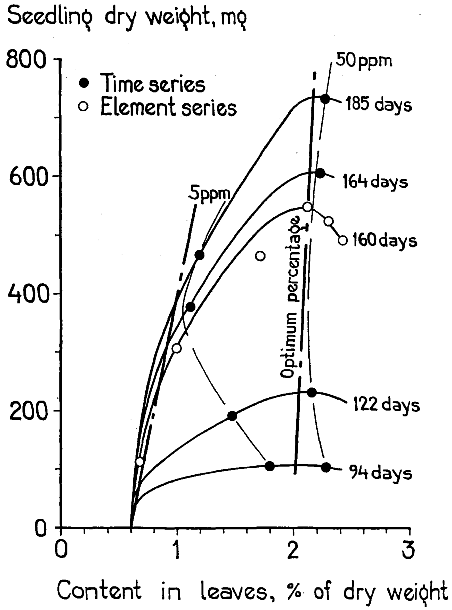


Figure 38. Principle diagram (nitrogen experiments with spruce) of the time variation of the seedling dry weight *at varying nitrogen concentration in the leaves.*

————	Curves connecting points representing the same length of the growth period
— — —	Curves connecting points representing the same initial nitrogen concentration in the nutrient solutions
—— – ——	Lines connecting the points of 100 and 50 per cent of maximum seedling dry weight.

In the spruce seedlings the percentages increase again in the longest growth times, which coincides mainly with the decreasing avtivity of the seedlings in the latest period (p. 60). In the pine and birch seedlings the tendencies are fundamentally the same but the internal concentrations never increase clearly within the experimental periods (Table 16, p. 46).

On all harvest occasions the maximum dry weight seems to coincide with about the same nitrogen concentration of the leaves (2.0—2.2 per cent of dry weight), which is shown in the diagram with a heavy long-short dashed line through the maximum points. It is also probable that the minimum concentration (*cf.* 96) is independent of the time and that it is about 0.6 per cent of the spruce leaf dry weight. This value is utilized to fix the time curves (solid curves) in the diagram of Figure 38, and it agrees also closely with the lowest value Tamm (175, Appendix II) has found in a great field material (about 0.7 per cent in current leaves).

A relative growth of 50 per cent of the maximum seems, however, to correspond to a slowly increasing concentration in the leaves with increasing growth time. This is shown in Figure 38 with a long-short dashed line through the minimum point. It is probable that this change with time cannot be very great and that it increases only to a certain limit. This means that *the shift in the relation between the concentration in the leaves and the dry matter production with time even at low supplies is not very great.*

The relations demonstrated for the nitrogen effects on spruce are also principially valid for the pine and birch seedlings and for potassium. The small variations of the concentrations in the leaves of the other elements in the controls with time (Table 17, p. 47) indicate that the principle holds true, on the whole, also for the other elements. One exception is, however, the calcium concentration in the birch leaves that tends to increase with time, and it seems as if the optimum calcium concentration increases with the age of the seedlings. This is not noticed in the pine and spruce seedlings within the experimental periods.

2. *Definitions*

The principle of the content/growth relation (Figure 38) is schematically demonstrated and it cannot be shown to be valid in detail on the basis of the present material. The relation is also known to be influenced to some extent by many external factors and it seems to be beyond the actual problems in forest tree nutrition to analyze the relation in detail here. Instead, it seems motivated to study the patterns more roughly and to distinguish intervals of percentages corresponding to certain defined growth levels. The following basis of classification will be used:

Strong deficiency: < 50 per cent of maximum growth.
Moderate deficiency: 50—90 per cent of maximum growth on the sub-optimum side.
Optimum nutrient status: 90—100—90 per cent of maximum growth.

As has been seen above the use of the term supra-optimum nutrient status is not justifiable here, because it is impossible in the material to decide with certainty whether it is the internal concentration of the nutrient elements that causes the growth reductions at the highest supplies or whether other factors may be of greater importance (*cf.* p. 50—56). This means that also the upper limits of the optimum range are not necessarily the upper limits

Table 26. Element concentrations in leaves (per cent of dry weight) corresponding to 50—90 per cent of maximum growth (range of moderate deficiency) and to 90 — 100 — 90 per cent of maximum growth (range of optimum)

Element	Pine		Spruce		Birch	
	Range of moderate deficiency	Range of optimum	Range of moderate deficiency	Range of optimum	Range of moderate deficiency	Range of optimum
N	1.1—2.4	2.4—3.0	0.9—1.8	1.8—2.4	2.4—3.4	3.4—4.0
P	0.08—0.15	0.15—0.4*	0.07—0.10	0.10—> 0.3	0.1*—0.2	0.2—0.4
K	0.44—0.9	0.9—1.6	0.3—0.7	0.7—1.1	0.5—1.5	1.5—3.1
Ca	0.03*—0.04	0.04—0.3	0.02*—0.09	0.09—0.6	0.06—0.16	0.16—0.6
Mg	0.05—0.12	0.12—0.18	0.02—0.09	0.09—0.16	0.10—0.17	0.17—0.5
S	0.06—0.20	0.20—0.25	0.09—0.13	0.13—0.18	0.22—0.29	0.29—0.32

* Extrapolated values.

of the internal optimum nutrient status. Yet, these limits are representative for the present experiments and may be considered as indications of unsuitable nutrient conditions, since the internal concentrations generally increase within the interval (Figures 6—23, p. 24—40).

Optimum curves have frequently been described mathematically (20), for instance, with parabolic functions (*e.g.* 131, 136) or with exponential equations (*e.g.* 5, 94, 113, 114). These equations may be used here and are doubtless of great value in reaching certain practical results. In the present study they do not seem to be called for because it is not the purpose here to generalize the results. Instead a graphic method is applied where the experimental results are used directly. Thus, the concentrations in the leaves corresponding to certain growth levels have been interpolated from the seedling dry weight curves (heavy solid lines) to the percentage curves of the leaves (heavy broken lines) in Figures 6—23. In the earlier papers (66, 68, 69) another method was applied in the interpolations (percentage/growth diagrams with smoothened curves were used), but since the results differ only to a small degree it may be concluded that the method used is of minor importance. By means of these interpolations the experimental results are compressed from many and unsurveyable data to few and uniform which are presented in Table 26.

In some cases the concentrations in the leaves corresponding to 50 per cent of maximum dry weight on the sub-optimum side or 90 per cent on the supra-optimum side cannot be interpolated, because the experimental results do not cover these ranges. Usually it is possible to make reasonable extrapolations according to the method used in the earlier papers and when such extrapolations are made this is remarked in the table. In one case, only a limit value can be given, namely in the phosphorus series with spruce where no certain supra-optimum supplies have been used.

Among the great bulk of analytical values from forest tree species found in the literature only a small part are utilizable for direct comparisons with the present material. The data are scattered on various species of Pinus, Picea, and Betula, various types of growth measurements have been used, and different types of materials have been analyzed. Further more, the basis varies on which the significance of the analytical values is defined, and seldom defined growth levels have been used as a basis. Often the contents are expressed in other units than used here but then they are always made out and cited as per cent element of dry weight. In many earlier works the sampling was not satisfactorily defined and the analytical methods were then not always developed to the same refinement as today. It is not possible to judge what these factors mean for the comparability but for lack of other data many such values will be subsequently discussed.

3. Nitrogen

a. Optimum

Pine. Optimum percentages reported earlier for Pinus silvestris are quite varying (2—3.2 per cent in shoots or leaves) but come from materials of very different conditions. In seedlings Gast (45) found 3 per cent in the leaves as optimum independent, on the whole, of the light intensity, and Björkman's (15) material indicates that 2.5—3 per cent in shoots correspond to the highest growth. Mitchell (109) found optimum at about 3.2 per cent in shoots of Pinus silvestris as well as P. strobus and found no greater differences between the species in their content/growth relations in spite of considerable differences in their absolute dry weights. Later (111) he reported 3.26 per cent nitrogen in the shoots as optimum in P. strobus. Tamm (175, 177) estimated on the basis of the diameter growth the optimum content in leaves from full-grown pine trees to be 2—2.5 per cent.

Also for other pine species optimum nitrogen percentages are reported. Bensend (10) determined the optimum content to 2.25 per cent in seedlings of Pinus banksiana from nurseries, but his material from sand culture experiments show the highest growth often at contents up to and above 3 per cent in the shoots. Swan (161) found for the same species a growth increase when the content increased from 2.12—2.47 per cent, but here it is not possible to estimate an optimum content because no higher supplies have been used. In Pinus taeda and P. Virginiana Fowells and Krauss (43) found in sand cultures that the highest growth corresponds to about 2.3 per cent nitrogen in the leaves and essentially lower growth was recorded at contents of 1.7 and 2.7 in P. taeda and 1.9 and 3.1 per cent in P. Virginiana.

They considered that 1.7—2.3 per cent indicates a satisfactory nitrogen status of these species but it is obvious that the optimum range in their material comprises also higher contents.

The optimum range found here (2.4—3 per cent, Table 26) corresponds quite well with the cited values for Pinus silvestris seedlings and also other species of Pinus. Tamm's (175, 177) values for full-grown trees are lower but refer also to another type of growth. Yet, Tamm's values correspond to 82—93 per cent of maximum seedling dry weight in the present material.

Spruce. Maximum growth corresponds to 1.8—2.4 per cent nitrogen in the spruce leaves of the present experiments (Table 26). This is in good agreement with the optimum estimated by Tamm (175) in full-grown trees (>2 per cent in current spruce leaves) and with results reported by Mitscherlich and Wittich (115). Swan's (161) material with Picea glauca and P. mariana does not permit conclusions about optimum nitrogen percentages, but it may be noticed that growth increases when the content increases from 1.94 to 2.82 per cent and 1.75 to 2.78 per cent in the shoots of the respective species. Leyton (85) reported data that indicate that Picea sitchensis produces best growth with a nitrogen content of the leaves of 1.4—1.5 per cent. The related data are, however, taken from experiments of different types and the optimum content cannot be regarded as conclusive, as Leyton also remarks.

Birch. Tamm (175) found it probable that the optimum nitrogen content in birch leaves is higher than 3.3 per cent, which agrees very well with the optimum interval found here (3.4—4.2 per cent, Table 26).

b. Deficiency

Pine. In the present experiments contents of 1.1—2.4 per cent nitrogen in the leaves correspond to moderate deficiency (Table 26). The results indicate that 0.6—0.7 per cent is minimum content. Tamm (175) found preliminarily that 1.1—1.6 per cent nitrogen in current leaves from full-grown trees is the deficiency level and reported (177) that contents below 1.75 per cent indicate an unsatisfactory nitrogen availability. This value corresponds to about 75—80 per cent of maximum seedling dry weight in the present study. Bozormenyi (21) found the interval 1.8—2 per cent between deficient and luxury consumption of seedlings. Mitchell (111) divided the deficiency range into two regions, "region of minima" and "working region" and reported for Pinus strobus seedlings the contents 0.70—1.33 and 1.33—2.70 per cent in the shoots for the respective interval. The ranges are divided primarily according to the nitrogen status of the root medium and not to the growth of the seedlings. If Mitchell's data are treated in the same way as here they show a pattern practically identical to that of the present experiments, which was demonstrated earlier (*cf.* 69). Thus, it is seen that the agreement is very good with earlier reported data.

Tamm (175) found 1.1 per cent as the lowest nitrogen content in the deficiency level but in Appendix II a great material shows contents down to about 0.7 per cent in current leaves. It seems, however, probable that the minimum content seldom is realized in the field and that values below 1 per cent are rather unusual. In an extremely nitrogen-poor area where the soil consists mainly of lime and where a competitive flora is lacking the author has during several years found contents of 0.7—0.8 per cent in leaves from about 40-year-old, planted pine trees. These have practically no growth and have often, in spite of their age, a height of some decimeters (unpublished data). The minimum content found in the present material corresponds also to that reported by Mitchell (111) for Pinus strobus.

Spruce. Strong deficiency corresponds to a content of < 0.9 per cent in the spruce leaves and moderate deficiency to 0.9—1.8 per cent (Table 26). The lowest content recorded was 0.61 per cent and it seems as if the minimum content is about 0.6 per cent. Tamm (175) found in Picea abies leaves 0.8—1.3 per cent to be the preliminary deficiency level. The upper limit corresponds in the present investigation to a growth of about 70 per cent of maximum. The lowest content found by Tamm (Appendix II) is about 0.7 per cent in the current leaves, which is in good agreement with the minimum level found here.

Birch. Tamm (175) reported 1.8—2.2 per cent nitrogen as the preliminary deficiency level in birch leaves. The upper limit corresponds, thus, to strong deficiency in the present material. Since the optimum content estimated by Tamm is close to that found here, it seems probable that the deficiency level extends essentially higher than the highest limit observed by Tamm from his relatively limited amount of data.

4. *Phosphorus*

a. Optimum

Pine. The optimum range is found at 0.15—0.4 per cent in the pine leaves (Table 26), which is generally in good agreement with earlier data. Fowells and Krauss (43) found 0.14—0.18 per cent as optimum in Pinus taeda and P. Virginiana leaves and Leyton (85) reported 0.15 per cent as optimum in Corsican pine leaves. Swan (161) found the highest growth of Pinus banksiana at 0.30 per cent phosphorus in the shoots and lower growth at 0.23 and 0.41 per cent. The comparatively high values found by Swan may depend on the presence of stems in the analyzed material, since it is found here that the content of phosphorus in the stems is higher than in the leaves (Figure 9). However, in some seedlings analyzed by Swan, this difference between the contents in stems and leaves was not recorded.

Björkman (15) reported data that indicate the optimum at 0.20—0.30 per cent in shoots of Pinus silvestris. Süchting (164) mentioned that fertilization increases growth when the phosphorus percentage in shoots is 0.12 per cent. Very contradictory to these results are the values reported by Mitchell (111) for Pinus strobus grown in sand cultures. He found the "region of minima" at 0.10—0.28 per cent phosphorus in the shoots, the "working region" at 0.28—0.56 per cent, the "region of tension" at 0.56—0.69 per cent, optimum at 0.67 per cent and the "toxic region" at 0.67 + per cent phosphorus. It is seen that the optimum found here, which is higher rather than lower than other comparable data, lies to a large extent within Mitchell's "region of minima". An optimum of 0.67 per cent phosphorus is very high also in comparison with other plants (*cf.* 48).

Spruce. The optimum range corresponds to 0.10 — > 0.3 per cent phosphorus in the spruce leaves (Table 26). Leyton (85) reported 0.13 per cent as an optimum in Sitka spruce. Swan (161) found low growth in Picea glauca and P. mariana at 0.15 and 0.14 per cent phosphorus respectively in shoots when compared to the growth corresponding to 0.51 and 0.40 per cent respectively. It is seen that Swan's values are high in the spruce species just as in Pinus banksiana.

Süchting (163) found that phosphorus fertilization produced a growth increase when the phosphorus content was 0.13 per cent in the shoots, reporting (169) that no deficiency is manifested when the content is 0.16—0.38 per cent. Nemec (120) observed growth responses after basic slag fertilization also at phosphorus contents of 0.35 per cent in the leaves. The results seem to show, however, that growth responses appear to correspond to increased phosphorus contents only when the percentage is as low as 0.14 per cent (*cf.* 120, table on p. 699). The optimum phosphorus content seems instead to fall within the range 0.14—0.20 per cent. The growth response recorded despite the high phosphorus contents may depend on secondary effects of the basic slag.

Birch. No optimum contents have been reported for phosphorus in birch as far as the author knows.

b. Deficiency

Pine. Moderate deficiency corresponds to 0.08—0.15 per cent phosphorus and the minimum content seems to be about 0.05—0.06 per cent. Tamm (175) found 0.09—0.10 per cent to represent the preliminary deficiency level in current leaves. The upper limit corresponds to a dry weight of about 75 per cent of maximum in the present material. Süchting (162, 163) reported deficiency at 0.09 per cent in shoots. The lowest content in current leaves reported by Tamm (175, Appendix II) is 0.08 per cent and is, thus, essentially higher than the lowest found here.

Spruce. The deficiency level reported by Tamm (175) is 0.07—0.08 per cent phosphorus in current spruce leaves and the lowest value in Appendix II is 0.07 per cent. In the present experiments the minimum content seems to be about 0.04—0.05 per cent and moderate deficiency corresponds to 0.07—0.10 per cent. The upper limit of the preliminary deficiency level found by Tamm corresponds to about 60 per cent of maximum seedling dry weight in the present study.

Birch. The upper limit of the deficiency level reported by Tamm (0.08—0.10 per cent phosphorus in birch leaves) corresponds to only about 50 per cent of maximum seedling dry weight in the present material where 0.1—0.2 per cent phosphorus represents the range of moderate deficiency (Table 26). It is probable, as in the case of nitrogen, that the level in the field may be higher than is seen from Tamm's values since these are based on a limited material.

5. Potassium

a. Optimum

Pine. The optimum range is found at 0.9—1.6 per cent (Table 26). Only few optimum contents of potassium in pine have been reported in the literature. Swan (161) found a small growth increase in Pinus banksiana seedlings when the percentage in the shoots increased from 1.09—1.16 per cent potassium. Mitchell (111) found the optimum content to be 1.72 per cent in shoots of Pinus strobus. The optimum range found here lies mainly within Mitchell's "working region" (1.02—1.49 per cent). Mitchell's values seem, as in the case of phosphorus, very high in comparison with other values. Süchting *et al.* (169) reported no deficiency present when the content in the shoots is 0.5—1.17 per cent. Süchting found later (163) the "normal" contents to be 0.33—0.83 per cent, which is lower than Mitchell's "region of minima" (0.82—1.02 per cent). Further more, Mitchell reported deficiency symptoms at the lowest potassium supply and the corresponding content in the shoots is 0.82 per cent. This value is 2—3 times higher than all such values in pine found in the literature (*cf.* Table 36).

Spruce. Also in the case of spruce few optimum data are available for potassium. The optimum range found here is 0.7—1.1 per cent (Table 26) and this is in agreement with the findings of Leyton (85). According to Leyton the ratio between nitrogen and potassium is about 1.4 at maximum growth, which means an optimum potassium content of about 1.0 per cent. Leyton assumed, however, an optimum nitrogen content of 1.4—1.5 per cent, which is low in comparison to the optimum nitrogen content found here (Table 26). The optimum N/K ratio is in the present study about 2—2.5. Swan (161) found a small growth increase in Picea glauca and P.

mariana when the contents in the shoots increased from 1.20 to 1.60 per cent and from 0.70 to 1.72 per cent respectively.

Birch. No optimum contents of potassium in birch have been proposed as far as the author knows.

b. Deficiency

The preliminary deficiency levels reported by Tamm (175) are low in relation to the results of the present study. The upper limit for pine (0.31 per cent in 1½ year-old-leaves) corresponds to 40 per cent of maximum seedling dry weight in the present material, for spruce (0.30 per cent in current leaves) to 65 per cent, and for birch (0.34 per cent in the leaves) to 20 per cent of maximum. The ranges of moderate deficiency reach in the present study essentially higher percentages, especially in birch (Table 26). In relation to the findings of, for instance, Süchting *et al.* (169) and Swan (161) discussed above in connection with the optimum there are reasons to believe that Tamm's preliminary deficiency levels do not cover the upper interval of the potassium deficiency region. Further field data are required to judge whether there are physiological differences in the potassium relations between young seedlings and older trees.

6. Calcium

Very few data about the relations between growth and the internal calcium concentration of forest tree species are found in the literature. The only optimum calcium content proposed seems to be Mitchell's (111) data for Pinus strobus seedlings, but, as for phosphorus and potassium, Mitchell's values appear to be very high. The optimum was found at 0.33 per cent in the shoots and the "region of minima" between 0.23 and 0.24 per cent. It is seen that the optimum found here for pine lies mainly below Mitchell's "region of minima". It may be mentioned that Themlitz (183) found good growth of Pinus silvestris at 0.25 per cent calcium in the leaves. Süchting *et al.* (169) reported about 0.3—1.3 as "normal" in pine and spruce shoots. Tamm (175) recorded contents in current leaves down to 0.16 per cent in pine and 0.11 per cent in spruce, but reported no signs of existing calcium deficiency. Nemec's observations in forest stands (*e.g.* 125, 126) on the calcium or lime status of the soil seems to have no bearing upon a physiological calcium deficiency of the trees, but possibly the soils may be regarded as lime poor.

The upper limit of the optimum ranges found here (Table 26) are low in comparison to common values found in the field (29, 70, 71, 72, 169, 172, 174, 175). The reason for this discrepancy is not known, but is is possible that the relations at high supplies of calcium discussed above (p. 50—56) involve secondary effects of the supply and that the growth curve is supressed also when the internal calcium concentration is relatively low. It is, however, also possible that the age of the seedlings and the growth conditions are of importance for the calcium content/growth relation and that young seedlings are sensitive to high internal concentrations or that older seedlings and trees have a greater requirement of calcium. There is, in fact, in birch such a trend with increasing growth time (Table 17, p. 47). Further more, in the field the lime factor makes the relations complicated and often it is not possible to distinguish between this and the calcium factor.

7. Magnesium

Conclusive data about the magnesium content/growth relations in forest tree species are practically lacking in the literature. According to Stone (154) there are no growth effects of magnesium deficiency in pine until they show severe symptoms, which corresponds to a magnesium content up to 0.12 per cent in the leaves. In Pinus banksiana seedlings Swan (161) found a growth increase when the magnesium content in the shoots increased from 0.13 per cent to 0.22 per cent. These values are high in comparison with the present data (Table 26). When it comes to the spruce species Swan found the highest growth at a content of 0.08 and 0.07 per cent in the shoots of Picea glauca and P. mariana respectively and lower growth was noticed at 0.14 and 0.16 per cent. These values are low rather than high compared to the present findings (Table 26), but Swan characterized the supply as very low when the growth was the highest and noticed deficiency symptoms in the seedlings.

8. Sulphur

No data have been found about the sulphur content/growth relations of forest tree species in the literature. It is of interest to notice, however, that the highest levels of content found in the field are close to the optimum contents found here (Table 26). Moyer *et al.* (117) reported 0.04 per cent as the lowest and 0.25 per cent as the highest sulphur content in current leaves of conifers from a nonindustrial area. Near geysers in Yellowstone Park 0.12 per cent was the lowest value and 0.29 per cent the highest in leaves of Pinus contorta. Thomas *et al.* (185) found in deciduous trees 0.24—0.50 per cent sulphur in the leaves. The variations are, thus, as in the present study, not very great. In many plants, however, the sulphur content is found to vary considerably and marked increases with age have often been reported (*cf.* 7).

9. Conclusions

As far as it has been possible to make comparisons between the present data and values found in the literature the correspondence is striking with regard to the great variations of the conditions behind the data. Earlier reported optimum contents fall as a rule very close to and often within the optimum ranges found here. Noticed differences seem to depend mainly on the definition of satisfactory or optimum nutrient status. Great differences, however, are recorded in comparisons to Mitchell's (111) values for phosphorus, potassium, and calcium in Pinus strobus seedlings grown in sand cultures. Mitchell's results lack support in the literature, and it seems probable that some error is present in them.

The optimum contents found in the present study are usually higher rather than lower than values reported earlier. This may depend on the fact that the nutrient solutions contain approximately optimum supplies of all elements except the varied one, which makes possible a good approach to the maximum growth in all element series. Yet, in comparisons with the preliminary deficiency levels reported by Tamm (175) there is often a very good agreement with the present results. The upper limits for Tamm's nitrogen and phosphorus levels for pine and spruce correspond to 60—80 per cent of maximum seedling dry weight in the present study. When it comes to birch and also potassium for pine Tamm's values correspond to a low growth here. It is to be remembered, however, that Tamm obtained his deficiency levels from available experiments in the field and that they are based on the condition that fertilization causes clear growth responses when the deficiency levels were found in leaves from unfertilized plots. Tamm regarded also the deficiency levels reported as preliminary because they are based upon a comparatively small material. Further more, it may be stated that a rather great response is required in a forest stand to be regarded as clear.

It may be questioned whether a physiological optimum can be recognized in the field because of the complicated influences of fertilization. As an example of the difficulties may be mentioned the results from experiments with soil disinfection and nitrogen fertilization in forest nurseries (*cf.* 72). It was found that the relative effects of ammonium sulphate compared with sodium nitrate fertilization on the growth of spruce seedlings was different on disinfected and non-disinfected areas. When growth was plotted against the nitrogen concentration of the leaves the optimum concentration appeared, therefore, to be different in the two cases and about 2.0 per cent on non-disinfected soil against about 2.5 per cent on disinfected soil. A strongly marked physiological optimum at 2.5 per cent in spruce leaves does not seem very probable in the light of the present and earlier data (*cf.* p. 82) and, therefore, the results were interpreted as a consequence of secondary effects of the fertilizer rather than of the nitrogen status of the seedlings. The fertilizers were supposed to be different in their action on the micro flora developed in the soil after disinfection, but other explanations are certainly possible. In any case, these experiments demonstrate that in the field it is necessary to interpret the relations between the element percentages in the leaves and growth with great care and that it is important to distinguish between the significance of the physiological nutrient status of the seedlings and the ecological effects of fertilization. The fundamental importance of knowledge about the meaning of the internal nutrient concentrations is also obvious.

A greater and more conclusive material from field experiments than is now available is required to obtain more valid data regarding the significance of the element concentrations in the leaves. Yet, the comparisons that have been possible to make indicate that the validity of the values in Table 26 is high despite the extreme growth conditions in the present experiments. As far as it is possible to judge today, therefore, *the present investigation furnishes strong evidence in support of the practicability of foliar analysis in the diagnosis of the nutrient status of forest trees.*

B. Relations between Element Percentages in Different Materials and Different Growth Values

In the previous section the relations between element content in the leaves and seedling dry weight have been discussed. It is seen from the cited data that many workers have used other materials for analysis and other growth measurements. For comparing different types of analytical values the distribution of the elements in the different seedling parts is of decisive importance.

1. Element Distribution in the Seedlings

The relations between supply and element percentages in leaves, stems, and roots are shown in Figures 6—23 (p. 24—40). The following general tendencies may be noticed:

1. In birch the percentages in the leaves are the highest except for phosphorus which shows the highest percentage in the roots. The percentages in the stems are the lowest except for calcium and magnesium which are low in the roots.

2. In pine and spruce the differences in percentages of the different organs are less pronounced and often the contents in the leaves are

comparatively low. The percentages in the leaves are highest only for calcium and then especially at high supplies.

3. The low percentages in the pine and spruce leaves in relations to that of the birch leaves depend mainly on morphological differences. Thus, the dry matter content is essentially higher in the former (30—40 per cent of the fresh weight against 18—25 per cent in birch).

Nitrogen and potassium are recognized as easily movable within the plants (*cf.* 42), and it is evident from the appearance of the deficiency symptoms (p. 27) that nitrogen is mobilized from the older to the younger leaves. In birch it may be noticed that the nitrogen percentage increases with the supply more pronouncedly in the leaves than in the stems and roots (Figure 8, p. 24), whereas potassium increases more evenly within the whole seedlings (Figure 14, p. 30). In the pine and spruce seedlings potassium behaves as in birch, but the nitrogen percentages in the leaves do not increase so markedly within the supra-optimum region (Figures 6—8, p. 24). It is possible that this depends on the observed toxicity of high nitrogen supplies (p. 53—54).

Phosphorus shows another distribution pattern than potassium and nitrogen. A physiologically important part of the phosphorus is regarded as easily movable in deficiency (*cf.* 7). Russel and Martin (145) found that relatively more phosphorus was retained in the roots at low and decreasing supplies. In the present material the tendency is the opposite, that is, the phosphorus percentage in the roots increases in relation to that of the shoots with increasing supply (Figures 9—11, p. 28). In spruce the phosphorus percentages in the roots increase, however, not so markedly as in pine and birch. In pine also the percentages of the stem increase and at supra-optimum supplies a strong increase is noticed in all three organs in birch. The results indicate that phosphorus is not so easily transported upwards from the roots, which is most pronounced in the spruce seedlings where also the uptake is restricted at high supplies.

Calcium is distributed in a third pattern with the highest percentages in the leaves and with a remarkable increase within the supra-optimum region that in all three species is least pronounced in the roots (Figures 15—17, p. 34). The results indicate that calcium is easily transported upwards but that it is not so easily remobilized from the leaves. This is in good agreement with earlier observations (*cf.* 42, 46, 144). Magnesium shows a similar tendency as calcium (Figures 18—20, p. 36), but the magnesium percentages in the pine and spruce seedlings are highest in the stems.

Sulphur is generally considered as not a very movable element within the plants, which is also seen from the fact that the deficiency symptoms appear at first in the youngest leaves. Biddulph *et al.* (14) found, however, that a

Table 27. Content ranges of moderate deficiency corresponding to various growth measurements and analyzed materials

Ele-ment	Content in	50—90 per cent of maximum dry weight of								
		PINE			SPRUCE			BIRCH		
		Seedlings	Shoots	Roots	Seedlings	Shoots	Roots	Seedlings	Shoots	Roots
N	Leaves	1.1—2.4	1.5—2.6	0.8—1.4	0.9—1.8	1.1—1.9	0.7—0.9	2.4—3.4	2.4—3.4	1.9—3.4
	Shoots	1.1—2.4	1.4—2.5	0.8—1.3	0.9—1.8	1.0—1.8	0.7—0.9	1.9—2.6	1.9—2.6	1.7—2.6
	Seedlings	1.2—2.4	1.5—2.5	1.0—1.4	1.0—1.9	1.2—2.0	0.8—1.0	1.9—2.6	1.9—2.6	1.7—2.6
P	Leaves	0.08—0.15	0.08—0.15	0.06—0.09	0.07—0.10	0.08—0.10	0.06—0.10	0.1*—0.2	0.1*—0.2	< 0.12
	Shoots	0.09—0.18	0.10—0.18	0.08—0.10	0.08—0.11	0.09—0.12	0.07—0.11	0.1*—0.2	0.1*—0.2	< 0.11
	Seedlings	0.10—0.24	0.11—0.24	0.08—0.12	0.10—0.13	0.11—0.13	0.09—0.13	0.1*—0.2	0.1*—0.2	< 0.12
K	Leaves	0.4—0.9	0.4—0.9	0.5—0.9	0.3—0.7	0.3—0.7	0.3—0.6	0.5—1.5	0.5—1.6	0.4—1.2
	Shoots	0.5—1.0	0.4—1.0	0.6—1.0	0.3—0.7	0.3—0.7	0.3—0.6	0.4—1.2	0.4—1.3	0.4—1.0
	Seedlings	0.5—1.2	0.5—1.1	0.7—1.3	0.3—0.7	0.3—0.7	0.3—0.6	0.3—1.3	0.3—1.3	0.3—1.0
Ca	Leaves	0.03*—0.04	0.03*—0.04	0.03*—0.06	0.02*—0.09	0.02*—0.13	0.02—0.10	0.06—0.16	0.06—0.16	0.05—0.16
	Shoots	0.03*—0.04	0.03*—0.04	0.03*—0.05	0.02*—0.09	0.02*—0.12	0.02—0.09	0.05—0.15	0.05—0.14	0.05—0.14
	Seedlings	0.03*—0.04	0.03*—0.04	0.03*—0.05	0.02*—0.09	0.02*—0.12	0.03—0.09	0.05—0.15	0.05—0.14	0.05—0.14
Mg	Leaves	0.05—0.12	0.05—0.12	0.04—0.13	0.02—0.09	0.02—0.10	0.02—0.08	0.10—0.17	0.10—0.17	0.10—0.17
	Shoots	0.05—0.13	0.05—0.13	0.04—0.14	0.02—0.10	0.02—0.11	0.03—0.09	0.09—0.14	0.09—0.14	0.09—0.14
	Seedlings	0.05—0.12	0.05—0.11	0.05—0.12	0.03—0.10	0.03—0.11	0.03—0.09	0.08—0.12	0.08—0.13	0.08—0.12
S	Leaves	0.06—0.20	0.06—0.21	0.05—0.07	0.09—0.13	0.10—0.13	0.07—0.17	0.22—0.29	0.23—0.29	0.16—0.28

* Extrapolated values (*cf.* p. 81).

part is retained in soluble form. The quite even distribution of the percentages in the leaves and roots (Figures 21—23, p. 40) indicates that the upward translocation occurs easily.

Few investigations are available with analytical results from different organs of forest tree seedlings. Mitchell (109) found that the nitrogen content in pine leaves is somewhat higher than in whole seedlings but that the variations are proportional. Judging from Bensend's (10) data the content is usually somewhat lower in the roots than in the shoots of Pinus banksiana. In the same species Swan (161) found that the nitrogen content in the stems was lower than in the leaves and that the difference is less pronounced for potassium, magnesium, and especially phosphorus. Fowells and Krauss (43) analyzed nitrogen and phosphorus in leaves, stems, and roots of Pinus taeda and P. Virginiana. The nitrogen percentages practically throughout were lowest in the stems and highest in the leaves and also the phosphorus percentage was lowest in the stems but of the same order in leaves and roots. These results differ from the present mainly in that the percentages in the stems are higher in the present study and that, consequently, the percentages in the shoots will be higher. The reason for the difference is undoubtedly that the lignification of the stems has not proceeded so far in the present experiments as in the others mentioned.

2. *Examples of Different Content/Growth Relations*

It is seen that in the present study the analytical results from any organ or from shoots or whole seedlings are, on the whole, utilizable for diagnosis of the nutrient status of the seedlings since all percentages varies univocally with the supplies or the growth of the seedlings. It is also evident, however, that the element concentrations are not always the same in all organs, and, therefore, the relations between internal content and growth will often depend on the material that is analyzed. Nor is it always of minor importance what growth measurements are used in the relation. A content that corresponds to moderate or even strong deficiency when related to the seedling or shoot dry weight may correspond to maximum or nearly maximum development of the roots.

In Table 27 the percentage intervals corresponding to moderate deficiency (*cf.* p. 80) are given when the growth is expressed as dry weight of seedlings, shoots, or roots and when the contents of leaves, shoots, or seedlings are used. The percentages are interpolated (or extrapolated) in the same way as described above (p. 81). It is seen that the percentage ranges vary differently depending on the element or species involved. Whereas the variations are relatively small in the case of potassium, calcium, and magnesium, except for potassium in birch, the intervals of nitrogen and phosphorus are sometimes very strongly influenced by the type of material analyzed or the growth measurements used.

3. *Conclusions*

The contents as per cent of dry weight are often different in the various parts of the seedlings and different growth characteristics are dependent on the nutrient status of the seedlings in a sometimes highly variable way. The internal element percentage in samples consisting of more than one organ depends partly on the fraction of the total dry weight of the organs and partly on the percentage levels in them. It is seen from the present investigation that the quotient between the dry weights of the leaves and stems is approximatively independent of the nutrient status of the seedlings (Table 32, p. 104), but in spruce and especially birch strongly dependent on the length of the growth period (Table 31, p. 102). It is also found that the time trend in the internal percentages is greater in the stems than in the leaves or roots in spruce as well as birch (Table 16, p. 46). In the pine seedlings these factors are of little importance within the experimental period. Thus, it is obvious that the significance of the analytical results obtained in certain organs or in samples composed of more than one organ may depend on the developmental stage of the seedlings.

It may be concluded that *the analyzed material and the growth measurements used in the percentage/growth relation ought to be well defined.* Analytical data from the roots are generally uncertain when solid root media are used. The stems are continuously lignified, which means a change with time in the significance of their nutrient percentages. *The leaves, therefore, may be regarded as preferable material for analysis,* especially in the field where they always can supply a comparatively uniform material from year to year (*cf.* 112).

Chapter VI. Morphological Effects of the Macro Nutrient Factors

A. Visual Deficiency Symptoms

1. *Description of the Deficiency Symptoms*

Deficiency symptoms of varying intensity were developed in each series of varied supply on one, two, or three treatments (Table 28). In pine and spruce the deficiency symptoms are very unspecific, but in birch certain patterns may be recognized for each element (*cf.* Chapter III, p. 25—47).

Table 28. Treatments causing deficiency symptoms

Element	Supply of respective element, ppm		
	Pine	Spruce	Birch
N	0.05, 0.5	0.5, 5.0	4.2
P	0.02	0.1	1.0
K	0.05, 0.5	0.15, 1.5	0.3, 3.0
Ca	0.004, 0.12	0.12, 1.2	0.4, 1.2, 12
Mg	0.015, 0.15	0.05, 0.15	0.5
S	0, 0.2	0, 0.2	0

Therefore, the symptoms in birch are summarized in Table 29, but a similar description of the symptoms in pine and spruce seems of little value.

In the earlier paper about birch (66) another potassium series was described than here. The potassium deficiency symptoms were in that series connected with strong chlorosis, which is generally not found in plants (*cf.* 192). In all later series a symptom picture similar to that of most other plants was developed and the first results could not be repeated. In the present paper the symptoms from the later potassium series are described.

Table 29. Descriptions of deficiency symptoms in birch

Element	Symptoms in the leaves	Symptoms in the roots
N	All leaves relatively small. Pale green to yellow colour. Anthocyanin spots on the underside Old leaves die.	Long and very thin roots.
P	Dark green colour and strong anthocyanin colouring on the underside. Leaf size not affected.	Violet to black root tips.
K	Old leaves dark green, young leaves with chlorotic margins. Buckled leaf-blades. In the chlorotic parts brown spots are developed.	Small and thin roots.
Ca	First dying leaf tips leading to more rounded leaves. Then whitened margins. Buckled leaf-blades fading from the tips. At last dying plant tops and formation of branches.	Short and very branched root systems.
Mg	First yellowing leaves with grey to brown spotted margins spreading over the whole leaf-blade. The leaves finally die.	No specific symptoms.
S	Colour as in nitrogen deficiency but no anthocyanin colouring. The symptoms restricted to the young leaves.	No specific symptoms.

a. Symptoms in the Leaves

Few descriptions of symptoms in birch are found in the literature. Nitrogen and potassium symptoms have been described by Tamm (175, 176) and Tamm and Ingestad (179), and manganese symptoms by Ingestad (67). In the earlier paper about birch iron deficiency symptoms were also described (66).

For pine and spruce, on the contrary, many symptom descriptions have been given, often in connection with colour pictures. Among the descriptions of micro nutrient deficiency symptoms may be mentioned iron (68, 69), manganese (67, 151), boron (90, 91, 151), copper (11, 138, 151), and zinc (151, 152, 198). Smith (151) also reported disturbances in connection with low molybdenum supplies in pine.

The macro nutrient deficiency symptoms are in the pine and spruce seedlings with exception of the phosphorus symptoms in pine all connected with chlorosis in the present experiments. This is in most cases in agreement with earlier results. The nitrogen deficiency symptoms consist of a diffuse chlorosis, short leaves, and dying older leaves. In the field it is characteristic that the leaves are short (175, 179) and in pine the leaves die early and are often shed after 1—1½ year. In nursery seedlings all leaves are generally chlorotic, and it is often found that the seedlings are darker green on the borders of a seedling bed than in the middle, which obviously is due to competition in the middle.

The chlorosis found in the youngest leaves of the spruce seedlings in phosphorus deficiency in the present study has not been observed in other investigations (*cf.* 73, 161) and it is possible that it depends on the continuous growth of spruce in the present experiments. Under other conditions the seedlings usually produce top buds and stop growing after a time. Purple colouration is found in old leaves of spruce but not of pine. Jessen (73) found no anthocyanin colour in spruce but Swan (161) reported this as the most characteristic symptom in Picea glauca and P. mariana. In pine van Goor (50) found dark green colour of the leaves, especially of the older, but mostly the symptoms are described as a purple colouration of the leaves (73, 111, 118). Swan (161) reported no such colouring in Pinus banksiana but brown leaf tips as most characteristic. In the author's experience from nurseries, pine is often coloured more or less dark purple in the autumn, which in practice is interpreted as a quite normal "winter colouring". However, the impression is that this colouring is dependent on both the nutrient status of the seedlings and hereditary properties.

Potassium deficiency symptoms seem to vary in spruce with age. Thus, in older trees chlorosis is found in the older leaves (179) but in seedlings the tops are coloured yellow to brown (16, 70, 74, 173). In the present investigation the symptoms were similar to those reported by Swan (161) with chlorosis of the young leaves and brown leaf tips. Similar in type are the calcium deficiency symptoms, which is in agreement with Mitchell's (111) and Davis' (31) results with pine.

The magnesium deficiency symptoms are fairly characteristic in the conifer seedlings, especially in spruce. The leaf tips are bright yellow with a sharp border against the green bases. In strong deficiency the green part is small and the leaf tips die and become brown. The symptoms are, thus, very similar to those reported earlier (*e.g.* 8, 9, 24, 65, 70, 71, 74, 118, 121, 128, 161, 181, 182, 183). It ought here to be mentioned that the nomenclature concerning potassium and magnesium deficiency is somewhat confusing. In the German literature the magnesium deficiency symptoms in pine have often been described as "Gelbspitzigkeit" (8, 128). A similar term has been used for potassium deficiency in spruce, namely "yellow tip disease" (16, 173), which also is used to denote copper deficiency in cereals, especially oats (22, 192).

The sulphur deficiency symptoms are connected with chlorosis of the young leaves. This pattern is not always found in plants. Baumeister (7) mentions in his review that sulphur deficiency symptoms typically are similar to those of nitrogen. Eaton (40) found that black mustard showed chlorosis first in the upper leaves as also soybean (38), tobacco (103) and the tea bush (155). On the other hand, Eaton (39) found no such gradation in sunflower, and Nightingale *et al.* (130) reported that the oldest leaves were affected first in tomato.

b. Symptoms in the Roots

In some cases deficiency symptoms are also found in the roots. For birch these symptoms are described in Table 29 and similar symptoms were found in the pine and spruce roots.

2. *Element Percentages in the Leaves Corresponding to Deficiency Symptoms*

The deficiency symptoms develop with time and there is generally no definite limit between presence and lack of symptoms. It is seen in the time series that the internal element concentrations decrease with time, especially at low supplies (Table 16, p. 46). The symptoms seem to appear first after a certain percentage level is reached. In the case of nitrogen there is a continuous change in the leaf colour from pale yellow to dark green with increasing content, which has also been pointed out earlier (*e.g.* 111). A characteristic limit of appearing symptoms, therefore, may be difficult to define in such a case, and it seems most appropriate to state a range of

Table 30. Element percentages in the leaves and relative growth levels corresponding to deficiency symptoms. Limit values are known only in some cases of weak symptoms. In other cases ranges corresponding to strong and no symptoms are given

Element	Pine		Spruce		Birch	
	Content, % of dry weight	Relative growth, % of maximum	Content, % of dry weight	Relative growth, % of maximum	Content, % of dry weight	Relative growth, % of maximum
N	0.7—1.6	28—72	1.0—1.7	56—85	1.5—3.1	20—72
P	0.06—0.09	28—68	0.05—0.11	22—100	0.12	69
K	0.3	39	0.3	64	0.5	56
Ca	0.05	98	0.02	77	0.12	85
Mg	0.06	69	0.02—0.07	52—74	0.06—0.18	22—100
S	0.07	86	0.13	69	0.06—0.21	9—43

percentages within which the yellowing is developed. In other cases the symptoms appear quite suddenly with decreasing internal element concentration, and then it is possible to determine an approximate limit value of the content corresponding to the appearance of symptoms.

In the present experiments deficiency symptoms of varying intensity were visible at the time of harvest in certain treatments but at the next higher supply symptoms were lacking. When the symptoms are weak, the corresponding percentage may be used as an approximate limit value, but when they are strong a limit value cannot be settled even if it may exist but, as for nitrogen, only a range corresponding to strong — no symptoms (Table 30).

It is obvious that the growth values corresponding to deficiency symptoms are not very certain because of the time factor and that the content/growth curves are usually steep within the region where symptoms appear. However, they are given in Table 30 only to demonstrate that symptoms in some cases may appear also when the seedling dry weight is very little affected (calcium). In other cases they are related with very strong growth reductions (sulphur in birch, potassium in pine and birch).

Nitrogen. Mitchell (111) reported visual nitrogen deficiency symptoms in Pinus strobus at nitrogen contents of 0.7—1.3 per cent in the shoots. Swan (161) found symptoms in Pinus banksiana at 1.32—1.52 per cent in the shoots and evident symptoms in Picea glauca and P. mariana at contents up to 1.28 and 1.01 per cent respectively. According to Süchting (163) symptoms occur at contents up to 1.2 per cent in pine as well as spruce and reported later (166) that 0.84—1.11 per cent in the shoots of pine corresponded to strong and 1.03—1.37 per cent to weak symptoms. These levels are in good agreement with the present results (Table 30). No corresponding values for birch have been found in the literature.

Phosphorus. Evident phosphorus deficiency symptoms are found by Swan (161) at 0.07 per cent in shoots of Pinus banksiana and at 0.10 per cent in Picea glauca and P. mariana. Fowells and Krauss (43) reported symptoms in Pinus taeda and P. Virginiana at 0.10 per cent phosphorus in the leaves. Süchting (162, 163, 164, 165) found 0.09 per cent in the shoots of both pine and spruce to be the limit value for deficiency symptoms but reported later (166) for pine that weak symptoms corresponded to contents up to 0.16 per cent and strong up to 0.09 per cent. The agreement with the values found here is generally good (Table 30).

Potassium. In all three species weak symptoms of potassium deficiency were found on some treatment in the present experiments and the corresponding percentages may be regarded as limit values (Table 30). The agreement with earlier reported values is very good. Heiberg and White (57) found symptoms in Pinus resinosa at 0.30 per cent potassium in the leaves and reported symptoms in Picea glauca and P. abies at 0.13—0.21 per cent. In Pinus strobus Walker (190, 191) found symptoms at 0.4 per cent in the leaves and the corresponding value for Pinus nigra was found at 0.30 per cent by van Goor (49). Swan (161) reported symptoms in Pinus banksiana at contents up to 0.39 per cent and in Picea glauca up to 0.26 per cent in the shoots. In Picea mariana Swan found strong symptoms at 0.20 per cent. In Pinus silvestris van Goor (49) reported 0.35 per cent and Wittich (200) 0.4 per cent in the leaves at weak symptoms. Süchting (162, 163, 165) found in pine and spruce symptoms at 0.33 per cent in the shoots.

Calcium. With the exception of Mitchell's (111) results no analytical data corresponding to calcium deficiency symptoms in forest tree species are found in the literature. Mitchell reported symptoms in Pinus strobus when the calcium content in the shoots appear to have been 0.23 per cent. This value is, thus much higher than the limit value found here for Pinus silvestris (Table 30). It is seen above (p. 85—87), that Mitchell's results are very divergent from other values of phosphorus, potassium, and calcium found here and in the literature. Nemec's observations in forest stands (*e.g.* 125, 126) do not seem to be related to calcium deficiency but rather to the lime status of the soil (*cf.* p. 87).

Magnesium. Swan (161) found strong symptoms in Pinus banksiana at magnesium contents in the shoots of 0.05 per cent, weak symptoms at 0.06 per cent and very weak symptoms at 0.13 per cent. In Picea glauca and P. mariana Swan found strong symptoms at 0.06 and 0.03 per cent and less pronounced symptoms at 0.08 and 0.07 per cent respectively. Becker-Dillingen (8, 9) reported contents of 0.0078—0.070 per cent in the leaves of pine with symptoms and healthy leaves at 0.037—0.080 per cent. Nemec (128) reported for Pinus strobus and P. silvestris symptoms at 0.078—0.089 per cent and healthy seedlings at 0.12—0.13 per cent magnesium. Stone (154) reported pronounced symptoms in Pinus resinosa, P. strobus, and P. banksiana at magnesium contents in the leaves of 0.08—0.12 per cent and weak symptoms up to 0.15 per cent. Themlitz (181, 182, 183) determined the limit percentage as 0.06 per cent magnesium in leaves of Pinus silvestris, which is in good agreement with the value found here and in nursery samples (*cf.* 70, 71).

Sulphur. No values for sulphur have been found in the literature corresponding to deficiency symptoms in forest tree species.

3. *Conclusions*

Deficiency symptoms are used for convenience in diagnosing insufficient nutrition. Many standard works have been published with colour pictures to faciliate the diagnosis (*e.g.* 22, 192. See also 7). In many cases the symptoms are specific enough for a safe diagnosis but not always. Pine and spruce have no differentiated leaf blade area that may show significant symptom patterns. In the field the symptoms are often disturbed by secondary damages caused by, for instance, fungi that easily attack affected leaves. Further more, the symptoms develop with time and may show many stages that sometimes are very different from each other. Often the symptoms develop slowly under a constantly low but not very low nutrient availability, in other cases they appear suddenly, for instance in connection with great rain amounts, and the resulting symptoms may be very different in type. Thus, there are many difficulties in the application of the diagnosis of visual symptoms, especially in the conifers. *It seems, therefore, generally important and sometimes necessary to complete the visual observations with leaf analysis for a safe diagnosis of the cause for the symptoms.*

The close agreement between different values corresponding to deficiency symptoms reported in the literature and between these and the present findings indicates that *the internal concentration level of the elements is of decisive importance for the symptom appearance and that the foliar analysis is very useful in the diagnosis of deficiency symptoms.* In one case, however, different observations are varying and contradictory, namely for magnesium. Thus, deficiency symptoms have been reported in pine at contents in the leaves from 0.0078 to 0.15 per cent, whereas healthy leaves have been found to contain as low as 0.037 per cent magnesium. This would mean that leaf analysis is not applicable for diagnosing magnesium deficiency. However, the correctness of a so low value as 0.0078 per cent magnesium in the leaves of pine may be questioned, since in the present material the minimum percentage does not seem to be lower than about 0.02 per cent (Figure 18, p. 36). The author has in forest tree nurseries confirmed very closely the values found in the laboratory and found great mutual similarity between different field samples (70, 71). The differences between the values in the literature seem to depend on lacking accuracy in the sampling and analytical methods, and it may be remembered that the deficiency symptoms in pine are very unspecific and that they are not always shown to be really caused by magnesium deficiency in earlier works.

The agreement between the values corresponding to deficiency symptoms found here and earlier reported values is usually better than for the optimum values. This is quite natural because deficiency symptoms represent an easily recognized status that is not the case of maximum growth. Further more, the symptoms seem to develop under relatively slight influences of other factors than the nutrients. The close agreement also confirmes the statement made above (p. 90) that the percentage values found here seem to have a high validity despite the extreme growth conditions in the present experiments.

Björkman (16) and Tamm (173) have discussed the possibility that high levels of calcium may induce potassium deficiency and proposed the use of quotients between the elements in the diagnosis. The present data do not support this view and in no case does a high supply of the cations cause such low contents of any of the others that they correspond to the levels of deficiency or deficiency symptoms. It is possible that interactions are of importance at certain limit conditions but a high or low quotient between the elements may as well indicate deficiency of one of the elements as toxicity of the other. In the present author's opinion the analytical values are, therefore, most practicable as such for diagnosing the cause for deficiency symptoms, but still under consideration of the percentages of the other elements as was also stated above (p. 71).

B. Toxicity Symptoms

In some cases toxicity symptoms were recorded in the experiments. Since at least two ions were supplied in high concentrations in these cases, it is not possible to establish certainly the cause (*cf.* p. 50—56). The toxicity symptoms consisted of brown spots of dead tissues in the margins and tips of the birch leaves and of brown leaf tips in pine and spruce. Sometimes chlorosis was present. The symptoms appeared at high supplies of nitrogen, calcium, and sulphur in pine and spruce and of potassium and sulphur in birch.

C. Other Morphological Effects

1. Changes in the Morphological Properties with the Age of the Seedlings

With increasing growth time the proportions between the different parts of the seedlings are changed (Figures 25—27, p. 45). The leaf fraction of the total dry weight decreases with time in all three species. The root/shoot quotient, on the other hand, increases in the pine and spruce seedlings, which is especially pronounced at low nitrogen supply, but is in the birch seedlings quite constant (Table 31). The stem/leaf quotient in pine is nearly constant throughout, but it increases in spruce and birch with time. Thus, in pine only the root fraction of the total dry weight increases with time and in birch only the stem fraction, whereas in spruce the root as well as the stem fraction increases.

The relations between the length and weight growth of the stems and roots are strongly affected by the growth time (Table 31). The weight increases several times more than the length and the quotient between them in the control seedlings of birch is nearly 10 times greater on the fourth harvest occasion than on the first in both roots and stems.

Table 31. Relations between different growth data at various lengths of the growth periods

Treatment	Harvest	Dry weights						Dry weight, mg/length, mm					
		Root/shoot			Stem/leaves			Roots			Stems		
		Pine	Spruce	Birch	Pine	Spruce	Birch	Pine	Spruce	Birch	Pine	Spruce	Birch
Control	1	0.23	0.15	0.11	0.24	0.30	0.37	0.16	0.22	0.16	0.21	0.24	0.19
	2	0.28	0.17	0.10	0.22	0.31	0.55	0.23	0.44	0.41	0.27	0.46	0.48
	3	0.40	0.21	0.10	0.23	0.57	0.74	0.44	0.63	0.90	0.35	0.97	1.06
	4	0.40	0.23	0.10	0.23	0.63	0.97	0.61	0.72	1.58	0.63	1.25	1.77
Low N	1	0.29	0.21	0.15	0.22	0.28	0.41	0.18	0.32	0.25	0.22	0.25	0.24
	2	0.35	0.39	0.14	0.21	0.28	0.52	0.26	0.54	0.39	0.26	0.33	0.48
	3	0.58	0.62	0.13	0.24	0.36	0.83	0.40	0.55	0.63	0.40	0.55	0.88
	4	0.76	0.64	0.15	0.24	0.46	0.88	0.56	0.70	1.06	0.48	0.77	1.16
Low K	1	0.15	0.19	0.23	0.30	0.29	0.36	0.08	0.22	0.26	0.30	0.22	0.14
	2	0.23	0.26	0.10	0.26	0.30	0.60	0.16	0.45	0.44	0.32	0.32	0.47
	3	0.33	0.30	0.14	0.25	0.37	0.61	0.28	0.46	0.81	0.33	0.63	0.71
	4	0.33	0.35	0.17	0.24	0.42	0.54	0.40	0.54	1.04	0.39	0.72	0.82

The relations between the different seedling parts are very different in the three species and with increasing growth time these differences become more and more pronounced (Figures 25—27, p. 45). The most obvious difference is that the conifer seedlings have a comparatively great dry weight fraction in the roots. At the same growth time the birch seedlings have utilized a greater fraction of the total dry matter production in the stems than the conifer seedlings and a smaller fraction in the leaves. The difference between the birch and conifer seedlings is also marked when it comes to the growth pattern of the root systems. Thus, the roots of the birch seedlings reach within a comparably short time a great degree of branching and, consequently, a high weight/length ratio of the roots (Table 31) in spite of the fact that the individual root threads are much thinner than in the conifer seedlings.

2. *Effects of Varied Nutrient Supply*

Shoot Development. In forestry the size of the tree crowns and amount of foliage have by many workers been related to the stem production and the crowns were found to have an optimum size (*e.g.* 25, 33, 159). Stålfelt (159) analyzed this optimum curve for spruce and came to the conclusion that the water and light (self-shading) factors were limiting the stem growth of trees with great foliage amounts. Thus, in the field there seem to be branches that have a low assimilation and that diminish the production rather than increase it. In the present experiments the water and light factors are practically constant for the seedlings and, therefore, it is possible to study the effects of the nutrients on *the stem/leaf quotient* of the seedlings. It is seen from Table 32 that *this quotient is practically independent of the nutrient factor* and that low values are found only at some of the lowest supplies. It was shown in the earlier papers in diagrams that the correlation is very strong and the ratio between the stem and leaf dry weights is close to 0.27, 0.47, and 0.56 for pine, spruce and birch respectively (66, 68, 69). The ratio, on the other hand, is influenced by the seedling age (Table 31).

It is seen that *the ratio between the weight and length of the stems* (Table 32) *is very strongly influenced by the nutrient factors.* This depends obviously on a strong diameter growth and probably also on the lignification and specific weight of the stems.

Root Development. The weight/length quotient of the root system is strongly influenced by the nutrient factors in all three species (Table 32) and it is seen that the highest values are generally found at optimum nutrition. Especially low values are found in nitrogen, potassium, and sulphur deficiency in pine and spruce and in all deficiencies but for phosphorus in birch where strong phosphorus deficiency is not reached

Table 32. Relations between different growth data at varied element supply

Element	Treatment	Dry weights						Dry weight, mg/length, mm					
		Root/shoot			Stem/leaves			Roots			Stems		
		Pine	Spruce	Birch	Pine	Spruce	Birch	Pine	Spruce	Birch	Pine	Spruce	Birch
Nitrogen	1	1.02	0.73	0.35	0.29	0.34	0.55	0.14	0.21	0.51	0.15	0.29	0.41
	2	1.04	0.60	0.12	0.35	0.43	0.58	0.21	0.38	0.91	0.22	0.53	0.81
	3	0.84	0.32	0.12	0.31	0.44	0.60	0.45	0.50	1.18	0.40	0.63	0.99
	4	0.38	0.26	0.12	0.27	0.46	0.55	0.43	0.56	1.00	0.55	0.75	0.84
	5	0.36	0.27	0.12	0.31	0.46	0.55	0.45	0.54	1.05	0.55	0.71	0.80
	6	0.27	0.23		0.23	0.50		0.36	0.46		0.61	0.74	
Phosphorus	1	0.78	0.65	0.18	0.25	0.30	0.57	0.17	0.26	1.01	0.20	0.28	0.80
	2	0.48	0.31	0.12	0.25	0.43	0.60	0.39	0.60	1.01	0.41	0.78	0.96
	3	0.34	0.28	0.12	0.27	0.43	0.60	0.39	0.55	1.18	0.52	0.71	0.99
	4	0.38	0.26	0.15	0.27	0.46	0.52	0.43	0.56	0.86	0.55	0.75	0.61
	5	0.36	0.27	0.14	0.29	0.48	0.50	0.42	0.53	0.86	0.52	0.79	0.66
	6	0.35	0.24		0.28	0.47		0.34	0.52		0.48	0.73	
Potassium	1	0.26	0.20	0.15	0.25	0.28	0.35	0.14	0.20	0.20	0.19	0.26	0.30
	2	0.28	0.34	0.14	0.24	0.42	0.61	0.28	0.46	1.20	0.32	0.62	1.24
	3	0.31	0.26	0.14	0.29	0.52	0.64	0.39	0.74	1.52	0.52	0.73	1.15
	4	0.38	0.26	0.12	0.27	0.46	0.59	0.43	0.56	1.55	0.55	0.75	1.27
	5	0.32	0.28	0.12	0.26	0.42	0.63	0.39	0.52	1.63	0.50	0.64	1.35
	6	0.36	0.23	0.18	0.25	0.41	0.45	0.36	0.42	1.67	0.42	0.56	1.06
Calcium	1	0.32	0.25	0.16	0.26	0.40	0.56	0.38	0.70	0.20	0.42	0.59	0.32
	2	0.32	0.24	0.12	0.26	0.39	0.46	0.38	0.72	0.79	0.51	0.67	0.75
	3	0.35	0.36	0.12	0.26	0.41	0.57	0.42	0.75	1.02	0.51	0.68	0.83
	4	0.38	0.26	0.12	0.27	0.46	0.60	0.43	0.56	1.18	0.55	0.75	0.99
	5	0.29	0.26	0.10	0.29	0.47	0.55	0.27	0.47	0.74	0.48	0.70	0.84
	6	0.29	0.22		0.27	0.44		0.36	0.31		0.49	0.62	
Magnesium	1	0.49	0.20	0.16	0.26	0.24	0.61	0.26	0.21	0.29	0.29	0.26	0.31
	2	0.36	0.24	0.16	0.28	0.28	0.54	0.35	0.40	1.06	0.45	0.39	0.69
	3	0.33	0.30	0.14	0.27	0.47	0.57	0.33	0.46	0.99	0.48	0.59	0.80
	4	0.38	0.26	0.14	0.27	0.46	0.55	0.43	0.56	0.87	0.55	0.75	0.69
	5	0.29	0.26		0.26	0.43		0.40	0.46		0.48	0.63	
Sulphur	1	0.50	0.56	0.32	0.31	0.49	0.67	0.06	0.22	0.13	0.13	0.24	0.22
	2	0.40	0.26	0.16	0.32	0.40	0.58	0.22	0.46	0.38	0.41	0.45	0.46
	3	0.33	0.18	0.12	0.25	0.44	0.62	0.29	0.56	0.88	0.35	0.58	0.79
	4	0.32	0.25	0.11	0.32	0.48	0.65	0.39	0.60	0.95	0.40	0.55	0.86
	5	0.30	0.22	0.12	0.25	0.44	0.55	0.38	0.44	0.34	0.39	0.50	0.52
	6	0.32	0.22	0.18	0.25	0.39	0.50	0.26	0.34	0.37	0.31	0.41	0.46

within the experiments. The weight/length ratio of the root systems is dependent on the diameter growth of the individual root threads, but it is visually noticed in the experiments that this factor may be considered to be of comparatively little importance. More decisive, no doubt, is the intensity of the branching of the root systems that varies to a considerable degree with varied element supply. The weight/length ratio may, therefore, be regarded as a rough expression of the branching intensity of the roots. Thus, it may be concluded that *the nutrient deficiencies lead to poorly branched roots and a predominating length growth except for calcium in pine and spruce.* The special effect of calcium deficiency on the root systems, namely that the meristems die leading to increased branching (Table 29, p. 95) is manifested in the weight/length ratio of the conifer seedlings. In birch the calcium deficiency leads to so strong effects that the root branches become very short and the root systems as a whole are, therefore, thin and have a low weight/length ratio also in calcium deficiency. The results of the calcium series of pine and spruce confirm the statement that the weight/length ration is a measure of the root branching as far as the general effect on the root development is not too strong as in birch.

The Root/Shoot Quotient. The relative growth of the roots in relation to the shoots is affected in certain nutrient deficiencies (Table 32). Thus, it is seen that *the root/shoot quotient is high in nitrogen and sulphur deficiency in all three species and also in phosphorus deficiency in pine and spruce.* In other cases the ratio is little or not affected by the nutrition.

3. Conclusions

It is seen that the nutrient status of the seedlings is of great importance for their morphological development. The stem growth, however, seems to depend on the amount of assimilating leaves and not on the nutrient factors directly, contrary to what is found for the relative root growth in certain deficiencies. The effect of especially nitrogen deficiency on the root/shoot quotient has long been known and was by Reid (140, 141) related to the nitrogen/carbon quotient of the plants. The nutrient status, however, influences also the growth type of the roots and the branching of the root systems.

In forestry practice an important procedure is the production of seedlings in nurseries for plantation. The central problem is then to produce seedlings that easily adapt themselves to the new locality and begin a valuable production. Thus, it is obvious that it is not at first hand a question of mass but of quality production and, consequently, the relation nutrition/growth is of less interest than the relation nutrition/quality in this context. Yet, little is known about the properties of the seedlings that are most important for the quality. Björkman (17, 18, 19) stated that mycorrhiza ought to be present in the seedlings and these are preferably developed under low fertilization (15). Nemec (120, 127), on the other hand, found that rich and balanced fertilized seedlings showed the best development after plantation. Very heavily and excessively fertilized (NPK) seedlings seem to have a good development after plantation, and frequently they are more vigorous than seedlings that are poorly or incompletely fertilized (18, 19). The question about appropriate fertilization in forest nurseries is, thus, quite confused. It seems, however, as if the mycorrhiza is of secondary importance and that other properties of the seedlings are more decisive.

Björkman (19) was of the opinion that the importance of a high root/shoot quotient has been exaggerated, stating it more important that the seedlings have a root system able to develop rapidly in the new site. A root system of this kind is characterized mainly by dense branching and this may be obtained by transplanting in the nursery or by root pruning (19), but probably also to a certain extent by an adequate fertilization judging from the present results. The occasionally used method of increasing the root/shoot ratio by low nitrogen fertilization seems inappropriate because a relatively large but long and thin root system is heavily reduced in the lifting and planting of the seedlings. The present data indicate that from a quality point of view the seedlings would be best at optimum nutrition.

Chapter VII. Comparisons between the Nutritional Properties of the Species

The properties of the three species studied are in many ways fundamentally different, which makes it difficult to distinguish clearly the physiological differences in nutrition. Thus, the growth rates at optimum nutrition are very different (Figure 24, p. 44), which made it necessary to use somewhat different experimental conditions (duration of the growth periods, composition of control solutions). Further more, it is seen that the morphological characteristics are different, which, among other things, means that the internal nutrient concentrations as expressed on dry weight basis lie on different levels (Table 26, p. 81). It is, however, also clear that certain differences are due to differences between the species in their specific nutrient physiology. The intention in this chapter is to demonstrate such specific differences.

From the earlier chapters the following differences may be summarized:

1. The birch seedlings have, on account of their higher growth rate, the highest nutrient uptake per seedling, and spruce has the lowest. If the nutrient uptake is put in relation to the dry weight of the seedlings the differences between the species are less pronounced. In relation to the fresh weight the nutrient uptake is nearly the same for the three species (*cf.* p. 67—70).

2. The birch seedlings have a tendency to utilize the supply most rapidly, and the spruce seedlings most slowly (p. 67).

3. The requirements of the various elements come in the same order for the three species except calcium, for which element the pine seedlings have a low requirement. The birch seedlings have in relation to the dry matter production a general tendency to a higher nutrient requirement than the pine seedlings. Within the sub-optimum region the requirements of the pine seedlings is also somewhat lower than those of the spruce seedlings. In relation to the fresh weight the differences between the species in requirements are less obvious (p. 76—77).

The relations between the species, however, may also be considered from another point of view. Thus, *they may be compared on the basis of their sensitivity to certain external or internal situations or changes in the nutritional conditions in relation to a certain defined status, for instance, the optimum.* This method was used by Mitchell and Chandler (112) in their comparison between the nitrogen requirements of some hard wood species. They divided the species into three groups: Group I, "nitrogen-deficiency tolerant" species "which are apparently capable of sustaining relatively satisfactory rate of growth in nitrogen-deficient soils, and which approach maximum radial increment at significantly lower levels of nitrogen supply than do species of the other two groups", Group II, "intermediate" species, and Group III, "nitrogen requiring" or "nitrogen demanding" species "which are infrequent or absent on poor sites, make relatively meagre growth in nitrogen-deficient soils, and attain maximum growth only at very high levels of nitrogen availability". They found also that "the only reliable basis for comparison, or index to nitrogen tolerance, is the degree to which trees growing on such (nitrogen-deficient) sites approach, in internal nitrogen concentration, the experimentally determined optimum for the species".

The concept of tolerance to describe the nutritional properties of different species has been used by Mitchell and Chandler in spite of the fact that it is usually used in connection with shade tolerance, because they were of the

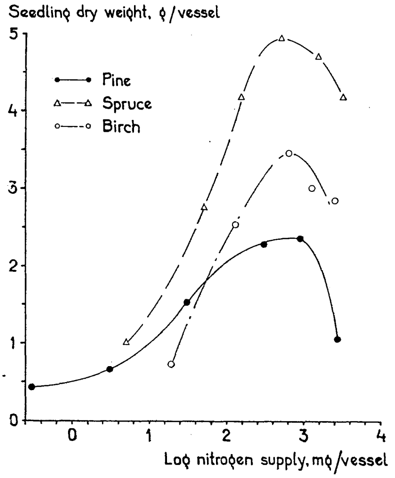


Fig. 39.

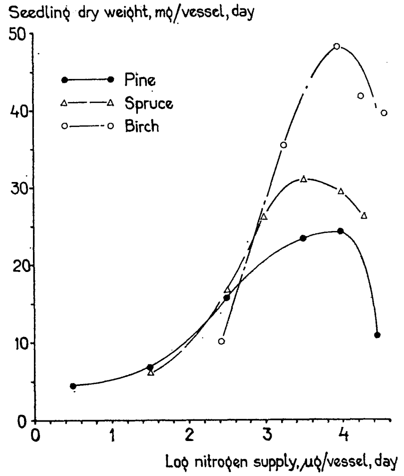


Fig. 40.

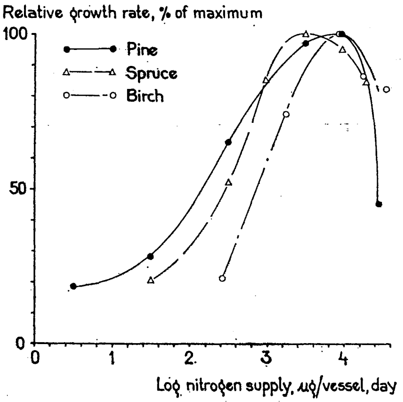


Fig. 41.

Figures 39—41. Relations between supply and growth in the nitrogen series.

Figure 39. Dry matter production per vessel at different total nitrogen supplies per vessel.

Figure 40. Average rates of dry matter production per vessel at different rates of nitrogen supply.

Figure 42. As in Figure 41 but with the growth rate maximum of each species put equal to 100.

opinion that the coining of a new term was not motivated. It seems to the present author that the nutritional properties of the forest tree species are very adequately described by means of the concept "nutrient tolerance", because the interesting problem is the differences between the species in sensitivity to the nutritional conditions of a site.

The concept of nutrient tolerance, in the meaning it will be used here, is best put in its connection by means of the general, ecological definitions used by Stålfelt (160, p. 19—20): "The optimum curve reflects the relative *sensitivity* or *tolerance* of the individual species to the ecological factor. A relatively great distance between the minimum and maximum values means a great tolerance, that is, the species is able to exist at comparably low as well as high degrees of strength of the actual factor; the species is said to have a great ecological amplitude for the factor or it shows a relatively low sensitivity to variations in the factor. In cases when a species is pronouncedly insensitive to variations in a factor, the optimum appears with a broad and flat course. The more sensitive the species is to a factor, the narrower the optimum and the shorter the distance between the minimum and maximum values; the broader the optimum, the greater the tolerance." (Translated from Swedish by the present author.)

1. Tolerance to Variations in the Nutrient Factors (Nutrient Tolerance)

In the present investigation the species have shown different dry matter production per vessel, which is demonstrated in Figure 39 by means of the nitrogen series. The curves here are not comparable because the growth periods are not of the same length for the three species. If the growth and supply values are divided by the growth time (number of days) attention is paid to a certain extent to this fact and then the curves in Figure 40 are obtained. It is now seen that the birch seedlings at low supplies show a lower rate of dry matter production per vessel than the pine and spruce seedlings, but at higher supplies the birch seedlings have the highest growth rate. Thus, *the birch seedlings are more nitrogen-requiring and especially the pine seedlings more nitrogen-deficiency tolerant.* The optimum nitrogen supply, however, is about the same for the pine and birch seedlings. In this respect the present results are different from the principle of Mitchell and Chandler (112) that a deficiency-tolerant species reaches the maximum at lower supplies than a requiring species (*cf.* Figure 17 in Mitchell and Chandler, 112). The essential difference lies instead in the course of the optimum curves in correspondence with the definition of Stålfelt as cited above; the nutrient tolerance and requirement for maximum growth are not related to each other. Thus, the optimum curve of the pine seedlings is comparatively broad and flat, that of the birch seedlings narrower (Figure 40), and *the pine seedlings have a high nitrogen requirement to reach maximum growth despite the relatively great nitrogen tolerance.*

These relations are best demonstrated in Figure 41, where the maximum growth is put equal to 100 for all three species and where the relative effects of a supply change on growth are seen. It is seen that the growth of the pine seedlings is changed from 50 per cent of maximum on the sub-optimum side to 90 per cent on the supra-optimum side if the rate of supply is changed (in logarithmic terms) from about 2.16 to 4.24, that is if the supply is increased about 120 times. The corresponding changes in the nitrogen supply for spruce and birch and in the other elements are approximately the following:

	N	P	K	Ca	Mg	S
Pine	120	650	200	40 000	3 000	3 000
Spruce	50	>250	200	1 500	250	1 000
Birch	30	200	150	150	150	150

It is seen that *with the exception of potassium there are differences, often very great, between the species in their nutrient tolerance and that pine may be regarded as the most and birch as the least tolerant.* In most cases the differences between pine and spruce are greater than between spruce and birch.

The tolerance to variations in the various elements is also different. Thus, *in all three species the tolerance is lowest in nitrogen and in pine and spruce highest in calcium. In birch the differences between the other elements except nitrogen are small. Especially remarkable is the extremely great tolerance of the pine seedlings to variations in the calcium supply.*

2. *Tolerance to Low Nutrient Supplies (Deficiency-Tolerance)*

When it comes to decisions about the more special question of the tolerance of the species to nutrient deficiencies, that is their ability to sustain growth at low nutrient availability (*cf.* 112), the growth must be studied entirely within the sub-optimum region. It is seen from Figure 41 that the lowest rate of nitrogen supply corresponds to 21 per cent of maximum growth in the birch seedlings. The same rate of supply means in spruce a growth of 48 per cent of maximum and in pine 62 per cent. Thus, birch has the lowest and pine the greatest relative dry matter production at this rate of supply. At the lowest supply in spruce this species has a growth of 20 and pine of 28 per cent of the maximum, which shows that the same relation

Table 33. Relative rates of dry matter production at low rates of supply. The lowest supplies of each species are represented

Element	Supply, microgram per vessel and day	Rate of dry matter production, per cent of maximum		
		Birch	Spruce	Pine
N	262	21	48	62
	31	—	20	28
	3.1	—	—	18
P	62	70	95	90
	6.2	—	22	54
	1.2	—	—	29
K	19	9	25	30
	9.4	—	14	24
	3.1	—	—	18
Ca	25	8	65	100
	7.5	—	51	100
	0.2	—	—	68
Mg	30	16	62	69
	3.1	—	24	50
	0.9	—	—	40
S	40	43	62	89
	0	14	24	20

exists between these species also at this lower supply rate. These values and the corresponding for the other elements are found in Table 33. It is seen that *the pine seedlings have the greatest and the birch seedlings the least tolerance to low supplies of the macro elements.* The difference between the species is relatively small for potassium and great for calcium.

3. *Nutrient Requirements for Maximum Growth*

The nutrient requirement to reach maximum growth is in most cases about the same for the three species (Figures 32—37). There is, however, a general tendency to a higher requirement of the birch seedlings than of the conifer seedlings. The pine seedlings have a tendency to a higher requirement of nitrogen, potassium, and sulphur than the spruce seedlings. The calcium requirement of pine is, on the other hand, very low in comparison to that of spruce and birch.

4. *Growth Response for Supply at Deficiency*

The tolerance of the species for variations in the nutrient supply and to deficiency is related to the width of the optimum curve and the growth at low supplies. The effect of a nutrient supply on growth when a deficiency exists may, on the other hand, be determined on basis of the width of the supply interval corresponding to 50—90 per cent of maximum growth on the sub-optimum side, that is an expression of the slope of the growth curve. How many times the supply has been increased to pass this growth interval is seen from the following approximate values for the different elements and species:

	N	P	K	Ca	Mg	S
Pine	10	15	5.5	5.0	150	25
Spruce	4.0	3.5	6.5	50	45	250
Birch	4.5	4.0	8.0	15	3.5	8.0

It is seen that *the pine seedlings show a comparatively small response to a nitrogen, phosphorus and magnesium supply and a strong response to a calcium supply in deficiencies of these elements. The birch seedlings respond, in comparison to the conifer seedlings, strongly for magnesium and sulphur. In the case of potassium the species are quite equal.*

5. Sensitivity to Variations in the Internal Nutrient Concentration

According to Mitchell and Chandler (112) the ability observed in a nitrogen-deficiency tolerant species to sustain growth in a soil with low nitrogen availability was "attributable to the fact that, on such sites, the internal nitrogen concentration of these trees is significantly greater, in relation to their respective optima, than for the intermediate or nitrogen-demanding species". In the present material this is not the case within the nitrogen series, which is seen from Figure 42 where the nitrogen percentage of the leaves expressed in relative values (the optimum percentage put equal to 100) is plotted against the rate of supply. It is found that *the species reach about the same relative values of nitrogen percentages in the leaves at the same rate of supply within the sub-optimum region despite great differences in their nitrogen-deficiency tolerance.*

The immediate explanation of the differences in nutrient tolerance between the species may be either differences in their uptake capacity at low supplies or differences in sensitivity to variations in the internal nutrient concentrations. The nutrient uptake capacity has been compared above (p. 67—70), and it was found that in the present experiments the birch seedlings commonly have a tendency to a greater uptake capacity in relation to the dry weight, whereas the difference between the species is small if the uptake

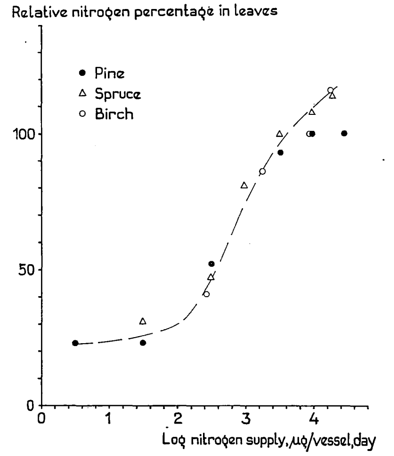
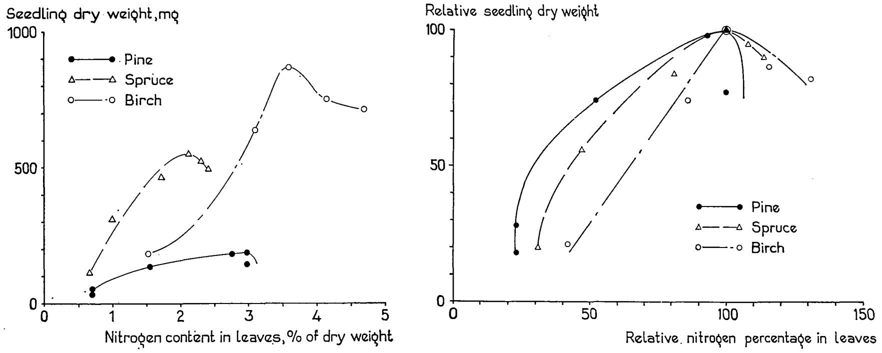


Figure 42. Relation between rate of nitrogen supply and relative nitrogen percentage in the leaves. The nitrogen percentage corresponding to the highest seedling dry weight is put equal to 100.

is put in relation to the fresh weight. Thus, the uptake capacity is rather opposite to the expected, since the least tolerant species (birch) has the greatest uptake capacity. Yet, for calcium it is noticed that the pine seedlings have a very high utilization at low supplies and a low utilization at high supplies and that they have a good growth also at high utilization (*cf.* p. 64) which may explain their great tolerance to variations in the calcium supply.

The sensitivity to variations in the nitrogen percentage of the leaves is seen from Figures 43 and 44. The growth and nitrogen content levels are very different in the three species and, therefore, the curves in Figure 43 are difficult to compare with regard to their sensitivity to variations in the percentages. In Figure 44 the maximum points of the three curves are put together (optimum percentages and maximum growth are put equal to 100). It is seen from this diagram that on the sub-optimum side the pine seedlings are less sensitive than the spruce seedlings to variations in the nitrogen percentage, in relation to their respective optima, and that the birch seedlings are most sensitive. Thus, *the explanation of the comparatively greater tolerance to variations in the nitrogen supply or to nitrogen deficiency of the pine seedlings seems to be mainly the lower sensitivity to variations in the sub-optimum nitrogen percentages in the leaves.* This low sensitivity is also present when it comes to the nitrogen percentage in the whole seedlings (Figure 32, diagram B).

The sensitivity to variations in the element percentage of the leaves in relation to the optimum may also be expressed in figures on the basis of the range of the percentage corresponding to the growth interval from 50 per cent of maximum on the sub-optimum side to 90 per cent on the supra-optimum side. On account of the difficulty in settling the optimum content



Figures 43—44. Relations between nitrogen percentage in the leaves and growth. In Figure 44 both percentage and growth are expressed relatively whereby the highest seedling dry weight of each species is put equal to 100 as also the corresponding percentages.

sufficiently accurately for most elements except nitrogen, it is not possible to get completely comparable values. If, however, the range of percentage is expressed as per cent of the mean value of the optimum content range (corresponding to 90—100—90 per cent of maximum growth) the following approximate values of comparison are obtained:

	N	P	K	Ca	Mg	S
Pine	70	115	95	160	85	85
Spruce	70	120	90	170	115	60
Birch	45	100	115	140	120	35

The range for nitrogen in pine is relatively narrow when calculated in this way, which depends on the steep course of the growth curve on the supra-optimum side (Figures 43 and 44). It is seen, however, that the birch seedlings are more sensitive to variations in the element percentages of the leaves, in relation to the respective optimum, than the conifer seedlings when it comes to nitrogen, phosphorus, calcium, and sulphur, but for potassium and magnesium they are less sensitive. The differences are greatest in the case of nitrogen and sulphur and are usually not so great between pine and spruce. *The lower nutrient tolerance of the birch seedlings seems, thus, to have its main explanation in the greater sensitivity to variations in the nutrient percentages of the leaves.* There is also a correspondence between the greater sensitivity to variations in the nitrogen percentage or the lower sensitivity in the calcium content variations and the fact that the species are found to be most tolerant to variations in the calcium supply and least tolerant to variations in the nitrogen supply.

On the other hand, it is seen that the sensitivity is great to variations in the sulphur percentage of the leaves but that the tolerance, nevertheless, is great to variations in the sulphur supply. This depends obviously on the fact that the sulphur uptake varies comparatively little with the supply (Figures 28—30, p. 65) as also, consequently, the sulphur percentages (Figures 21—23, p. 40). This means a high growth effect by a change in the sulphur percentage and a great uptake adaptation to the sulphur supply. This relation is still more pronounced for calcium in the pine seedlings. The very great tolerance to calcium supply variations is not connected with a correspondingly low sensitivity to variations in the calcium percentage of the leaves when pine is compared with the other two species. The explanation to this seems to be that the pine seedlings have a great capacity to utilize low calcium supplies and to grow at high utilization (p. 64), whereas high supplies are utilized to a small degree (Table 22, p. 62). *The great calcium tolerance of the pine seedlings seems, thus, to depend mainly on a great ability of adaptation in the calcium uptake to variations in the supply.*

6. *Conclusions*

From the experimental results certain conclusions have been drawn about the physiological nutrient properties of the species in comparison to each other, both in the relation between the seedlings and the nutrient medium and between the seedlings and the internal nutrient status. The differences

Table 34. Comparisons between the species in their nutritional properties

Properties		Pine	Spruce	Birch	Remarks
Nutrition tolerance		high	intermediate	low	Small difference for K
Deficiency tolerance		high	intermediate	low	
Requirement for maximum growth	N	high	low	high	Small difference for P and Mg
	K	intermediate	low	high	
	Ca	low	high	high	
	S	intermediate	low	high	
Response to supply at deficiency	N	low	high	high	Small difference for K
	P	low	high	high	
	Ca	high	low	intermediate	
	Mg	low	intermediate	high	
	S	intermediate	low	high	
Sensitivity to variations in the leaf percentages	N	low	intermediate	high	Comparably small differences for the other elements
	S	low	low	high	

between the species are summarized in Table 34. It is seen that the pine seedlings have a great tolerance to variations in the nutrient supply (nutrient tolerance) and a great deficiency-tolerance. The high tolerance is usually combined with a low response to a supply at deficiency. This, however, is not the case of calcium on account of a steep course of the growth curve on the sub-optimum side and the fact that the growth maximum is reached rapidly. The nutrient requirement for maximum growth is generally intermediate or low for the pine seedlings but in the case of nitrogen they have about as high a requirement as birch.

The birch seedlings have a low nutrient tolerance and deficiency-tolerance, a high requirement, and usually also a high response to supplies at deficiency. The spruce seedlings are mostly intermediate between pine and birch. The many observations in practice (*cf.* p. 7) that indicate that pine is the most suitable forest tree species on sites poor in nutrients (nitrogen) and that birch is nitrogen-requiring are, thus, in agreement with the present results and seem, therefore, to have a physiological background.

Chapter VIII. Summary

The investigation presented has been carried out to study the physiological background for the leaf analysis method as an instrument for defining the macro nutrient status of forest trees and to compare the nutritional properties of the three dominating forest tree species in Sweden. The purpose has not been to obtain detailed data but fundamental and broad information about the reactions of young seedlings to varied nutrient supply under strictly controlled external conditions.

Pine, spruce, and birch seedlings have been grown, after a germination period, in nutrient solutions with varied supplies of N, P, K, Ca, Mg, and S for periods of about 95, 160, and 75 days respectively. The elements were varied, one at a time, starting from control solutions that, on the basis of preliminary experiments, were supposed to give the highest growth under the experimental conditions used. The significance of the length of the growth period for the results has been studied in experiments comprising controls and one low supply of nitrogen and of potassium harvested on four occasions. The more important experimental data from individual vessels in these main experiments are given in Tables I—IV at the end of the paper. The results of the different treatments are presented in Chapter III (p. 25—47). Some results from a preliminary experiment with birch seedlings in flowing

water cultures with varied pH and two nitrogen sources are given on p. 17—19. The results and conclusions may be summarized as follows.

1. It is shown that the supply of an element has been varied under conditions of otherwise nearly optimum nutrition. Thus, the control seedlings have throughout the highest or very close to the highest dry weight within each series of varied element supply. The percentages in the leaves of the unvaried elements (Table 7—12, p. 26—39) are within or very close to the ranges found to be optimum (Table 26, p. 81) except in some cases of very low supplies when earlier well-known interactions are recognized (p. 70—71).

2. With increasing supply the seedling dry weight may generally be described by an optimum curve, whereas the internal concentrations of the varied element increases more or less continuously with increasing supply (Figures 6—23, p. 24—40). At the high supplies, however, it has not been possible to distinguish between different effects of the supplied salts (p. 50—56) and, consequently, it is not shown that the growth reductions are entirely caused by supra-optimum supplies of the nutrient *elements* or by supra-optimum internal percentages of them. Still, the growth and internal percentages do, of course, reflect the influences of the salts under the conditions used. Within the deficiency and optimum regions no secondary effects of the nutrient salts seem to have been of importance for the results and conclusions.

3. A low supply permits a growth and nutrient uptake that in the beginning is as high as at control supply, and deficiency does not appear until a certain time has passed; the lower the supply is, the shorter the time (p. 57—59). The amount of supply in the controls has, in the beginning, been unnecessarily high; a certain low supply suffices at this time. After a longer growth period also the control solution becomes insufficient. There is, thus, a trend in the supply/growth relation towards higher concentrations in the solutions or rates of supply to get a certain relative growth (p. 50). These relations depend on the experimental methods and the fact that the growth of the seedlings is undeterminated. At a rate of supply that is adapted for the rate of growth per vessel and the specific needs of the seedlings, that is for the actual nutrient uptake per vessel, a lower total amount of supply is required than at a constant rate of supply to produce a certain relative seedling size. The composition of the control (optimum) solution is, consequently, dependent on the experimental conditions, and in the present experiments it is especially devised for the conditions of the element series.

4. The internal concentrations of the elements generally decrease with the time, especially at low supplies (Table 16, p. 46). However, there is

Table 35. Optimum contents (per cent of dry weight). Values within brackets are estimates by the persent author

Species	Analyzed material	Reference	N	P	K	Ca	Mg	S
		PINE						
P. silvestris	Leaves	Present paper (Optimum range)	2.4—3.0	0.15—0.4	0.9—1.6	0.04—0.3	0.12—0.18	0.20—0.25
	„	Gast (45)	3					
	„	Tamm (175)	2—2.5					
	Shoots	Boszormenyi (21)	1.8—2					
P. banksiana	„	Bensend (10)	2.25					
	„	Swan (161)		(0.30)	(1.16)		(0.13—0.22)	
P. taeda, Virginiana	Leaves	Fowells & Krauss (43)	1.7—2.3	0.14—0.18				
P. strobus	Shoots	Mitchell (111)	3.26	0.67	1.72	0.33		
P. nigra	Leaves	Leyton (85)		0.15				
		SPRUCE						
P. abies	Leaves	Present paper (Optimum range)	1.8—2.4	0.10—$>$ 0.3	0.7—1.1	0.09—0.6	0.09—0.16	0.13—0.18
	„	Tamm (175)	>2					
P. glauca	Shoots	Swan (161)					(0.08—0.14)	
P. mariana	„	Swan (161)					(0.07—0.16)	
P. sitchensis	Leaves	Leyton (85)	1.4—1.5	0.13	(1)			
		BIRCH						
B. verrucosa	Leaves	Present paper (Optimum range)	3.4—4.0	0.2—0.4	1.5—3.1	0.16—0.6	0.17—0.5	0.29—0.32
	„	Tamm (175)	>3.3					

Table 36. Contents (per cent of dry weight) corresponding to visual deficiency symptoms

Species	Analyzed material	Reference	N	P	K	Ca	Mg	S
		PINE						
P. silvestris	Leaves	Present paper	0.7—1.6	0.06—0.09	0.3	0.05	0.06	0.07
	Shoots	Süchting (166)	1.0—1.4	0.09—0.16	0.33			
	Leaves	van Goor (49)			0.35			
	„	Wittich (200)			0.4			
	„	Nemec (128)					0.09	
	„	Themlitz (181—183)					0.06	
	„	Ingestad (71)					0.06	
P. strobus	Shoots	Mitchell (111)	0.7—1.3					
	Leaves	Walker (190, 191)			0.4			
	„	Nemec (128)					0.09	
	„	Stone (154)					0.08—0.15	
P. banksiana	Shoots	Swan (161)	1.3—1.5	0.07	0.39		0.06	
P. taeda, Virginiana	Leaves	Fowells & Krauss (43)		0.10				
P. resinosa	„	Heiberg & White (57)			0.30			
	„	Stone (154)					0.08—0.15	
P. nigra	„	van Goor (49)			0.30			
		SPRUCE						
P. Abies	Leaves	Present paper	1.0—1.7	0.05—0.11	0.3	0.02	0.02—0.07	0.13
	„	Björkman (16)			0.32			
	Shoots	Süchting (161)	1.2	0.09	0.33			
	Leaves	Heiberg & White (57)			0.21			
	„	Ingestad (70)					0.04—0.05	
P. glauca	Shoots	Swan (161)	1.3	0.10	0.26		0.08	
P. mariana	„	„ (161)	1.0	0.10	0.20		0.07	
		BIRCH						
B. verrucosa	Leaves	Present paper	1.5—3.1	0.12	0.5	0.12	0.06—0.18	0.06—0.21

evidence that the relation between the element concentration of the leaves and the growth is affected only to a rather small degree by the length of the growth period (p. 78—80). This means that a low supply has produced a relatively high internal element percentage and good growth in the beginning that is not represented in the content/growth relation obtained at the harvest of the element series. However, the higher internal percentage levels occur when the growth rate and reactivity of the seedlings is low, and, therefore, the error caused by this factor in the estimation of the content/growth relation will be small.

5. It is found that there is a strong relation between the element percentages of the leaves and the growth and development of the seedlings. On account of the good agreement between the values found here to represent the content/growth relation (Table 26, p. 81) and many earlier reported data (*cf.* p. 82—88, and Table 35) there are reasons to believe that the values in Table 26 have a high degree of validity despite the extreme growth conditions of the present experiments. *The leaf analysis method seems, therefore, to have a strong physiological basis as a diagnostic tool in the studied species.* It is also found that analysis of different seedling parts and different growth characteristics are utilizable for a description of the nutrient status, but not with identical numerical values (p. 93—94). However, the leaves alone seem most suitable as analytical material because of the less pronounced morphological changes with time in this organ.

6. A strong correlation between the element percentages of the leaves and the appearance of visual deficiency symptoms is noticed (Tables 30, p. 98, and 36). Because the deficiency symptoms, especially in the conifer seedlings, are usually quite unspecific, the diagnosis of the cause by means of the visual symptoms directly requires much practice and sometimes seems to be impossible (p. 94—97). *For an accurate diagnosis of the symptoms the leaf analysis method appears to be very helpful.*

7. The nutrient status of the seedlings is of great importance for the morphological properties of the seedlings (p. 102—106). The root/shoot quotient is high at deficiencies of N, P, and S. The type of the root system and especially its branching intensity is dependent on the nutrition. In deficiency the degree of root branching is low, except for calcium, and is generally highest at optimum nutrition. The stem and leaf dry weights are, on the other hand, strongly correlated, independent on the whole of the varying nutrient factors.

8. The growth rate is at control supply much higher in the birch than in the conifer seedlings and somewhat higher in pine than in spruce (Figure 24, p. 44). The nutrient uptake rate and requirement is also much higher of the birch than of the conifer seedlings (Table 21, p. 60). In

relation to the dry weight, and especially the fresh weight, the differences between the species in the uptake (Tables 24 and 25, p. 69) and requirements (Figures 32—37, p. 74—75) are less pronounced.

9. It is found that the nutrient requirement is highest for N and K in all three species and that pine has an extremely low Ca demand (p. 76).

10. *The pine seedlings are found to be least sensitive or most tolerant to variations in the nutrient supply, whereas the birch seedlings are least tolerant;* the optimum curves of pine are comparatively broad and flat and of birch narrow (p. 109—111). In all three species the tolerance is lowest to nitrogen supply variations. The pine seedlings show a remarkably great tolerance to variations in the calcium supply. This relation between the species is also found in the tolerance to low supplies. *Despite the comparatively great nutrient tolerance of the pine seedlings they have a rather high requirement of N, K, and S for maximum growth. The great tolerance of the pine seedlings is, on the other hand, often connected with a comparatively low response to a supply in deficiency and the least tolerant birch seedlings show the highest response.* In the case of calcium, however, the growth curve of the pine seedlings is relatively steep on the sub-optimum side and the response to calcium is, thus, higher in pine than in spruce and birch. The explanation of these differences between the species seems to be mainly the differences in their sensitivity to variations in the internal nutrient concentrations; the pine seedlings are least, the birch seedlings most sensitive. In the case of sulphur, and especially of calcium in the pine seedlings, there is a high sensitivity to variations in the internal percentages despite a low sensitivity to variations in the supply. This depends obviously on a great ability of the seedlings to adapt their uptake when the supply of these elements is varied. The differences between the species in their nutritional properties are summarized in Table 34 (p. 115).

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Sammanfattning

Inverkan av varierad makronäringstillförsel på tall-, gran- och björkplantor i näringslösningar

I. Inledning

I föreliggande undersökning har tall *(Pinus silvestris,* L.), gran *(Picea abies,* Karst.) och björk *(Betula verrucosa,* Ehrh.) odlats från groddstadiet i näringslösningar. Tillförseln av de sex makronäringselementen (kväve, fosfor, kalium, kalcium, magnesium och svavel) har varierats och plantornas tillväxt och inre näringskoncentrationer har bestämts. Avsikten med undersökningen har i första hand varit, att studera de nämnda arternas näringsfysiologiska egenskaper speciellt med tanke på bladanalysen som diagnostiskt hjälpmedel. Lagatu och Maume (80), som studerade vinrankans näringsfysiologi, introducerade begreppet "bladdiagnostik" år 1924 och särskilt Lundegårdh (92—94) har demonstrerat bladanalysens användbarhet för diagnostiska ändamål i jordbruket.

Mitchell (109—111) och Mitchell och Chandler (112) betraktade bladanalysmetoden som ett hjälpmedel vid skogsmarkens bonitering, men denna möjlighet har ifrågasatts av bl. a. Tamm (171, 174). Tamm (171, 175) ansåg att bladanalysen kan erbjuda en bekväm metod för diagnos av näringsbrist hos träd eller bestånd. Tillgången på faktiska data är dock starkt begränsad, vilket betonats av Leyton (85, 86), Tamm (171, 174, 175) och andra.

Bladanalysmetoden är komparativ och dess användbarhet hänger på att analysvärdenas innebörd, som är mer eller mindre artspecifik, är känd. Tillgängliga data om skogsträd kommer emellertid från olika arter och täcker som regel endast ett begränsat antal element eller nivåer av elementen. På nuvarande stadium är därför ett av de mest framträdande problemen, hur skogsträdens näringstillstånd skall kunna definieras. I denna undersökning har därför frågan ställts, om det finns en fysiologisk bakgrund för bladanalysen som diagnosmetod för näringstillstånd hos de studerade arterna och, om så är fallet, vilka halter, som under kontrollerade betingelser motsvarar brist, och vilka, som motsvarar maximal tillväxt.

I en sådan undersökning är många metoder användbara (se 6, 12, 48, 61), men författaren har valt att börja med en grundläggande studie över inverkan av varierad tillförsel av ett element i taget, då näringstillförsel, temperatur och ljus strängt kontrolleras. Plantorna har sålunda odlats i näringslösningar i ett konstantrum med artificiellt ljus. Fördelen med denna metod är, att tillväxtbetingelserna och näringstillförseln kan definieras väl och varieras inom mycket vida gränser. Å andra sidan är resultatens tillämpning i fält osäker. Undersökningen har därför planerats så, att laboratorieförsöken kompletteras med gödslingsförsök i plantskolor för att en vidare giltighet av resultaten och mera detaljerade data skall kunna erhållas. Dessa fältförsök har pågått sedan några år, men icke tillräckligt länge för att medge säkra slutsatser. Här redovisas därför endast laboratorieförsöken.

Temperatur- och ljusförhållandena har anpassats för att en snabb utveckling av friska plantor skulle vara möjlig. Näringslösningarnas sammansättning har baserats på villkoret, att ett element skulle kunna varieras under i övrigt optimala eller nästan optimala näringsbetingelser. Undersökningen startades därför med en serie preliminära försök, som ledde till den sammansättning, som använts i *kontrollösningarna.* Dessa antogs innebära en nära nog optimal näringstillförsel för respektive art i de slutliga försöken.

Förutom de mätningar, som behövts för att studera huvudproblemet, har andra utförts för att ytterligare belysa näringens inverkan på plantorna. Sålunda har en serie tillväxtmätningar utförts för att möjliggöra ett studium av näringsfaktorernas formativa effekter, som är av intresse bl. a. för relationerna mellan gödsling och plantkvalitet i plantskolor (jfr. 1, 17, 18, 19, 120, 127). Bristsymptom har noterats för att studera möjligheten att skilja mellan olika bristtillstånd direkt visuellt eller genom bladanalys. Den kemiska analysen har utförts på såväl blad som stam och rot för att erhålla upplysningar om bl. a. den totala näringsupptagningen och innebörden av näringskoncentrationen i olika delar av plantorna. Vidare har blad och rötter analyserats på så många som möjligt av makroelementen för att medge dels en studie av samspel mellan elementen och dels en bättre uppskattning av plantornas näringstillstånd.

Förutom försöken med varierad makroämnestillförsel (elementserier) har försök utförts med plantor, som skördats efter olika lång tid, varvid såväl kontroller som en låg kväve- och en låg kaliumgiva använts (tidsserier). Vidare redovisas resultaten från serier med samma proportioner mellan elementen som i kontrollösningarna, men med varierad totalkoncentration. Även ett preliminärt försök med björk i näringslösningar med varierat pH och två olika kvävekällor omnämnes. Näringslösningarna har i detta försök fått rinna kontinuerligt genom odlingskärlen.

För att underlätta läsningen av figurer och tabeller ges en ordlista efter sammanfattningen.

II. Metodik

Försöksplantorna valdes ut ur ett stort antal utgrodda frön och placerades i glasbägare innehållande näringslösningarna. Bägarna ställdes på ett bord i ett konstantrum med lysrör som enda ljuskälla (Figur 1 och 2). Temperaturen hölls under dagen (18 timmar per dygn) vid 20° C för tall och gran och vid 25° C för björk. Under natten sänktes temperaturen, vanligen till 12° C. Odlingstiden var i elementserierna c:a 75 dagar för björk, 160 dagar för gran och 95 dagar för tall. Antalet plantor i varje bägare vid skörd framgår av Tabellerna I—IV i slutet av avhandlingen.

Näringslösningarna byttes en gång i veckan och hade en volym av en halv liter. Näringslösningarnas sammansättning framgår av Tabellerna 2 och 3. I Tabell 2 återfinns förrådslösningarnas sammansättning. Om dessa späds 1 : 100 erhålles kontrollkoncentrationerna. I tabellen anges de använda salterna, antalet gram per liter för respektive trädslag samt i vilka försöksserier salterna har använts (× anger de salter, som icke varierats, + anger det salt, som använts för att variera det aktuella elementet). I Tabell 3 anges koncentrationerna i kontrollösningarna av de olika elementen uttryckta som ppm (delar av million, mg per liter).

Som utgångspunkt för variationen av lösningarnas elementkoncentrationer användes de genom förförsök erhållna kontrollösningarna. Kontrollerna har sålunda ingått som ett gemensamt led i samtliga serier med varierad elementkoncentration. Vilka koncentrationer (uttryckta som ppm), som använts, framgår av de vänstra kolumnerna i Tabellerna 7—12 samt I—IV (i slutet av avhandlingen). På grund av plantornas ömtålighet användes vid försökens början utspädda lösningar (1:4 och 1:2), varvid det varierade elementet utelämnades i respektive serier. Lösningarna har kontinuerligt genomluftats med kompressorluft.

Lösningarnas pH har praktiskt taget genomgående legat mellan 4 och 5. Denna nivå kan, av tidigare resultat att döma (se t. ex. 30, 82, 167, 168, 169), anses vara lämplig för skogsträdsplantor. I ett preliminärt försök med kontinuerligt byte av näringslösningarna (kemostat) visade björkplantor en tämligen ringa variation i tillväxten inom ett brett pH-intervall, speciellt om ammoniumsulfat användes som kvävekälla. Detta framgår av Tabell 4, där resultaten från detta försök redovisas. Tabellen anger pH, kvävekälla (natriumnitrat och ammoniumsulfat), planttorrvikt och elementhalt i blad (procent av torrvikt).

I försöken saknar plantorna mykorrhiza. Betydelsen av detta faktum för försöksresultaten är icke känd, men det är uppenbart, att plantorna även utan mykorrhiza kan utvecklas fullt normalt och ha en mycket hög tillväxthastighet jämfört med vad som vanligen registreras i fält.

Den tillämpade provbehandlingen och analysgången har i allmänhet följt gängse rutinmetoder på Avdelningen för botanik och marklära vid Statens skogsforskningsinstitut.

Försöken har vanligen utförts med en upprepning och det procentuella metodfelet i medeltalet mellan två bestämningar framgår av Tabell 5 för plantfriskvikt, planttorrvikt, bladtorrvikt, rottorrvikt, stamlängd, halter i blad och halter i rötter. Uppskattningen av metodfelet har utförts på basis av hela materialet inom elementserierna med hjälp av variansanalys på de logaritmiska värdena.

III. Experimentella resultat

Försöksresultaten redovisas i en serie diagram och tabeller. I Tabellerna I—IV i slutet av avhandlingen visas de viktigaste enskilda mätresultaten individuellt för varje bägare.

Resultat från elementserierna. I Tabell 6 återfinns barrlängderna hos tallplantor vid varierad kväve- och fosforgiva i ett preliminärt försök. I Tabellerna 7—12 ges halterna i blad och rötter av de icke varierade elementen. I Figurerna 6—23 redovisas i de övre diagrammen halterna i blad, stammar och rötter av de varierade elementen och i de nedre diagrammen en rad tillväxtresultat. Nyckeln till symbolerna anger: (punkter) hela plantor, blad, stammar och rötter samt (linjer) torrvikt, längd och elementhalt. I Tabell 13 har data om försök med varierad totalkoncentration men samma proportioner mellan elementen i lösningarna samlats. I dessa försök saknas upprepningar med björk. I tabellen återfinns den relativa koncentrationen (kontrollkoncentrationerna = 1), planttorrvikt samt halter i blad och rötter.

Resultat från tidsserierna. I Tabell 14 har uppgifter om behandlingarna i tidsserierna sammanställts. I den övre delen återfinns odlingstiden för de olika skördetillfällena, i den nedre delen anges koncentrationerna i näringslösningarna av kväve och kalium vid kontrollgivan samt vid låg tillförsel av respektive element. I Tabell 15 anges odlingstid, tillväxthastighet samt stam- och rotlängder vid skörd. I Tabell 16 har analysresultaten av kväve och kalium samlats och Tabell 17 omfattar halterna av fosfor, kalcium och magnesium i kontrollbladen. I Figur 24 ges planttorrvikten av kontrollerna efter olika lång odlingstid och i Figurerna 25—26 har några torrviktsdata från tidsserierna samlats. Kurvorna anger torrvikterna av rötter, rötter + stammar samt hela plantor.

IV. Inverkan av lösningarna

A. Samband mellan giva och torrsubstansproduktion

Försöksresultaten visar, att kontrollösningarna inneburit optimal eller nästan optimal tillförsel av makroelementen under de aktuella betingelserna. Endast i tre av elementserierna har kontrollerna icke givit den högsta planttorrvikten, nämligen i kväveserien med tall, fosforserien med gran och kaliumserien med björk (Figurerna 6—23). Även i dessa fall är dock kontrollplantornas torrvikt praktiskt taget densamma som i maximum (98, 99 respektive 96 procent av högsta planttorrvikt). Kontrollplantorna uppvisar den högsta tillväxten också i serierna med varierad totalkoncentration men med samma proportion mellan elementen (Tabell 13). De effekter, som framkommit vid variation av ett element, har sålunda icke påverkats av i övrigt extrema makronäringsgivor. Inga tecken på att en extrem mikronäringssituation skulle föreligga har framkommit i försöken.

I elementserierna har som regel en reducerad tillväxt noterats vid lägre givor än i kontrollerna (Figurerna 6—23) och ju lägre givorna är, desto lägre är tillväxten. Vid de högre givorna har likaledes en klar tillväxtreduktion i allmänhet framkommit. Ibland har förgiftningssymptom utvecklats och plantor dött. Orsaken till dessa effekter är icke nödvändigtvis en hög koncentration av makroelementen själva utan kan också vara höga givor av salterna med vilka elementen varierats. Det är sålunda av vikt att konstatera, att överoptimala givor eller inre koncentrationer av *elementen* ej säkert kan fastställas, även om en hög inre elementkoncentration kan anses spegla en hög och överoptimal koncentration av det varierade saltet.

Ett speciellt förhållande föreligger i kväveserierna, där de högsta givorna (av ammoniumnitrat) lett till kraftiga tillväxthämningar (Figurerna 6—8), förgiftningssymptom och många plantors död. Trots detta är varken den inre kvävekoncentrationen eller värdena av de sekundära faktorerna i lösningarna så höga (Tabell 19), att detta kan förklara effekterna. Det finns emellertid skäl att tro, att nitratet kan vara orsaken genom giftverkan vid högre givor. Det visar sig nämligen i försöken med björk i kemostat, att plantorna växer bättre med ammonium än med nitrat som kvävekälla (Tabell 4) och många försök med barrträdsplantor i krukor och plantskolor tyder på liknande förhållanden hos dessa (t. ex. *72*, 123, 124, 161), vilket också bekräftats i flera ännu icke publicerade plantskoleförsök med såväl tall som gran. För att närmare utreda kvävekällans betydelse för dessa arter, krävs ytterligare försök.

B. Samband mellan giva och upptagning

Sambanden mellan näringstillförsel och plantornas utveckling är knutna till näringsupptagningen och dennas beroende av tillförseln. För att beräkna näringstillförseln genom lösningarna, måste hänsyn tas till att försöken startades med låg koncentration i lösningarna och med utelämnande av det varierade elementet utom i kontrollerna. Den genom fröna tillförda näringsmängden kan som regel försummas. Vid de lägsta givorna är emellertid tall- och granfrönas näringsinnehåll ibland av samma storleksordning som den upptagna näringsmängden. Frönas näringsmängd framgår av Tabell 1, som anger 1000-kornvikt samt näringsinnehållet som procent av torrvikt och som mikrogram per frö. I Tabellerna 20—25 har frönas näringsinnehåll (enligt Tabell 1) dragits ifrån den upptagna näringsmängden, eftersom studiet här gäller upptagningen ur lösningarna. I en del fall har icke alla delar av plantorna kunnat analyseras och näringsupptagningen kan då icke beräknas. Dessa fall markeras i tabellerna.

Det framgår av Tabellerna 20 och 21, att näringsupptagningen och näringsupptagningshastigheten ökar med tiden, hastigt i kontrollerna men långsammare vid låg giva, då upptagningshastigheten tenderar att bli konstant (maximalt utnyttjande av givan) under senare utvecklingsstadier. Hos gran sker dock en minskning i upptagningshastigheten under perioden 164—185 dagar, då dessa plantor synes gå in i en period av allmänt lägre aktivitet. En liknande aktivitetsminskning hos tall under perioden 72—94 dagar kan tänkas ha påverkat resultaten i denna serie. Man finner, att en låg, men icke extremt låg kvävegiva inneburit en lägre upptagning än i kontrollerna först efter en tid (Tabell 20). En jämförelsevis ännu lägre kaliumgiva betyder en hastigare minskning i upptagningen i förhållande till upptagningen vid kontrollgiva. Detta sammanhänger med utnyttjandet av givorna och det framgår av Tabell 20, att utnyttjandet av den låga kvävegivan är väsentligt högre än av kontrollgivan, åtminstone i början. Plantorna har sålunda genom att utnyttja den lägre kvävegivan i mycket hög grad till en början förmått upprätthålla en lika hög upptagning som vid kontrollgiva, vilken utnyttjas mindre effektivt. Då kvävet utnyttjas med mer än c:a 60 procent påverkas emellertid såväl upptagning som tillväxt (Tabellerna 20 och 15). Kalium synes icke kunna utnyttjas i samma grad som kväve utan påverkan av upptagning och tillväxt.

Upptagningshastigheten ökar sålunda med tiden och med plantornas storlek. Om upptagningshastigheten i kontrollerna divideras med plantornas genomsnittliga torrvikt, så blir förändringen i värdena liten för kväve, medan en tendens till minskning med tiden föreligger för kalium (Tabell 21). Ökningen i upptagningen beror sålunda främst på plantornas ökade storlek och icke på en ökning av upptagningsförmågan per torrviktsenhet. I stället t. o. m. minskar upptagningsförmågan av kalium med tiden, åtminstone hos tall- och granplantorna (Tabell 21).

Data om upptagningen i elementserierna har sammanfattats i Tabell 22, som anger giva, upptagning och utnyttjandeprocent. Det framgår, att upptagningen hastigt ökar med givan inom det underoptimala området och sedan allt långsammare (se också Figurerna 28—30, där plantornas näringsinnehåll ställts mot näringsgivan). Endast i undantagsfall minskar upptagningen med ökad giva. Särskilt markant är detta inom svavelserierna, där upptagningen hos alla tre arterna minskar vid övergången från optimala till överoptimala givor för att sedan åter öka. En liknande tendens finner man för fosfor hos björk. Det verkar sannolikt, att denna effekt beror på en giftverkan av givan.

I elementserierna har de låga givorna ibland utnyttjats i mycket hög grad, medan de höga givorna har utnyttjats dåligt. Vid samma tillförselhastighet av elementen har dessa utnyttjats i sjunkande grad i stort sett enligt följande serier:

Tall: $N > K > P > Ca > Mg$

Gran, björk: $N > K > P > Mg > Ca$

Svavel kan icke inbegripas i dessa serier, eftersom den totala upptagningen ej är känd, men det finns tecken, som tyder på, att svavlet utnyttjas ungefär som fosfor. Det framgår, att olika element i allmänhet utnyttjas olika mycket och att högre givor i de flesta fall utnyttjas sämre än lägre givor.

Vid en jämförelse mellan trädslagen, finner man, att vid samma odlingstid har björkplantorna tagit upp väsentligt mer näring än tall och tall mer än gran (Tabell 20). Det framgår också, att björkplantorna då utnyttjat näringsgivan bäst och gran något sämre än tall. Å andra sidan har björkplantorna också den högsta och granplantorna den lägsta tillväxthastigheten (Figur 24). Frågan är nu, om skillnaden mellan arterna vid näringsupptagningen beror uteslutande på detta faktum eller om de har olika upptagningskapacitet i förhållande till torr- eller friskvikten. I Tabellerna 24 och 25 har elementupptagningen i kontrollerna från tids- respektive elementserierna uttryckts som procent av torr- och friskvikten. I Tabell 24 anges för tidsserierna kväve- och kaliummängderna överst som procent av torrvikten och i nedre delen som procent av friskvikten. I Tabell 25 anges för elementserierna upptagningen för de olika elementen och arterna till vänster som procent av torrvikten och till höger som procent av friskvikten. Det framgår av tabellerna, att granplantorna i allmänhet har haft den lägsta och björkplantorna den högsta upptagningen i förhållande till torrvikten. Upptagningsförmågan i förhållande till friskvikten är mycket lika hos arterna. Björkplantorna har dock fortfarande en tendens till högst upptagningsförmåga.

C. Inverkan av elementvariationen på upptagningen av andra element

Halterna av de icke varierade elementen i blad och rötter från elementserierna återfinns i Tabellerna 7—12. Det framgår, att dessa elementhalter varierar ganska litet. Vissa tidigare välkända samspel kan emellertid urskiljas. Sålunda finner man ofta ett samspel mellan elementen, som givits i form av positiva joner, vilket kan bero på jonantagonism (26). Vidare finner man låga kvävehalter vid låga svavelgivor. Denna effekt har ansetts bero på en minskad nitratreduktion vid svavelbrist (40, 79).

De något höga eller något låga halter av icke varierade element, som noterats, kan betraktas som en del av bilden vid vissa näringsbrister och är därför icke av avgörande betydelse för studiet av sambanden mellan inre halt och tillväxt, men visar å andra sidan att det är nödvändigt att ta hänsyn till flera element för säker diagnos av näringssituationen på basis av bladanalysmetoden.

D. Några anmärkningar angående näringslösningarnas funktion

Näringslösningarnas koncentration har varierats i försöken och därmed den totalt tillförda näringsmängden. Plantorna har ofta utnyttjat givan i mycket hög grad (Tabell 22) och lösningarnas koncentration kan därför icke alltid anses vara konstant. Den ursprungliga koncentrationen är emellertid ett uttryck för tillförselhastigheten av elementen och ppm-värdet (mg/liter) är lika med mg per två veckor eftersom lösningarna har en volym på en halv liter och byts ut en gång i veckan.

Tidsserierna visar, att en låg kvävegiva till en början leder till ungefär samma tillväxt och kväveupptagning som i kontrollerna (Tabellerna 15, 20, 21). Vidare visar det sig, att kvävehalterna i bladen samtidigt ligger nära det optimumintervall för kväve, som uppskattats i elementserierna (Tabellerna 16 och 26, Figur 31). Senare betyder den lägre givan i förhållande till kontrollgivan en mer och mer reducerad kväveupptagning och torrsubstansproduktion. Det inre kvävetillståndet försämras samtidigt ned till en viss nivå. Dessa förhållanden illustreras i principdiagrammet i Figur 31 med hjälp av kväveserierna med gran. I det övre diagrammet har kvävehalten i bladen ställts mot den totalt tillförda kvävemängden och i det undre diagrammet finner man samma abskissa men med planttorrvikten på ordinatan.

Av Figur 31 framgår, att en låg tillförselhastighet ger en högre planttorrvikt än en hög tillförselhastighet vid samma mängd totalt tillfört kväve. Vid samma längd av odlingstiden betyder en högre tillförselhastighet en högre torrvikt upp till ett optimalt värde, som ökar med tiden. Den giva, som i elementserierna befunnits vara optimal (50 ppm kväve för gran), är sålunda för hög i början och blir för låg vid längre odlingsperioder. Plantornas optimala behov av kvävetillförsel synes vara approximativt lineärt korrelerat med plantornas storlek (Figur 31), vilket också är att vänta, eftersom egenskaperna vid upptagningen och den optimala inre halten icke har ändrats med tiden. Genom att anpassa näringstillförselhastigheten successivt efter plantornas behov, skulle en väsentligt mindre total mängd näring behövas för maximal tillväxt, vilken dessutom skulle bli något högre. Detta demonstreras i Figur 31 med en kurva markerad "Adapted rate" och med × markerande maximumpunkter efter olika odlingstider.

Dessa förhållanden visar, att den väsentliga egenskapen hos näringslösningarna för plantornas näringsupptagningshastighet och tillväxt är den mängd näring, som tillföres per tidsenhet, och icke primärt elementkoncentrationerna. Detta synes främst bero på att plantornas näringsstatus (den inre näringskoncentrationen) påverkas av relationen mellan tillväxthastighet och näringstillförselhastighet. Den mängd näring, som behövs, för att upprätthålla ett visst näringstillstånd och en viss tillväxthastighet beror också på plantornas förmåga att utnyttja näringsgivan.

Näringstillförseln kan i försök baseras på något av följande villkor: konstant tillförselhastighet, konstant koncentration eller adapterad tillförsel i överensstämmelse med plantornas aktuella behov. I de föreliggande försöken har konstant tillförselhastighet tillämpats, vilket kräver högre total giva än adapterad tillförsel, som representerar minsta möjliga behov av tillförsel och som (så när som på mängderna i den ursprungliga lösningen) är approximativt den av plantorna upptagna mängden eller det "inre näringsbehovet". Vidmakthållande av konstant koncentration i lösningarna kräver kontinuerligt byte eller stor volym av lösningarna. De näringsmängder, som då behövs, är stora.

Behovet av näringstillförsel för en viss relativ planttorrvikt (procent av maximum) demonstreras i Figurerna 32—37. I vänstra diagrammen (A) anges behovet vid konstant näringstillförselhastighet uttryckt i formen $\left(\frac{\text{total giva, mg}}{\text{planttorrvikt, g}}\right)$. I de högra diagrammen (B) anges minsta möjliga behov uttryckt som näringshalt i plantorna (procent av torrvikten). Behovet av olika element framgår av följande serie med sjunkande behov:

Vid konstant tillförselhastighet (diagram A):

Tall: $N > K > Mg > S,P > Ca$
Gran, björk: $N > K, Ca > Mg > S,P$

Vid adapterad tillförselhastighet (diagram B):

Tall: $N > K > P > Mg > Ca$
Gran, björk: $N > K > P > Ca > Mg$

I de senare serierna kan svavel ej placeras in, eftersom hela plantornas svavelinnehåll ej är känt utan endast innehållet i blad + rötter. Behovet av svavel synes emellertid också i dessa serier vara ungefär detsamma som av fosfor. Behovet av olika element kommer sålunda i samma ordning hos de tre arterna utom då det gäller kalcium, för vilket element tall har ett mycket lågt behov.

Då arterna jämförs, finner man, att vid konstant tillförselhastighet (diagram A) är skillnaderna små inom optimumregionen, men praktiskt taget genomgående är björkplantornas behov störst och tallplantornas minst inom det suboptimala området. Vid adapterad tillförselhastighet (diagram B) har granplantorna det lägsta kvävebehovet medan skillnaderna mellan tall och gran i övrigt är små. Däremot har björkplantorna en allmän tendens till högre behov än barrträdsplantorna även i detta fall.

Dessa resultat gäller näringsbehovet för en viss torrsubstansproduktion. Om behovet i stället uttrycks på basis av friskvikten, blir skillnaderna mellan arterna genomgående små vid adapterad tillförselhastighet, men fortfarande finns en tendens till större behov hos björkplantorna.

V. Betydelsen av det inre näringstillståndet

A. Samband mellan bladens elementhalt och torrsubstansproduktionen

Av resultaten från tidsserierna framgår, att de inre näringskoncentrationerna tenderar att minska med odlingstiden (Tabell 16, Figur 31). Det finns emellertid tecken på att bladens optimumhalter förändras endast i ringa utsträckning med tiden. Sålunda finner man t. ex. att den låga kvävegivan har medfört en mycket hög relativ tillväxt i början (Tabell 15) och bladens kvävehalt (Tabell 16) är då också nära den optimumnivå, som framkommit i elementserierna (Tabell 26). För björkplantorna har den lägre kvävegivan medfört t. o. m. högre planttorrvikt än kontrollgivan vid första skördetillfället och kvävehalten i bladen överensstämmer också bättre med optimumnivån vid den lägre givan än i kontrollerna.

Dessa resultat stöder den uppfattningen, att näringshalten i de gröna delarna är den avgörande faktorn för näringens inverkan på plantorna (jfr. Lundegårdh, 94), men visar också, att en låg giva betyder ett bättre näringstillstånd hos plantorna vid början av försöken än vid skörd och att den inre halten och planttorrvikten då icke helt motsvarar varandra. Vid låg giva har emellertid plantorna vid försökens början liten förmåga att utnyttja det bättre näringstillståndet för produktion av torrsubstans. Senare, då produktionsförmågan ökar, blir förändringen i den inre halten mindre. Man kan sålunda helt allmänt konstatera, att förändringen i den inre halten har väsentligt mindre betydelse för planttorrvikten vid skörd, än vad som framgår av haltnivåerna under de tidigare stadierna. Detta illustreras schematiskt i principdiagrammet i Figur 38, som bygger på kväveserierna med gran.

Det framgår, att den högsta planttorrvikten sannolikt inträffar vid en kvävehalt på ungefär 2—2,2 procent i bladen oberoende av odlingstiden. Även tillväxtnivån 50 procent av maximum synes sammanfalla med en halt, som varierar inom ett begränsat intervall. Det förefaller sålunda troligt, att sambandet mellan inre halt och tillväxt i stort sett varit oberoende av odlingstiden.

Dessa relationer har demonstrerats schematiskt och gäller icke i detalj. Avsikten har emellertid icke varit en detaljstudie utan att urskilja intervall av halter motsvarande vissa definierade tillväxtnivåer. Följande klassificering användes:

Stark brist: $<$ 50 procent av maximumtillväxten.
Måttlig brist: 50—90 procent av maximumtillväxten på den underoptimala sidan.
Optimalt näringstillstånd: 90—100—90 procent av maximumtillväxten.

De olika halterna motsvarande denna klassificering har bestämts grafiskt mellan kurvorna för planttorrvikt och halt i bladen (de tjockare linjerna) i Figurerna 6—23. I vissa fall täcker icke försöksserierna hela tillväxtintervallet, men då har som regel extrapoleringar kunnat utföras på ett tillfredsställande sätt i diagram av typen halt/tillväxt. I ett fall kan dock optimumintervallets övre värde icke bestämmas (fosforserien med gran, Figur 10). I Tabell 26, där intervallerna i halter motsvarande måttlig brist och optimalt näringstillstånd har sammanfattats för de olika elementen och arterna, anges i vilka fall extrapolationer tillgripits.

Vid jämförelser mellan värdena i Tabell 26 och en rad värden funna i litteraturen finner man, att överensstämmelsen är mycket stor trots olikheter i grundvalen för de olika värdena (se Tabell 35, som anger optimumvärden funna i olika undersökningar). Tamm (175, 177) har rapporterat en rad preliminära ”bristnivåer”, dvs. halter, som bestämts på material från ogödslade ytor i fältförsök, där gödsling medfört en klar tillväxteffekt. Tamm (177) fann, att hos tall motsvarade $<$ 1,75 procent kväve i barren brist. 1,75 procent kväve i bladen motsvarar i föreliggande undersökning ca 75—80 procent av maximumtillväxten. Även i andra fall motsvarar de övre gränsvärdena i Tamms (175) bristnivåer hög tillväxt i detta material, trots de mycket stora olikheterna i de experimentella förutsättningarna och den preliminära karaktären i Tamms värden.

Detta tyder på att ett starkt fysiologiskt samband föreligger mellan elementens halt i bladen och tillväxten. Så långt det för närvarande är möjligt att döma föreligger ett starkt stöd för bladanalysmetodens användbarhet som ett medel för diagnos av skogsträdens näringstillstånd och för att de här funna halt/tillväxt-relationerna (Tabell 26) har hög grad av giltighet, trots de extrema odlingsbetingelserna.

B. Samband mellan elementhalter i olika plantdelar och olika tillväxtvärden

De olika elementen förekommer i varierande halter i olika delar av plantorna och olika tillväxtvärden är icke alltid korrelerade med varandra (Figurerna 6—23). Detta innebär, att sambanden mellan inre halt och tillväxt är beroende av vilket plantmaterial, som analyserats, och vilka tillväxtmätningar, som utförts. I Tabell 27 har olika intervall av halter motsvarande måttlig brist sammanställts. I tabellen anges elementhalt i blad, skott eller hela plantor, motsvarande tillväxt uttryckt som torrvikt av plantor, skott eller rötter. Värdena har grafiskt interpolerats (eller extrapolerats) på liknande sätt som beskrivits ovan.

Det framgår av Tabell 27, att intervallen i halter varierar olika för olika element och olika arter. Oftast är emellertid variationerna icke särskilt stora i detta material, vilket till stor del beror på att plantorna icke kommit så långt i utvecklingen att t.ex. stammarnas sekundära tillväxt och förvedning inverkat helt avgörande på analysresultaten. Det är dock uppenbart, att det analyserade materialet och de tillväxtmätningar, som utförts, bör vara väl definierade i en angiven halt/tillväxt-relation. Bladen kan anses vara att föredra som analysmaterial framför andra plantdelar, eftersom de sekundärt förändras jämförelsevis litet och eftersom de i fält kan erbjuda ett någorlunda enhetligt material från år till år.

VI. Morfologiska effekter av makroelementen

A. Visuella bristsymptom

I samtliga elementserier har bristsymptom av varierande styrka uppträtt vid de lägsta givorna. De givor, som lett till symptom, finns angivna i Tabell 28. Bristsymptomen är hos tall- och granplantorna mycket ospecifika och består i de flesta fall av kloros med vissnande barrspetsar. Detta överensstämmer i stort sett med tidigare beskrivningar (t. ex. 16, 70, 71, 118, 121, 128, 175, 176, 179). Till de mera karakteristiska symptomen hos gran hör de, som orsakas av magnesiumbrist. Symptomen består av gula barrspetsar med markant gräns mot de gröna barrbaserna. Vid stark brist blir spetsarna bruna och de gröna delarna allt mindre. Symptomet är då mindre typiskt.

Hos tallplantorna är symptomen vid kalium-, kalcium- och magnesiumbrist mycket lika varandra.

Hos björkplantorna, som har en differentierad bladskiva, är symptomen i allmänhet mera karakteristiska och liknar de symptom, som beskrivits för andra bladväxter (jfr. *22*, *179*, *192*).

Även rötterna uppvisar symptom på näringsbrist, speciellt vid kalciumbrist, då rötterna är starkt förgrenade och verkar stympade på grund av att rotspetsarna dör. Vid kvävebrist blir rötterna mycket långa och tunna och vid fosforbrist färgas ofta rotspetsarna violetta till svarta. Vid kaliumbrist blir rotsystemen små och tunna. Dessa symptom är ungefär desamma hos alla tre arterna.

På grund av barrträdsplantornas i allmänhet diffusa symptombilder, synes det oftast vara vanskligt att göra säkra diagnoser enbart på basis av de visuella iakttagelserna. Dessutom växlar symptomens karaktär med årstid, uppkomstsätt och bildningen av sekundära skador (bl. a. svampskador). Det är därför av intresse, att undersöka i vad mån bladanalysmetoden är användbar för att avgöra orsaken till symptomen. I Tabell 30 har analysvärden av de olika elementen vid bristsymptom samlats, antingen som en halt motsvarande begynnande bristsymptom eller ett intervall inom vilket symptomen har utvecklats. I tabellen anges också de mot halterna svarande relativa tillväxtnivåerna (procent av maximumtillväxten). I Tabell 36 jämförs dessa haltvärden med sådana, som rapporterats i litteraturen.

Den mycket goda överensstämmelsen mellan halterna i Tabell 36 tyder på att den inre näringskoncentrationen är av avgörande betydelse för uppkomsten av symptom och att bladanalys är en värdefull diagnosmetod. I ett fall är emellertid överensstämmelsen mindre god, nämligen för magnesium. Författaren har därför insamlat prov i en rad plantskolor för att pröva variationen i bladens magnesiumhalt vid brist (*70*, *71*). Resultaten av dessa prov överensstämmer överraskande väl med resultaten i laboratorieförsöken, vilket tyder på att bladanalysmetoden bör vara ett värdefullt hjälpmedel även vid diagnos av magnesiumbrist. Variationerna i de rapporterade värdena kan bero på mindre exakta provinsamlings- och analysmetoder samt osäkerhet angående orsaken till symptomen i äldre undersökningar.

B. Förgiftningssymptom

Vid höga givor av kväve, kalcium och svavel i tall- och granserierna samt av kalium och svavel i björkserierna har symptom på förgiftning uppträtt, ibland med många döda plantor som följd. Som påpekats ovan (sid. 137) kan orsaken till förgiftningarna icke säkert avgöras, eftersom åtminstone två joner varierats samtidigt. Förgiftningssymptomen är ganska ospecifika och består av bruna fläckar i bladens kanter och spetsar. Ibland förekommer också kloros.

C. *Andra morfologiska effekter*

Med ökad odlingstid förändras proportionerna mellan de olika plantdelarnas torrvikter (Figurerna 25—27). Dessa förändringar har sammanfattats siffermässigt i fyra kvoter i Tabell 31, nämligen mellan rötternas och skottens torrvikt, mellan stammarnas och bladens torrvikt samt mellan rotsystemens och stammarnas torrvikt och längd. Rotsystemens vikt/längdkvot kan betraktas som ett uttryck för deras grenighet, eftersom de enskilda rottrådarnas tjocklek varierar föga i jämförelse med grenigheten i försöken.

Motsvarande kvoter från elementserierna återfinns i Tabell 32. Det framgår, att näringsfaktorerna påverkar rot/skott-kvoten mycket kraftigt i flera fall. Hög rot/skott-kvot finner man speciellt vid kvävebrist, men även vid brist på fosfor, magnesium och svavel. Stam/blad-kvoten påverkas däremot genomgående mycket litet av näringstillståndet. Rötternas och stammarnas vikt/längd-kvoter varierar kraftigt inom samtliga serier utom för kalcium, där rötternas ökade grenighet vid brist gör att kvoten är hög även vid låga givor. Annars är dessa två kvoter i allmänhet högst vid optimala givor.

Plantornas näringstillstånd är sålunda av stor betydelse för deras morfologiska utveckling. Av speciellt intresse är näringens effekt på rötternas utveckling. Många forskare har ansett, att rot/skott-kvoten bör vara hög hos plantskoleplantor för att deras möjlighet att överleva efter utplantering skall vara så stor som möjligt (t. ex. Aldrich-Blake, 1). Björkman (19) var av den uppfattningen, att betydelsen av rot/skott-kvoten har överskattats och att det är av större betydelse att rotsystemen har möjlighet att snabbt utvecklas i den nya jorden. Sådana rotsystem skulle karakteriseras av en rik förgrening, som kan åstadkommas bl. a. genom omskolning eller rotbeskärning. I föreliggande undersökning har de mest förgrenade rotsystemen uppkommit vid optimal näringstillförsel och ur denna synpunkt skulle alltså den högsta plantkvaliteten vara att vänta vid riklig och balanserad gödsling. Detta överensstämmer med Nemecs (120, 127) resultat i plantskole- och planteringsförsök. En hög rot/skott-kvot, som här förekommer vid vissa bristtillstånd, synes vara av litet kvalitetsvärde, eftersom de långa, svagt grenade rotsystemen vid t. ex. kvävebrist kommer att bli starkt reducerade då rötterna tas upp och senare klipps av för att göra plantorna lämpliga för plantering. Björkman (17, 18, 19) har emellertid hävdat, att plantorna bör ha mykorrhiza vid utplanteringen. Mykorrhizan utvecklas bäst vid liten eller måttlig gödsling enligt Björkman (15). Mycket kraftigt gödslade plantor synas emellertid ofta ha utvecklats bättre efter utplantering än svagt eller ofullständigt gödslade plantor (Björkman, 18, 19). För närvarande är sålunda sambanden mellan gödsling och plantkvalitet oklara. Mycket tyder dock på att det optimala tillståndet är att föredra, men för att utreda detta krävs ytterligare försök.

VII. Jämförelser mellan arternas näringsfysiologiska egenskaper

Arterna har i diskussionen jämförts på olika sätt och det har bl. a. framgått, att näringsupptagningen (sid. 12) och näringsbehovet (sid. 17) är olika och vanligen högst hos björk. De kan emellertid också jämföras på basis av deras känslighet för olika tillstånd eller förändringar i den yttre eller inre näringssituationen i förhållande till ett visst, definierat tillstånd, t. ex. optimum. Denna metod använde sig Mitchell och Chandler (112) av vid jämförelser mellan några lövträds kvävebehov. Metoden är lämplig för skogsträd, bl. a. därför, att man i skogsbruket måste välja trädslag efter ståndorten utan möjlighet att ändra näringsfaktorerna till förmån för ett önskat trädslag. Vad man vill veta är alltså arternas känslighet eller okänslighet för näringsvillkoren. Som uttryck för tillväxtförmågan vid olika yttre näringsbetingelser, dvs. optimets bredd i giva/tillväxt-kurvan, används i fortsättningen begreppet tolerans i överensstämmelse med den definition Stålfelt (160, sid. 19—20) använt. Begreppet bristtolerans används för att beskriva toleransen vid de låga givorna i överensstämmelse med Mitchell och Chandlers (112) definition.

I Figurerna 39—41 demonstreras sambanden mellan kvävegiva och tillväxt hos de tre studerade arterna. I det första diagrammet har försöksresultaten använts i obearbetad form. Som framhållits ovan (sid. 13—17) är odlingstiden av betydelse för sambandet mellan giva och tillväxt. I Figur 40 har hänsyn tagits till detta och i Figur 41 har för jämförelsens skull tillväxthastigheterna i maximum satts lika med 100 för alla tre arterna. Det framgår, att tall- och björkplantorna kräver högre kvävegiva än gran för att nå maximumtillväxt, men vid låga givor växer tall bäst och björk sämst i förhållande till respektive maximum. Tallplantorna uppvisar sålunda den största toleransen och björkplantorna den minsta för variationer i kvävegivan. Siffermässigt kan toleransen uttryckas på basis av den intervallbredd i givan, som motsvaras av en förändring i tillväxten från 50 procent av maximum på den underoptimala sidan till 90 procent av maximum på den överoptimala sidan. I en sifferuppställning på sidan 111 anges hur många gånger givan av de olika elementen har måst ökas för att åstadkomma denna tillväxtförändring. Det framgår, att skillnaderna mellan arterna med undantag för kalium är mycket stora i flera fall och att tallplantorna kan betraktas som mest och björkplantorna som minst toleranta. Speciellt anmärkningsvärd är tallplantornas stora tolerans för variationer i kalciumgivan.

Bristtoleransen kan uttryckas på basis av tillväxten vid de lägsta givorna i försöken. I Tabell 33 återfinns dessa tillväxter uttryckta som relativ tillväxthastighet (procent av maximum). Värdena har delvis interpolerats i giva/tillväxtdiagram. Det visar sig, att tallplantorna praktiskt taget genomgående har den största och björkplantorna den minsta bristtoleransen.

Näringsbehovet för maximal tillväxt är som regel större hos björkplantorna än hos barrträdsplantorna (Figurerna 32—37). Tallplantorna har dock ett jämförelsevis stort behov av kväve, kalium och svavel för maximumtillväxt, trots deras stora tolerans. Tallplantornas behov av kalcium är däremot extremt litet.

Tillväxtsvaret vid en näringstillförsel då brist föreligger kan uttryckas på basis av lutningen av tillväxtkurvans underoptimala del eller intervallbredden i giva motsvarande tillväxtintervallet 50—90 procent av maximum på den underoptimala sidan. Antalet gånger givan måste ökas för att förändra tillväxten på detta sätt finns angivet i en sifferuppställning på sidan 112. Denna visar, att tallplantorna ofta ger ett lägre svar på en giva än gran- och björkplantorna. Då det gäller kalcium är tallplantornas tillväxtsvar dock relativt stort.

Enligt Mitchell och Chandler (112) var i deras material den väsentliga skillnaden mellan de kvävebristtoleranta och de kvävekrävande arterna den, att de förra uppnådde en högre inre kvävekoncentration i förhållande till optimumhalten på lokaler med låg kvävetillgänglighet. Så är icke fallet med de här studerade arterna. I Figur 42, där den relativa kvävehalten (procent av optimum) ställts mot logaritmen för hastigheten i kvävetillförseln, visar det sig, att arterna uppnår ungefär samma kvävehalt i förhållande till optimum vid samma tillförselhastighet, trots stora olikheter mellan dem i bristtolerans. I stället är arterna olika känsliga för variationer i bladens kvävehalt, vilket framgår av Figurerna 43 och 44, där tillväxt ställts mot kvävehalt i bladen. I Figur 43 har de obearbetade försöksresultaten redovisats och i Figur 44 har den optimala kvävehalten och den maximala tillväxten båda satts lika med 100. Förklaringen till arternas olika kvävebristtolerans synes sålunda vara olikheter i deras känslighet för variationer i den inre kvävehalten inom det underoptimala området. I stort sett gäller samma förhållanden för de övriga elementen för vilka arterna visar olikheter i tolerans.

Det föreligger också en motsvarighet i sambanden hos en art mellan känslighet för inre haltvariation och låg tolerans för variation i giva då man jämför olika element. Sålunda är alla tre arterna mest toleranta för variation i kalciumgivan och minst toleranta för variation i kvävegivan, vilket motsvaras av låg känslighet för variation i kalciumhalten och hög känslighet för variation i kvävehalten. Å andra sidan är känsligheten för variationer i svavelhalten mycket hög, men icke desto mindre är toleransen för variationer i svavelgivan också hög. Detta beror uppenbarligen på det faktum, att svavelupptagningen (Figurerna 28—30) liksom svavelhalten (Figurerna 21—23) varierar jämförelsevis litet med givan. Detta förhållande är ännu mer uttalat för kalcium hos tall. Den stora toleransen för variationer i kalciumgivan är icke förenad med en i motsvarande grad låg känslighet för variationer i den inre kalciumhalten. Den höga toleransen hos tallplantorna för variation i kalciumgivan tycks därför huvudsakligen bero på en stor förmåga att reglera kalciumupptagningen.

Jämförelserna mellan arterna har sammanfattats i Tabell 34, där olika egenskaper (tolerans för variation i giva, bristtolerans, behov för maximal tillväxt, svar på giva vid brist samt känslighet för variation i bladens elementhalter) klassificeras i tre grader: hög, intermediär och låg.

MS mottaget den 26/2 1962.

Ordlista över några ords och begrepps betydelse i tabeller och figurer

Adapt, anpassa, *adapted rate (of supply),* tillförselhastighet anpassad efter plantornas behov. *Amount,* mängd. *Average,* genomsnittlig.

Beaker, bägare (även *vessel). Birch,* björk.

Calcium (Ca), kalcium. *Chlorine* (Cl), klor. *Compound,* kemisk förening. *Concentration,* koncentration. *Constant,* konstant. *Content,* innehåll. *Control,* kontroll, representerande det i förväg antagna optimet, *control solution (seedling),* kontrollösning (-planta). *Correspond,* motsvara.

Day, dag, dygn. *Decrease,* minska, minskning. *Deficiency,* brist, *deficiency symptom,* bristsymptom. *Different,* olika. *Dry,* torr, *dry matter (weight),* torrsubstans (-vikt).

Element, element, grundämne. *Equal,* lika. *Extrapolate,* extrapolera.

Factor, faktor. *Flowing solution,* rinnande l. kontinuerligt bytt lösning, kemostat. *Fresh,* frisk, *fresh weight,* friskvikt.

Growth, tillväxt, *growth period (time),* odlingsperiod (-tid), *growth rate,* tillväxthastighet.

Harvest, skörd, *harvest occasion,* skördetillfälle. *High,* hög.

Increase, öka, ökning. *Intermediate,* intermediär. *Interval,* intervall.

Leaf, blad, barr (pl. *leaves). Length,* längd. *Level,* nivå. *Litre,* liter. *Low,* låg.

Magnesium (Mg), magnesium. *Maximum,* maximum, *maximum growth,* högsta tillväxt i en försöksserie. *Measurement,* mätning. *Microgram,* µg, mikrogram, tusendels mg. *Moderate,* måttlig, *moderate deficiency,* måttlig brist (motsvarande 50—90 procent av maximumtillväxt på den underoptimala sidan).

Nitrogen (N), kväve. *Number,* antal. *Nutrient,* näring, *nutrient solution (uptake),* näringslösning (-upptagning).

Occasion, tillfälle. *Optimum,* optimum, motsvarande högsta tillväxt (maximum), *optimum content (supply),* optimumhalt (-giva), *optimum range,* optimumområde (motsvarande 90—100—90 procent av maximumtillväxt).

Per cent, procent. *Percentage,* procentuell halt. *Percentile,* procentuell. *Phosphorus* (P), fosfor. *Pine,* tall. *Potassium* (K), kalium. *ppm, part per million,* delar av millionen, mg per liter. *Production,* produktion. *Proportion,* proportion, andel.

Range, område, intervall. *Rate,* hastighet. *Relation,* samband, förhållande. *Relative,* relativ, *relative growth (percentage),* relativ tillväxt (halt), procent av maximum (optimum). *Requirement,* behov. *Root,* rot.

Salt, salt. *Seed,* frö. *Seedling,* planta. *Sensitivity,* känslighet. *Series,* serie. *Shoot,* skott. *Sodium* (Na), natrium. *Solution,* lösning, näringslösning. *Source,* källa. *Spruce,* gran. *Stage,* stadium. *Stem,* stam. *Strong,* stark. *Sulphur* (S), svavel. *Supply,* giva.

Time, tid. *Tolerance,* tolerans, uttryck för giva/tillväxt-kurvans bredd. *Total,* total, sammanlagd. *Treatment,* behandling.

Uptake, upptagning. *Utilization,* utnyttjande, *utilization per cent,* utnyttjandeprocent (upptagen mängd näring som procent av tillförd mängd).

Variation, variation. *Vary,* variera. *Vessel,* kärl, bägare. *Weak,* svag. *Weight,* vikt.

Table I. Experimental data from the elementseries with pine. Control supplies in italics

Element	Compound	Supply, ppm element	Total element supply, mg/vessel	Length of growth period, days	Number of seedlings per vessel	Length, mm/seedling		Fresh weight, mg/seedling		Dry weight, mg/seedling			Element content, per cent of dry weight		
						Stem	Root	Shoot	Seedling	Leaves	Shoot	Seedling	Leaves	Stem	Root
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
N	NH_4NO_3	0.05	0.30	97	12	27	150	33.3	112	12.7	16.2	31.9	0.64	0.66	1.00
					13	24	110	55.4	166	13.7	17.8	36.6	0.76	0.65	0.85
		0.5	3.0		13	34	120	65.4	231	20.4	27.9	54.9	0.72	0.62	0.96
					12	28	140	71.6	240	18.3	24.4	51.0	0.69	0.69	1.16
		5.0	30		13	39	140	188	508	45.5	59.9	109	1.49	1.20	1.52
					10	44	140	320	822	65.9	85.5	163	1.61	1.31	1.67
		50	*300*		13	45	100	562	935	93.7	117.1	164	2.60	2.57	2.65
					12	60	130	533	882	116.1	149.9	203	2.91	2.84	2.40
		150	900		13	62	130	542	919	103.3	137.5	188	3.02	2.52	2.88
					12	56	90	593	946	108.4	139.3	188	2.94	2.29	2.75
		450	2 700		4	38	95	425	675	108.2	131.7	174	2.81	3.42	3.74
					12	32	75	341	489	76.8	96.2	117	3.15	3.64	3.50
P	NaH_2PO_4	0.02	0.12	97	13	30	130	80.8	208	22.2	28.7	53.0	0.067	0.14	0.12
					13	26	130	94.7	225	24.3	29.2	49.8	0.055	0.13	0.094
		0.2	1.2		13	36	130	162	369	42.8	54.1	87	0.055	0.12	0.12
					11	40	110	395	836	81.3	101.3	159	0.12	0.18	0.17
		2.0	12		13	55	125	492	808	112.9	143.1	181	0.16	0.39	0.48
					13	52	110	599	1 012	97.6	123.5	174	0.17	0.38	0.44
		20	*120*		13	45	100	562	935	93.7	117.1	164	0.21	0.46	0.76
					12	60	130	533	882	116.1	149.9	203	0.25	0.43	0.68
		60	360		12	51	100	471	792	91.0	115.4	158	0.29	0.52	0.81
					9	62	120	607	1 020	107.0	140.4	191	0.30	0.54	0.76
		180	1 080		12	55	120	533	854	96.0	124.7	165	0.35	0.62	0.91
					12	60	140	543	934	100.0	126.7	174	0.34	0.59	0.88
K	KCl	0.05	0.30	97	9	34	60	50.0	63	17.0	22.4	28.2	0.205	0.27	
					12	26	55	105.0	157	29.8	36.0	45.8	0.159	0.25	
		0.5	3.0		11	35	70	127	173	39.0	47.8	60.2	0.326	0.38	0.81
					12	32	50	222	329	52.3	65.6	84.8	0.272	0.37	0.51
		5.0	30		11	57	90	546	877	109.3	139.7	185	1.03	1.13	1.72
					13	53	130	468	738	87.9	114.4	149	0.95	1.34	1.75
		50	*300*		13	45	100	562	935	93.7	117.1	164	0.76	1.33	2.24
					12	60	130	533	882	116.1	149.9	203	1.09	1.24	2.01
		150	900		11	55	110	527	827	103.5	128.2	170	1.24	1.48	2.16
					11	55	125	606	1 015	109.8	140.5	185	1.25	1.77	2.50
		450	2 700		11	55	115	477	741	92.6	118.1	154	1.88	2.29	3.06
					11	55	110	526	863	90.8	111.3	155	1.97	2.47	2.26
Ca	$CaCl_2$	0.004	0.024	97	12	44	70	342	508	76.2	93.8	124	0.034	0.01	0.06
					12	51	100	391	590	79.7	102.0	134	0.040	0.01	0.03
		0.12	0.72		13	58	105	515	781	100.1	130.5	169	0.050	0.01	0.05
					12	53	120	574	932	116.1	142.4	191	0.050	0.02	0.06
		4.0	24		11	55	110	546	873	110.1	139.7	188	0.20	0.12	0.09
					13	52	110	527	888	98.6	124.1	168	0.23	0.13	0.07
		40	*240*		13	45	100	562	935	93.7	117.1	164	0.26	0.22	0.09
					12	60	130	533	882	116.1	149.9	203	0.27	0.20	0.11
		120	720		11	52	120	418	609	79.0	100.0	126	0.46	0.33	0.26
					12	53	125	512	845	93.2	121.6	161	0.36	0.30	0.20
		360	2 160		6	57	110	500	758	104.4	132.2	171	0.82		0.27
					1										
Mg	$MgCl_2$	0.015	0.09	97	13	30	90	127	242	32.4	40.1	61.6	0.06	0.04	0.04
					12	38	90	203	388	45.8	58.0	84.0	0.03	0.03	0.03
		0.15	0.90		13	46	110	300	492	62.1	81.2	109	0.06	0.10	0.04
					12	44	90	408	694	82.4	104.0	144	0.06	0.09	0.04
		1.5	9.0		10	51	100	405	635	81.1	103.2	134	0.11	0.13	0.07
					10	50	130	526	893	97.8	124.2	169	0.12	0.19	
		15	*90*		13	45	100	562	935	93.7	117.1	164	0.12	0.24	0.11
					12	60	130	533	882	116.1	149.9	203	0.14	0.25	0.10
		150	900		11	60	80	527	777	100.0	124.9	160	0.20	0.36	0.13
					13	53	110	541	863	103.3	131.6	170	0.17	0.38	0.12
S	Na_2SO_4	0	0	99	9	38	170	94.4	176	16.8	21.6	33.1	0.05		0.06
					9	41	170	98.9	190	16.0	21.4	31.3	0.04		0.05
		0.2	1.2		9	58	180	371	653	69.3	94.3	135	0.06		0.06
					9	54	185	364	638	74.4	95.5	136	0.09		0.07
		2.0	12		9	65	140	537	841	90.4	113.0	148	0.19		0.23
					9	57	110	456	769	80.4	101.0	138	0.23		0.26
		20	*120*		9	73	90	531	832	87.8	117.9	152	0.22		0.26
					9	69	110	536	880	91.9	119.5	163	0.25		0.25
		60	360		9	64	110	569	926	100.6	125.6	163	0.18		0.38
					9	58	85	516	832	91.6	114.4	150	0.14		0.30
		600	3 600		9	61	120	429	740	72.3	92.1	123	0.46		0.46
					9	53	100	387	630	69.1	84.3	110	0.43		0.58

Table II. Experimental data from the element series with spruce. Control supplies in italics

Element	Compound	Supply, ppm element	Total element supply, mg/vessel	Length of growth period, days	Number of seedlings per vessel	Length, mm/seedling		Fresh weight, mg/seedling		Dry weight, mg/seedling			Element content, per cent of dry weight		
						Stem	Root	Shoot	Seedling	Leaves	Shoot	Seedling	Leaves	Stem	Root
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
N	NH_4NO_3	0.5	5.0	160	9	57	310	178	456	48.8	65.5	114	0.71	0.59	0.84
					9	57	180	167	444	47.9	64.1	110	0.61	0.54	0.98
		5.0	50		9	96	370	522	1 411	129	181	303	0.85	0.77	1.33
					9	124	260	656	1 411	140	204	312	1.13	0.73	1.51
		15	150		9	170	230	1 267	2 089	216	311	415	2.03	1.57	2.26
					9	169	220	1 278	2 144	276	396	513	1.41	1.15	2.45
		50	*500*		9	165	220	1 467	2 100	299	432	547	2.13	1.73	2.94
					9	199	180	1 600	2 144	301	442	552	2.12	1.66	2.48
		150	1 500		9	178	210	1 533	2 222	283	410	519	2.17	2.01	2.80
					9	188	200	1 444	2 133	281	416	527	2.43	1.83	3.12
		300	3 000		9	177	220	1 367	2 122	229	350	445	2.58	1.97	3.42
					8	183	170	1 562	2 225	311	457	543	2.25	2.75	3.84
P	NaH_2PO_4	0.1	1.0	160	9	65	170	211	433	54.2	70.9	106	0.060	0.12	
					9	57	200	189	500	56.5	73.6	133	0.043	0.08	0.10
		1.0	10		8	147	250	1 388	2 188	305	427	562	0.11	0.14	0.23
					9	178	190	1 333	2 000	289	422	546	0.11	0.12	0.21
		3.0	30		9	178	190	1 544	2 178	337	484	614	0.21	0.25	0.36
					9	182	240	1 367	2 078	260	369	471	0.27	0.27	0.40
		10	*100*		9	165	220	1 467	2 100	299	432	547	0.22	0.28	0.42
					9	199	180	1 600	2 144	301	442	552	0.24	0.25	0.40
		30	300		9	164	200	1 544	2 311	302	441	549	0.26	0.33	0.60
					9	192	240	1 500	2 344	277	418	542	0.25	0.27	0.53
		60	600		9	187	210	1 578	2 100	301	447	548	0.36	0.42	0.45
					9	195	200	1 611	2 256	293	426	536	0.28	0.30	0.50
K	KCl	0.15	1.5	160	6	78	110	333	450	83.6	106.2	126	0.26	0.24	0.29
					9	58	60	156	222	42.4	55.8	68	0.25	0.26	0.42
		1.5	15		9	116	160	822	1 233	188	258	337	0.32	0.30	0.37
					9	134	220	900	1 433	185	272	368	0.29	0.34	0.41
		15	150		9	185	170	1 444	2 178	267	401	527	0.74	0.82	1.13
					9	197	120	1 422	1 856	268	416	504	0.74	0.72	0.96
		50	*500*		9	165	220	1 467	2 100	299	432	547	0.92	0.67	1.08
					9	199	180	1 600	2 144	301	442	552	0.93	0.86	1.04
		150	1 500		9	179	230	1 500	2 167	294	410	523	1.23	0.93	1.72
					9	176	190	1 389	1 989	244	357	459	0.95	0.82	1.30
		300	3 000		9	190	210	1 378	1 989	250	350	434	1.45	1.24	1.60
					9	190	190	1 478	2 044	268	379	464	1.23	1.05	1.60
Ca	$CaCl_2$	0.12	1.2	160	8	125	110	812	1 125	172	237	300	0.015	0.02	0.05
					9	105	70	700	944	168	239	296	0.027	0.02	0.03
		1.2	12		9	138	130	1 122	1 567	262	356	447	0.029	0.04	0.04
					9	147	100	1 133	1 478	228	324	399	0.019	0.04	0.03
		12	120		9	164	190	1 333	2 200	249	353	482	0.12	0.12	0.11
					9	164	180	1 378	1 933	298	417	566	0.11	0.11	0.10
		40	*400*		9	165	220	1 467	2 100	299	432	547	0.19	0.19	0.23
					9	199	180	1 600	2 144	301	442	552	0.19	0.13	0.21
		120	1 200		9	194	230	1 422	2 111	266	397	502	0.56	0.32	0.17
					9	183	220	1 489	2 156	300	433	541	0.43	0.26	0.17
		360	3 600		0										
					8	158	230	1 162	1 625	224	322	393	0.99	0.63	0.20
Mg	$MgCl_2$	0.05	0.5	160	8	90	140	362	512	112.6	138.1	163	0.013	0.03	0.04
					9	86	90	278	400	80.4	101.0	123	0.020	0.05	0.08
		0.15	1.5		9	138	160	833	1 233	202	260	326	0.020	0.05	0.05
					9	126	120	633	922	156	198	244	0.018	0.05	0.05
		1.5	15		8	171	250	1 238	1 912	220	323	425	0.07	0.10	0.08
					9	171	170	1 211	1 878	206	305	392	0.07	0.11	0.07
		15	*150*		9	165	220	1 467	2 100	299	432	547	0.12	0.18	0.08
					9	199	180	1 600	2 144	301	442	552	0.10	0.15	0.08
		45	450		9	180	210	1 422	2 044	285	404	518	0.22	0.27	0.08
					9	158	200	1 089	1 600	210	304	379	0.19	0.30	0.08
S	Na_2SO_4	0	0	155	13	69	140	88	215	36.6	52.9	84	0.03		0.07
					13	60	100	104	215	26.1	40.7	63	0.03		0.06
		0.2	2.0		9	116	100	656	956	141	192	247	0.13		0.06
					9	130	125	667	967	137	196	244	0.13		0.06
		2.0	20		9	166	110	1 067	1 378	208	301	354	0.13		0.25
					7	140	80	1 029	1 371	195	280	331	0.14		0.25
		20	*200*		9	170	120	1 122	1 556	196	289	358	0.18		0.26
					9	170	120	1 067	1 556	191	284	358	0.18		0.29
		60	600		9	152	140	1 022	1 389	182	262	315	0.14		0.23
					9	143	100	844	1 178	149	216	266	0.16		0.31
		600	6 000		9	133	120	667	944	128	180	223	0.27		0.40
					9	116	110	656	933	133	183	220	0.34		0.42

Table III. Experimental data from the element series with birch. Control supplies in italics

Element	Compound	Supply, ppm element	Total element supply, mg/vessel	Length of growth period, days	Number of seedlings per vessel	Length, mm/seedling		Fresh weight, mg/seedling		Dry weight, mg/seedling			Element content, per cent of dry weight		
						Stem	Root	Shoot	Seedling	Leaves	Shoot	Seedling	Leaves	Stem	Root
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
N	NH_4NO_3	4.2	18.9	72	4	118	90	478	865	84.2	130.4	169	1.54	0.73	1.25
					4	114	95	510	1 010	89.5	139.8	196	1.50	0.99	1.22
		28	126		4	240	85	2 165	2 772	294.5	460.3	517	2.62	1.08	2.63
					4	272	75	2 802	3 628	422.8	671.2	758	3.59	0.97	2.14
		140	*630*		4	306	70	3 470	4 395	491.6	771.4	864	3.79	1.22	3.22
					4	280	90	3 345	4 132	476.4	776.6	871	3.42	1.34	3.43
		280	1 260		4	282	85	2 615	3 365	345.6	557.6	628	4.25	1.78	3.43
					4	288	75	3 510	4 310	517.7	782.5	870	4.08	1.96	3.31
		560	2 520		4	276	70	2 975	3 615	400.8	624.7	693	4.70	2.00	3.91
					4	284	70	3 108	4 045	419.8	646.5	725	4.70	2.13	3.72
P	NaH_2PO_4	1.0	4.5	72	4	226	90	1 888	2 845	302.9	472.9	560	0.12	0.08	0.18
					4	241	90	2 225	3 155	356.4	563.4	659	0.12	0.08	0.18
		3.0	13.5		4	306	90	3 325	4 050	469.0	746.6	829	0.23	0.15	0.35
					4	266	80	2 875	3 700	449.8	719.6	808	0.23	0.14	0.39
		100	*450*		4	306	70	3 470	4 395	491.6	771.4	864	0.38	0.28	1.14
					4	280	90	3 345	4 132	476.4	776.6	871	0.40	0.30	1.35
		200	900		4	259	80	2 050	2 780	299.9	452.4	521	0.63	0.38	1.31
					4	259	80	2 462	3 412	307.5	469.5	538	0.62	0.38	1.68
		400	1 800		4	227	90	2 075	2 912	285.3	422.3	480	0.88	0.49	1.89
					4	234	70	2 312	3 325	324.0	491.4	566	0.94	0.51	2.13
K	KCl	0.3	1.5	80	4	70	55	325	445	69.0	93.1	107	0.25	0.18	0.30
					5	68	65	278	360	51.2	68.7	79	0.30	0.18	0.34
		3.0	15		4	212	80	2 252	2 890	362.2	560.1	643	0.49	0.24	0.31
					3	210	80	3 123	3 963	500.7	826.2	935	0.54	0.21	0.37
		30	150		4	334	95	4 142	5 232	590.2	967.3	1 096	1.78	0.92	1.67
					4	332	80	4 085	4 998	611.9	997.9	1 133	1.50	0.91	1.42
		126	*570*		4	294	80	4 418	5 638	612.6	949,6	1 073	2.20	1.18	2.38
					4	302	85	4 200	5 215	673.7	1 092.5	1 225	1.80	1.07	1.91
		300	1 500		3	284	70	4 440	5 277	627.1	1 025.6	1 123	2.22	1.18	2.27
					4	327	85	4 502	5 455	676.7	1 104.1	1 262	2.25	0.99	2.21
		1 000	5 000		2	256	95	4 710	6 605	633.0	926.9	1 096	2.90	1.98	4.12
					3	262	90	4 583	6 130	584.8	840.8	982	3.99	3.02	4.15
Ca	$CaCl_2$	0.4	1.8	72	4	66	45	178	265	39.7	57.5	67	0.03	0.02	0.016
					4	58	45	140	212	32.8	54.0	63	0.05	0.01	0.010
		1.2	5.4		4	202	70	1 655	2 142	260.5	377.9	423	0.03	0.05	0.046
					4	201	80	2 325	3 000	407.1	594.7	670	0.08	0.05	0.032
		12	54		4	320	75	3 258	4 115	508.6	780.9	870	0.11	0.07	0.07
					4	268	85	2 620	3 562	345.0	558.4	631	0.13	0.09	0.06
		120	*540*		4	306	70	3 470	4 395	491.6	771.4	864	0.30	0.24	0.14
					4	280	90	3 345	4 132	476.4	776.6	871	0.30	0.22	0.18
		240	1 080		4	299	90	2 962	3 512	477.5	723.5	779	0.87	0.70	0.32
					4	258	85	2 582	3 395	372.5	592.6	665	0.63	0.62	0.26
Mg	$MgCl_2$	0.5	2.2	73	3	133	60	600	833	71.0	112.4	130	0.062	0.03	0.016
					3	153	70	800	1 117	76.4	125.7	145	0.053	0.03	0.016
		4.8	22		4	272	75	2 788	3 962	353.0	549.2	647	0.19	0.09	0.07
					4	276	95	2 588	3 238	349.8	528.9	607	0.18	0.09	0.04
		48	*216*		4	236	70	2 275	3 025	335.7	532.0	610	0.37	0.13	0.12
					4	262	90	2 800	3 425	362.0	564.6	643	0.42	0.15	0.12
		144	648		4	233	75	2 088	2 675	277.8	430.4	487	0.50	0.18	0.17
					4	240	80	2 375	3 100	315.5	490.6	569	0.55	0.17	0.14
S	Na_2SO_4	0	0	73	6	95	105	192	308	32.3	53.9	67	0.06		0.031
					6	70	100	150	292	21.2	34.8	48	0.06		0.073
		0.64	2.9		4	200	110	1 325	1 988	179.9	288.2	349	0.24		0.07
					4	182	85	850	1 050	118.4	184.7	203	0.18		0.10
		6.4	29		4	247	75	2 475	3 262	323.2	514.1	579	0.26		0.21
					4	279	75	2 562	3 300	347.6	569.8	630	0.34		0.23
		64	*288*		4	270	70	2 738	3 550	379.4	609.4	677	0.41		0.27
					4	255	65	2 238	2 812	316.0	535.7	596	0.23		0.34
		192	864		4	207	100	1 175	1 725	153.5	242.9	274	0.35		0.52
					4	216	100	1 700	2 162	244.4	374.4	411	0.40		0.36
		640	2 880		4	158	100	762	1 200	119.2	168.5	195	1.84		0.68
					4	219	140	1 438	2 150	220.8	342.8	408	1.22		0.64

Table IV. Experimental data from the series with varied length of the growth period. The growth time corresponding to that of the element series in italics

Species	Length of growth period, days	Treatment	Supply, ppm		Total supply, mg/vessel		Number of seedlings per vessel	Length, mm/seedling		Fresh weight, mg/seedling		Dry weight, mg/seedling			Content, per cent of dry weight					
															Nitrogen			Potassium		
			N	K	N	K		Stem	Root	Shoot	Seedling	Leaves	Shoot	Seedling	Leaves	Stem	Root	Leaves	Stem	Root
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
PINE	59	Control	50	50	175	175	9	32	50	138	198	24.1	29.2	35.5	3.24	2.89	2.50	1.33	1.42	2.42
							9	31	60	187	269	32.0	39.1	48.9	3.22	3.24	2.75	1.38	1.54	2.30
							9	35	60	200	294	34.7	43.5	53.3	3.06	2.59	2.80	1.28	1.63	2.38
		Low N	5		17.5		9	32	60	168	267	31.4	38.1	48.9	2.86	1.93	2.42			
							9	32	60	159	246	29.3	35.9	45.6	3.04	2.21	2.36			
		Low K		0.75		2.6	9	18	50	121	155	21.4	27.4	31.1				0.59	0.58	0.71
							9	22	50	119	159	19.9	26.3	31.1				0.56	0.64	0.66
	72	Control	50	50	225	225	9	40	60	239	350	43.6	53.7	67.8	3.08	2.66	2.43	1.30	1.29	1.88
							9	42	80	296	456	54.5	66.4	85.6	3.10	2.42	2.64	1.26	1.46	2.01
							9	40	80	273	410	50.8	61.6	78.9	3.18	2.52	2.28	1.26	1.40	2.12
		Low N	5		22.5		9	38	80	249	440	50.3	61.0	82.2	2.51	1.61	1.62			
							9	37	80	239	409	47.9	57.7	77.8	2.53	1.74	1.86			
		Low K		0.75		3.4	9	25	60	220	291	32.9	42.3	52.2				0.40	0.51	0.55
							9	25	50	204	266	29.8	36.6	44.4				0.55	0.67	0.69
	94	Control	50	50	300	300	9	53	100	356	640	70.8	86.4	124	3.14	2.02	2.44	1.08	1.01	1.61
							9	57	80	478	801	92.3	112.3	152	3.01	2.70	2.37	1.07	1.20	1.71
							9	55	90	402	735	82.2	104.0	147	3.02	2.55	2.46	1.00	1.21	1.78
		Low N	5		30		9	42	120	307	740	67.2	82.2	136	1.60	1.42	1.64			
							9	38	120	307	595	65.7	83.3	127	1.54	1.32	1.54			
		Low K		0.75		4.5	9	31	60	203	315	42.0	52.4	68.9				0.35	0.43	0.42
							9	29	60	227	343	40.6	51.3	67.8				0.38	0.46	0.47
	115	Control	50	50	375	375	9	62	130	572	1 158	158	196	273	2.87	2.99	2.63	0.68	0.90	1.52
							9	58	130	670	1 207	171	205	281	2.97	2.69	2.98	0.95	0.98	1.43
							9	60	130	553	1 094	150	188	271	3.18	2.86	2.45	1.06	0.99	1.16
		Low N	5		37.5		9	46	155	337	1 046	98.4	122	220	1.60	1.59	1.31			
							9	50	160	305	902	89.5	112	191	1.54	1.72	1.39			
		Low K		0.75		5.6	9	43	75	292	464	70.6	88.9	116				0.43	0.42	0.47
							9	45	70	297	478	70.4	85.4	116				0.35	0.39	0.42
SPRUCE	94	Control	50	50	275	275	9	80	60	301	372	59.2	75.6	86.7	2.37	2.03	2.95	1.25	1.42	1.73
							9	88	60	316	398	60.0	80.9	93.3	2.15	1.95	2.87	1.03	1.34	1.74
							9	94	70	473	584	91.1	117.1	134.4	2.35	1.95	3.09	1.13	1.30	1.60
		Low N	5		27.5		9	86	60	350	501	72.5	93.9	114.4	1.82	1.21	2.32			
							9	75	60	336	476	65.1	82.9	100.0	1.77	1.55	2.18			
		Low K		0.75		4.1	9	68	60	282	359	54.0	68.4	81.1				0.35	0.38	0.47
							9	68	50	207	280	44.8	59.5	71.1				0.38	0.48	0.52
	122	Control	50	50	375	375	9	108	60	816	1 033	165	219	251	2.28	1.80	2.64	0.89	1.02	1.52
							9	100	80	702	918	141	185	216	2.02	1.69	2.60	0.98	1.12	1.73
							9	91	80	686	902	138	177	212	2.16	1.72	2.43	0.96	1.18	1.34
		Low N	5		37.5		9	90	100	467	781	96.8	122	160	1.68	1.28	1.72			
							9	86	100	512	1 044	116.1	149	219	1.26	0.89	1.54			
		Low K		0.75		5.6	9	71	60	333	467	83.2	106	130				0.31	0.34	0.38
							9	77	60	364	535	80.7	107	138				0.30	0.32	0.39
	164	Control	50	50	525	525	9	181	160	1 322	1 866	235	376	460	2.50	1.95	2.96	0.92	1.07	1.63
							9	187	170	1 707	2 427	353	544	667	2.13	1.86	2.57	0.82	0.99	1.23
							9	196	170	1 824	2 413	368	583	690	2.02	1.56	2.71	0.85	1.00	1.26
		Low N	5		52.5		9	108	260	584	1 540	172	236	370	0.97	0.73	1.51			
							9	117	270	700	1 720	175	235	394	1.27	0.87	1.26			
		Low K		0.75		7.9	9	78	140	578	982	154	208	270				0.28	0.38	0.40
							9	90	120	506	799	134	186	244				0.24	0.30	0.30
	185	Control	50	50	600	600	9	169	200	1 696	2 372	372	583	708	2.39	1.74	3.21	0.83	0.76	1.09
							9	191	180	1 861	2 553	371	616	752	2.22	1.26	3.15	0.83	0.76	1.15
							9	192	200	1 782	2 658	355	590	744	2.15	1.41	2.38	0.91	0.80	0.98
		Low N	5		60.0		9	107	280	724	1 804	167	248	408	1.35	0.86	1.26			
							9	127	250	901	2 325	226	325	534	1.05	0.76	1.13			
		Low K		0.75		9.0	9	85	100	527	860	132	182	248				0.27	0.24	0.29
							9	89	170	690	1 151	165	241	321				0.25	0.25	0.25
BIRCH	49	Control	140	126	350	315	4	80	45	282	370	45.2	56.6	61.8	4.61	2.78	3.07	2.06	2.68	3.87
							4	97	50	375	493	50.0	68.2	75.5	4.36	2.30	3.30	2.09	2.50	3.99
							4	116	50	470	512	60.4	87.5	99.0	4.58	2.22	3.55	2.25	2.34	3.70
		Low N	14		35		4	114	55	538	696	66.6	95.6	110.0	4.16	1.96	3.14			
							4	100	55	482	670	61.7	84.5	97.5	4.15	1.97	2.92			
		Low K		1.3		3.2	4	90	40	235	295	26.7	37.1	45.0				0.95	0.96	0.75
							4	83	35	258	326	39.9	53.7	65.0				0.92	0.86	0.78
	63	Control	140	126	490	441	3	190	60	1 180	1 740	166	246	274	3.83	1.81	3.30	2.31	1.96	4.15
							4	185	60	1 240	1 660	154	248	278	4.43	1.66	3.49	2.36	2.02	3.55
							4	195	60	1 360	1 850	178	276	288	4.28	1.79	2.99	2.37	2.22	4.11
		Low N	14		49		4	170	80	1 060	1 470	164	246	282	3.54	1.26	2.56			
							4	166	85	1 050	1 420	143	221	250	3.81	1.53	2.45			
		Low K		1.3		4.4	4	142	50	710	900	82	133	150				0.56	0.31	0.50
							4	134	40	1 040	1 250	160	254	278				0.66	0.28	0.53
	76	Control	140	126	630	567	4	252	70	2 640	3 340	377	637	705	3.74	1.78	3.09	2.04	1.22	2.63
							4	269	75	2 740	3 370	367	646	700	3.48	1.54	3.12	2.15	1.20	2.64
							4	274	75	3 040	3 580	400	710	785	3.62	1.66	2.87	1.95	1.14	2.46
		Low N	14		63		4	232	90	1 790	2 410	263	500	565	2.55	1.06	2.07			
							4	218	90	1 520	2 040	215	373	422	2.99	1.45	2.39			
		Low K		1.3		5.7	4	148	50	1 280	1 640	211	326	365				0.36	0.19	0.39
							4	172	55	1 040	1 390	163	276	322				0.43	0.22	0.42
	91	Control	140	126	770	693	4	348	80	4 250	5 150	596	1 153	1 275	3.41	1.54	3.21	2.11	1.10	2.16
							4	317	80	4 250	5 210	606	1 171	1 345	3.52	1.27	3.23	2.06	1.32	2.25
							4	358	75	4 800	5 660	662	1 336	1 420	3.34	1.54	3.49	1.94	0.92	1.74
		Low N	14		77		4	261	100	2 650	3 550	371	707	822	2.29	1.03	1.59			
							4	300	100	2 750	3 460	373	689	788	2.57	0.96	2.16			
		Low K		1.3		6.9	4	172	70	1 560	2 010	253	378	440				0.35	0.18	0.27
							4	182	65	1 610	2 130	288	454	535				0.29	0.15	0.30