Studies on Forest Nutrition

Studier över skogens näringsförhållanden

I. Seasonal Variation in the Nutrient Content of Conifer Needles

I. Årstidsvariationen i näringsinnehållet hos tall- och granbarr

by

CARL OLOF TAMM

MEDDELANDEN FRÅN
STATENS SKOGSFORSKNINGSINSTITUT
BAND 45 · NR 5

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Introduction

Under the heading "Studies on forest nutrition" some investigations will be reported which deal with nutritional problems of forest trees and forest stands in Sweden.

The role of plant nutrients as yield-determining factors in the forest is very imperfectly known, although experiments have shown that in certain habitats at least an addition of nutrients may increase forest growth several times (MITCHELL & CHANDLER 1939, MALMSTRÖM 1949, 1952). Comparative investigations have shown good correlations between forest yield and amounts of certain nutrients or minerals in the soil, when habitats with similar climate and water supply are studied (*e.g.*, O. TAMM 1937, VIRO 1951). On the other hand the water factor seems to determine—directly or indirectly—the forest type and forest growth within large areas of north Sweden, where mineralogical composition of the moraines is rather uniform but moisture conditions vary with altitude, slope, exposure, coarseness of the substrate, *etc.* (cf. O. TAMM & WADMAN 1945, MALMSTRÖM 1949). It is thus clear that both hydrology and the geological and mineralogical nature of the soil are of great importance for Swedish forests, but the interaction between these two complexes of factors makes it difficult to find soil characteristics directly related to forest growth, except in special cases. There seems little hope of finding such properties by analysis of the humus layer instead of the subsoil, to judge from the large variation in humus layer properties found by MALMSTRÖM (1949) within each forest type. There are at least two probable physiological explanations of the difficulty in finding a strict correlation between soil data and forest yield: 1) The nutrient status of the stand and the nutrient content of the top soil are both variable, and their variation is perhaps not always positively correlated. 2) It is not at all easy to decide which soil properties are of most immediate importance for the trees. Nutrient uptake by roots (or mycorrhizas) and chemical extraction are very different things.

While we recognize forest nutrition, and the possibilities of improving nutrient supply to the forest, as among the most important topics in forest research today, a simple method of evaluating the nutrient status of a stand is still lacking. Although the possibility exists of experimenting with different combinations of nutrients, there is great need for a more convenient and less expensive and time-consuming method.

Foliar analysis offers some hope of estimating the nutrient status of a forest more directly than by the various soil analysis methods (cf. MITCHELL & CHANDLER 1939). Therefore the Department of Botany and Soils at the Forest

Research Institute of Sweden took up this method in 1949, in order to test its value for forest research and practice. From the beginning of the work we have studied the nutrient physiology and ecology of the forest trees, feeling that without a safe physiological foundation the method would be of considerably less significance (cf. LUNDEGÅRDH 1945). The rather negative conclusions of AALTONEN (1950), published at an early stage of our work, have been taken as a confirmation of our opinion in that respect.

The central point in our investigation has been the relation between internal nutrient concentration in the trees, particularly their leaves and needles, and growth. Each nutrient of ecological importance and each tree species must be studied in this respect. Moreover, the relation between internal nutrient level and growth is different under conditions of deficiency, sufficiency, and excess of a nutrient. As the occurrence of nutrient deficiencies, and their diagnosis is of most immediate interest, we began our work with a study of leaf nutrient concentrations in birch at localities known or suspected to be deficient in certain nutrients (TAMM 1951 a, b). Similar investigations are also being carried out for pine and spruce. A survey of the composition of leaves and needles from "normal" stands has been made as well. A preliminary report on the results so far achieved was read at the Botanical Congress in Paris 1954 (TAMM 1955). A more extensive paper on the same subject will follow later in this series.

Before we can apply a physiological method such as foliar analysis more generally, we must ascertain to what extent nutrient content may vary in the studied organs, both in relation to nutrient supply and other factors. In the present series some of these variations in nutrient content will be described, in special paper when they are considered of direct physiological or ecological interest, otherwise in connection with the description of sampling technique. The first paper in this series, concerned with seasonal variation in the composition of conifer needles, contains material of physiological as well as technical interest; a similar report on birch leaves has been published earlier (TAMM 1951 c).

In connection with the work on foliar analysis, experiments with fertilizers have been carried out. Their results will also be reported in this series, which will thus consider the problems of forest nutrition from a more general aspect than that of foliar analysis alone. The second paper thus describes a fertilizer experiment using radioactive phosphate.

Unfortunately some of the more complex physiological problems—interrelations between nutrient supply and other growth factors, or between the supply of different nutrients—are difficult to study in natural stands. Particular attention will therefore be devoted to such problems in our studies of the nutrition of forest tree seedlings, which will be reported elsewhere (INGESTAD, TAMM & INGESTAD, in prep.).

I. Seasonal Variation in the Nutrient Content of Conifer Needles

Experimental Section

Collections from April 1950 to April 1951.

The present investigation was started in April 1950, in order to determine the most suitable sampling period should the composition of conifer needles prove useful as a guide to the nutrient status of forest trees or stands. Satisfactory knowledge on this point is one of the most important prerequisites for the use of foliar analysis (MITCHELL 1936, AALTONEN 1950, TAMM 1951 c). Needle samples were therefore collected at different seasons between April 1950 and April 1951 from one pine (*Pinus silvestris* L.) and one spruce (*Picea Abies* KARST.). Some data on the sample trees are given in Table I and II respectively. They were growing in the same habitats as the birches sampled simultaneously (TAMM 1951 c), an old gravel pit (the pine) and a "park meadow" (the spruce), not far from the coast of the Baltic (lat. N. 59°52′, long. E. from Greenw. 18°55′). In both cases the trees were growing in rather open vegetation.

The pine needles were removed from the shoots before drying, while the spruce needles were left to dry on the shoots. In both cases the different annual shoots were separated shortly after the sampling. On each occasion two branches (sometimes one) were collected from much the same height and aspect on the sample tree. The needles were then dried and analyzed for nitrogen (KJELDAHL micro-determination), phosphorus (colorimetrically), potassium and calcium (flame-photometrically), using methods described earlier (TAMM 1951 c, 1953). Reproducibility of the analytical methods is good in all cases (standard deviation of single determinations within a few per cent), but it is known that somewhat larger errors may occur in the flame-photometric determination of calcium (see below). The results are expressed as dry weight percentages in Table I and Fig. 1 (pine), and Table II and Fig. 2 (spruce). In pine all living generations of needles (usually three) have been analyzed; in spruce the three youngest ones. Some nitrogen determinations have been carried out on still older spruce needles.

The most notable feature in Figs. 1 and 2 is the decrease in most elements in spring and early summer, and the corresponding increase during late summer and autumn. These regular, cyclic variations were at first surprising, particularly since very little confirmation could be obtained from the literature (see Discussion, p. 20). The relatively small number of samples in Tables I and II made a new series of determinations from different seasons desirable.

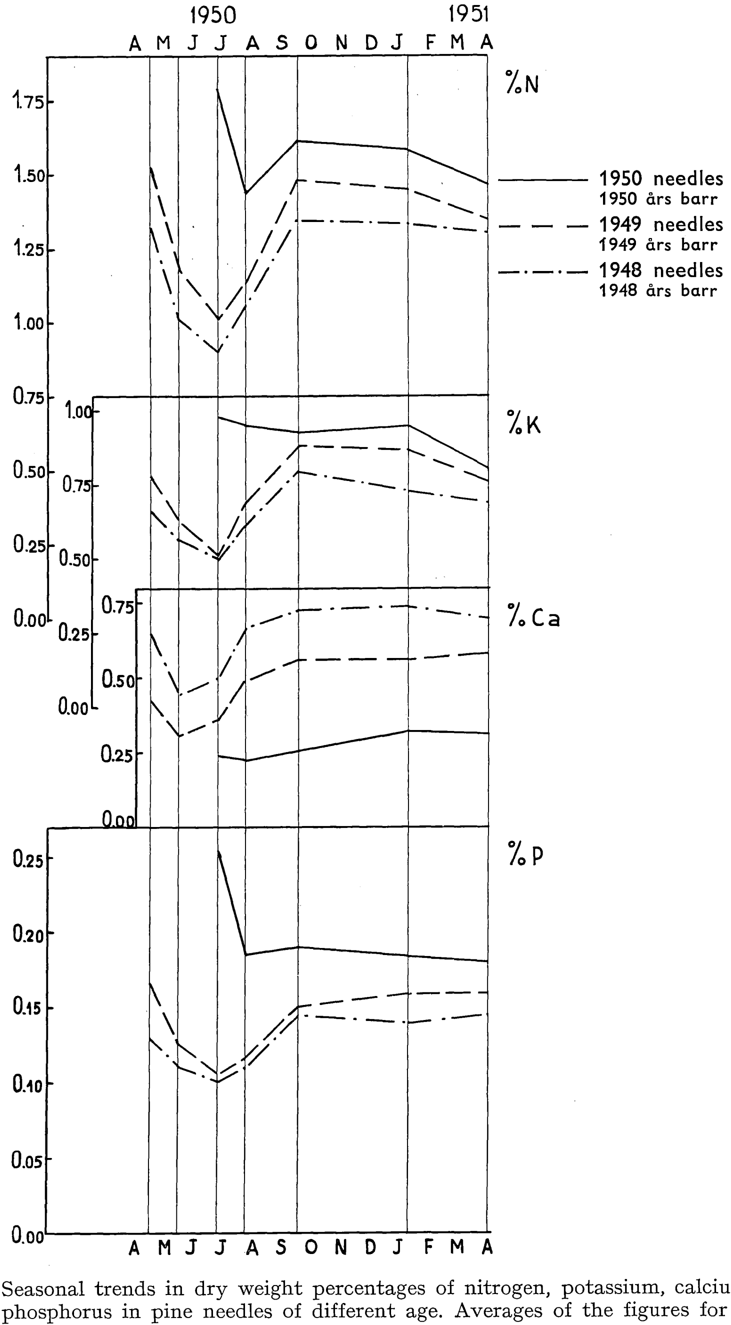

Fig. 1. Seasonal trends in dry weight percentages of nitrogen, potassium, calcium, and phosphorus in pine needles of different age. Averages of the figures for south-exposed and north-exposed branches in Table I.

Årstidsvariationen i halten av kväve, kalium, kalcium och fosfor (% torrvikt) i tallbarr av olika ålder. Medeltal av värdena för syd- och nord-exponerade barr i tab. I.

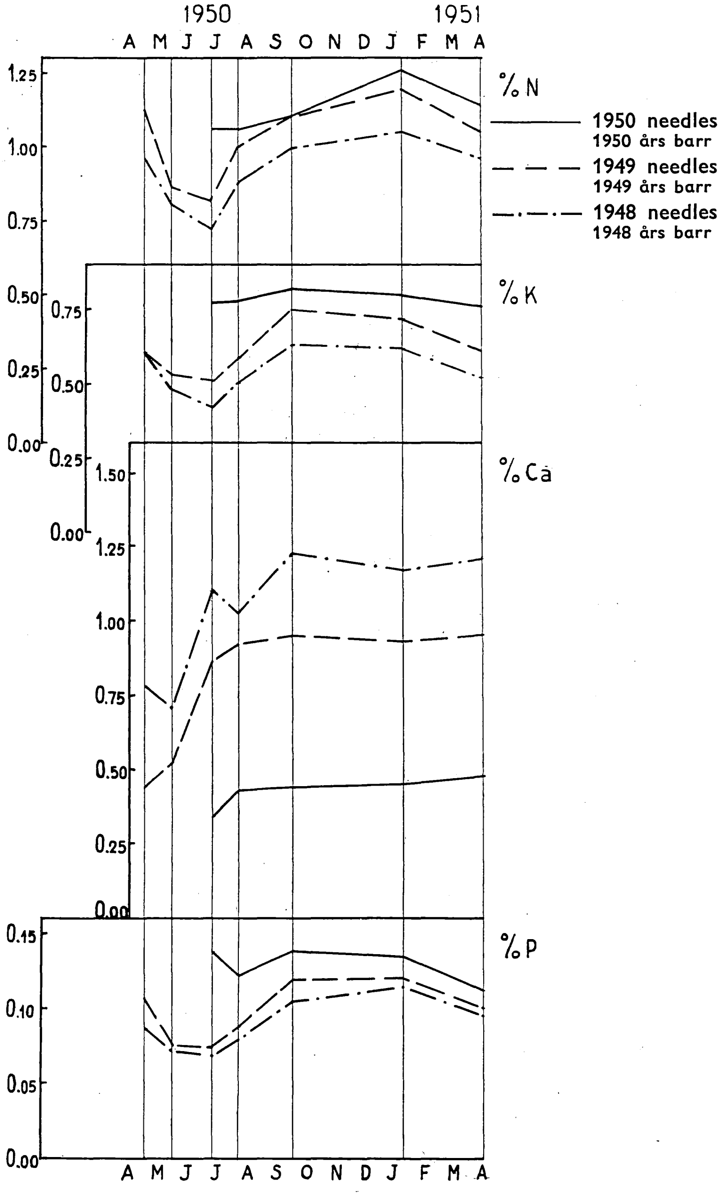

Fig. 2. Seasonal trends in dry weight percentages of nitrogen, potassium, calcium, and phosphorus in spruce needles of different age. Data from Table II.
Årstidsvariationen i halten av kväve, kalium, kalcium och fosfor (% torrvikt) i granbarr av olika ålder. Se vidare tab. II.

Collections from April 1951 to November 1952.

Both the sample trees in the new series were chosen in the park meadow, close to each other and not far from the spruce in Table II. From a pine two well-exposed branches were collected at each sampling, usually one facing south-west and one facing south-east, both from the upper part of the crown. From a spruce also two branches were taken each time, but one from the south (or south-west) side and one from the north (or north-east) side. Both branches were taken from a height of approximately 5 m; the spruce was 8.5 m high in April, 1951.

The analytical methods differed slightly from those used in the preceding series: the mineral elements were determined after dry ashing at 600° C, and calcium was determined both gravimetrically and flame-photometrically. Dry ashing was employed in order to examine the variation in ash and silica. Silica is of particular interest in this connection, as it is usually considered as even more "immobile" in the needles than calcium (note however TULLIN 1954). The silica content of the *pine* needles was too small and variable to allow any conclusions. Regarding analytical methods it should be mentioned that dry ashing of samples rich in silica (in this case the spruce needles) may result in erroneous low values of potassium and calcium, presumably due to the formation of insoluble silicates (Mrs. K. KNUTSON, personal communication). A small error in these both elements is thus likely, but affects all the data of Table IV in the same direction. As the calcium readings on the flame-photometer may be depressed by addition of phosphoric acid (cf. LEYTON 1954 b) and some other reagents, or increased in the presence of potassium, a comparison has been made with gravimetric determinations on the same ash extracts. The flame-photometrically determined values were higher both in pine and spruce, but only in spruce was the difference statistically significant (5.1 ± 0.4 per cent of the calcium value; in pine 0.8 ± 0.9 per cent). Evidently the depressive effect of phosphoric acid is compensated for by some other influence under the condition used (*i.a.*, extreme dilution). Of course this does not mean that results of comparable accuracy can always be expected by the flame-photometric method for analysis of plant ash. Yet a rough estimate of the calcium content may often prove satisfactory even if more accurate figures are desired for nitrogen, phosphorus and potassium, and in such cases the convenient flame-photometric method may be recommended.

As shown by Figs. 3 and 4 and Tables III and IV, the results of the second series of samples are essentially the same as those of the first series. The only difference of any importance is the absence of a summer minimum in calcium in Fig. 3; such a minimum occurred in the first series in pine (but not in spruce). The original purpose of the investigation is then fulfilled, at least for the climate and habitat under examination. The existence of a summer minimum and a winter maximum in the nutrient percentages of evergreen conifer needles seems established beyond doubt.

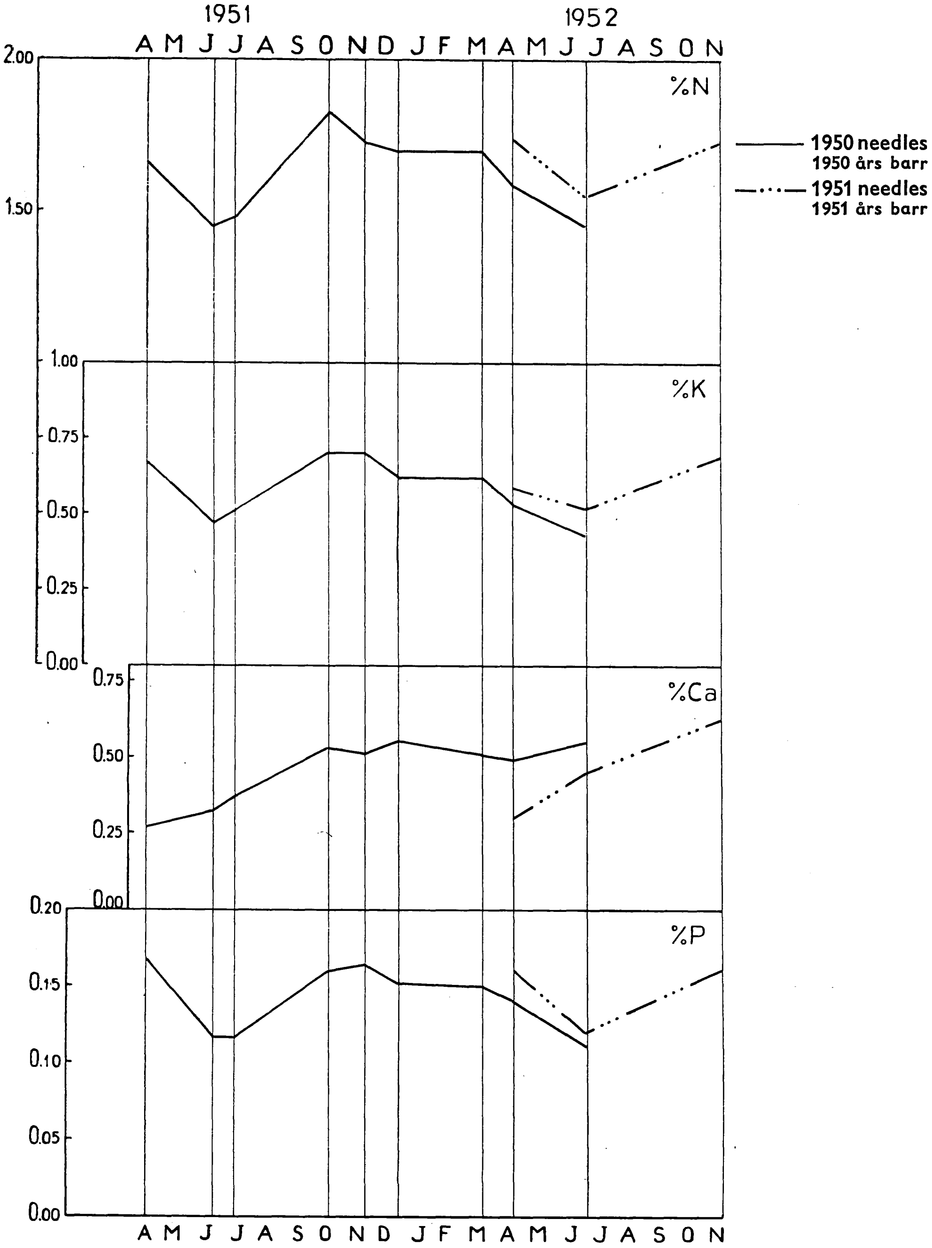

Fig. 3. Seasonal trends in dry weight percentages of nitrogen, potassium, calcium, and phosphorus in one- to two-year-old pine needles. Data from Table III.
Årstidsvariationen i halten av kväve, kalium, kalcium och fosfor (% torrvikt) i ett- till tvååriga tallbarr. Se vidare tab. III.

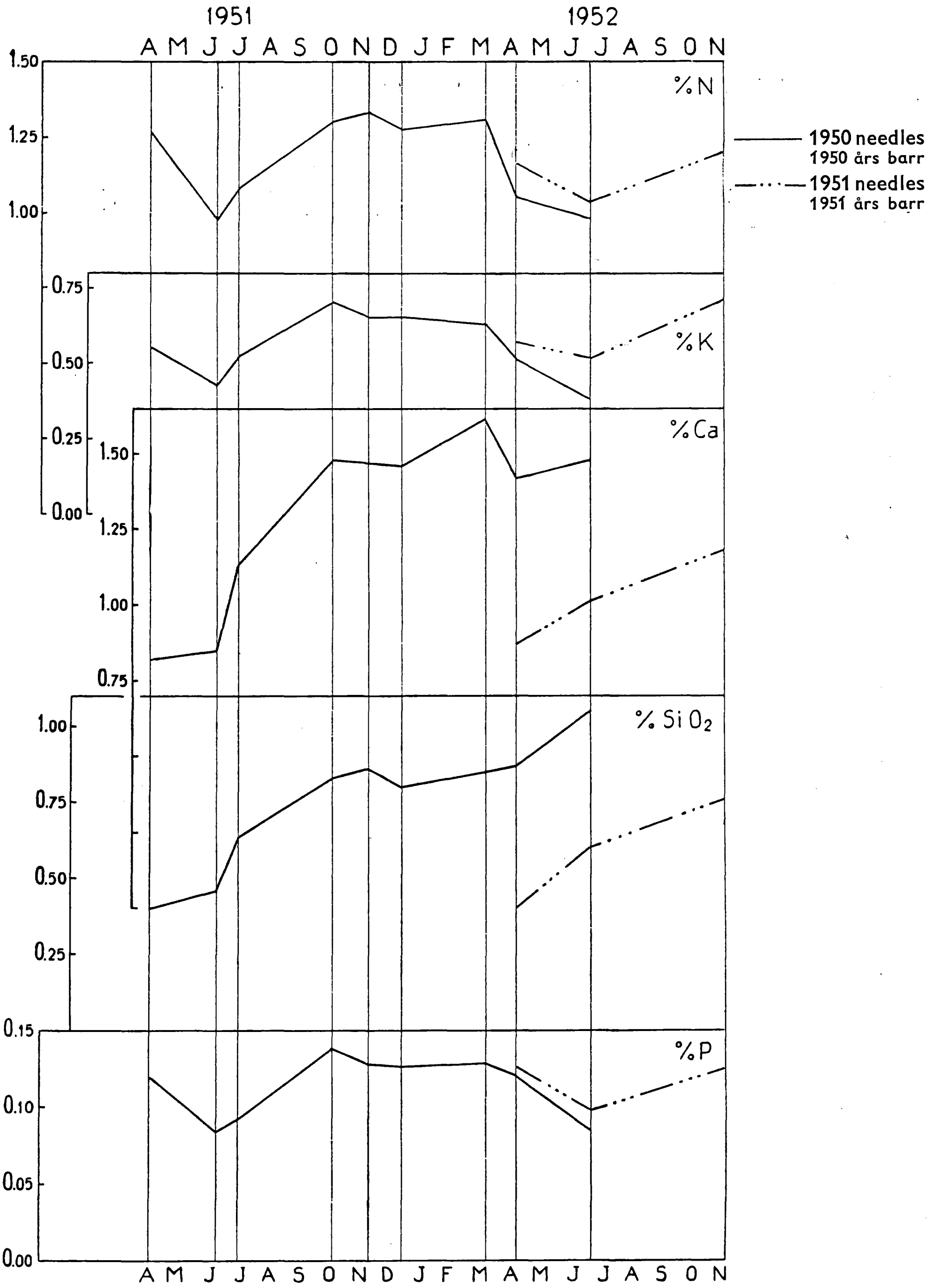

Fig. 4. Seasonal trends in dry weight percentages of nitrogen, potassium, calcium, silica, and phosphorus in one- to two-year-old spruce needles. Averages of the figures for south-exposed and north-exposed branches in Table IV.

Årstidsvariationen i halten av kväve, kalium, kalcium, kiselsyra och fosfor (% torrvikt) i ett- till tvååriga granbarr. Medeltal av värdena för syd- och nordexponerade grenar i tab. IV.

Collections from March 1953 to June 1954. Pine.

Nothing has so far been revealed concerning the causes of variation in nutrient percentages. For this reason a third series of samples was collected from March 1953 to June 1954. This time the technique was altered and needles from marked shoots were sampled—which made it possible to calculate the changes in both dry weight and the absolute content of nutrients in the needles. As dry weight and nutrient content may change with time of day, all samples were taken about noon (somewhat before noon in the case of pine from 26. III. 1953 and 6. VI. 1953).

The sample trees were two pines growing about 10 m apart in the park meadow mentioned before. Both were about 16 years old at the start of the investigation. On the larger pine (4 m high) four different branches were marked, and at each sampling 10 to 30 (most often 15 to 20) needle pairs were taken with a pair of forceps from each segment of the branch leader. An effort was made to have all parts of the shoots, and all aspects equally well represented. All four sample branches were moderately sun-exposed and about 1.5 m above ground. Branches *a* and *b* (see Table V) faced south-east; *b* was weaker and slightly less exposed. Branches *c* and *d* faced south-west; *c* was a vigorous branch similar to *a*, while *d* was a weak side-branch. The other pine was 2.3 m high, and only the top shoot was sampled (branch *e* in Table V). Here a complication arose—the needles being very often joined three and three together on each dwarf shoot, particularly those developed during 1953. Such triplets were avoided in sampling, but as normal needle pairs were not uniformly distributed, the figures for branch *e* in Table V are less accurate, particularly in the case of the 1953 needles.

The samples were placed in polythene bottles and weighed fresh, either immediately after the collection on a simple balance, or the day after on an analytical balance in the laboratory. The latter method was used on most occasions, and the figures so obtained are given to 0.1 mg in Table V. The dry weights were determined after 48 hours at about 55° C in a vacuum drying oven. The nitrogen and phosphorus analyses were then carried out in the usual way (wet ashing in the case of phosphorus). The dwarf shoots were included in the fresh and dry weights, but they were removed before grinding for analysis. The nitrogen and phosphorus figures in Table V are means of duplicate determinations. The standard deviations of the Table figures are approximately 0.009 per cent nitrogen and 0.0014 per cent phosphorus, calculated from the average difference between the duplicates, which were 0.014 per cent nitrogen and 0.0022 per cent phosphorus. This "chemical error" can thus hardly affect the conclusions from Table V and Figs. 5 and 6.

However, "errors" due to physiological causes may also occur. There are several such possibilities. In so far as the "biological errors" are random, their importance may be studied in at least two ways: 1) The samples are taken from five different branches and usually from three different annual segments, making up about 15 independent measures of the changes in needle weight. As a rule there is an excellent agreement between the different branches and segments. Although the independent measures are fewer in the case of nitrogen and, in particular, phosphorus, the agreement between them is very good too. 2) A special test on the homogeneity of some

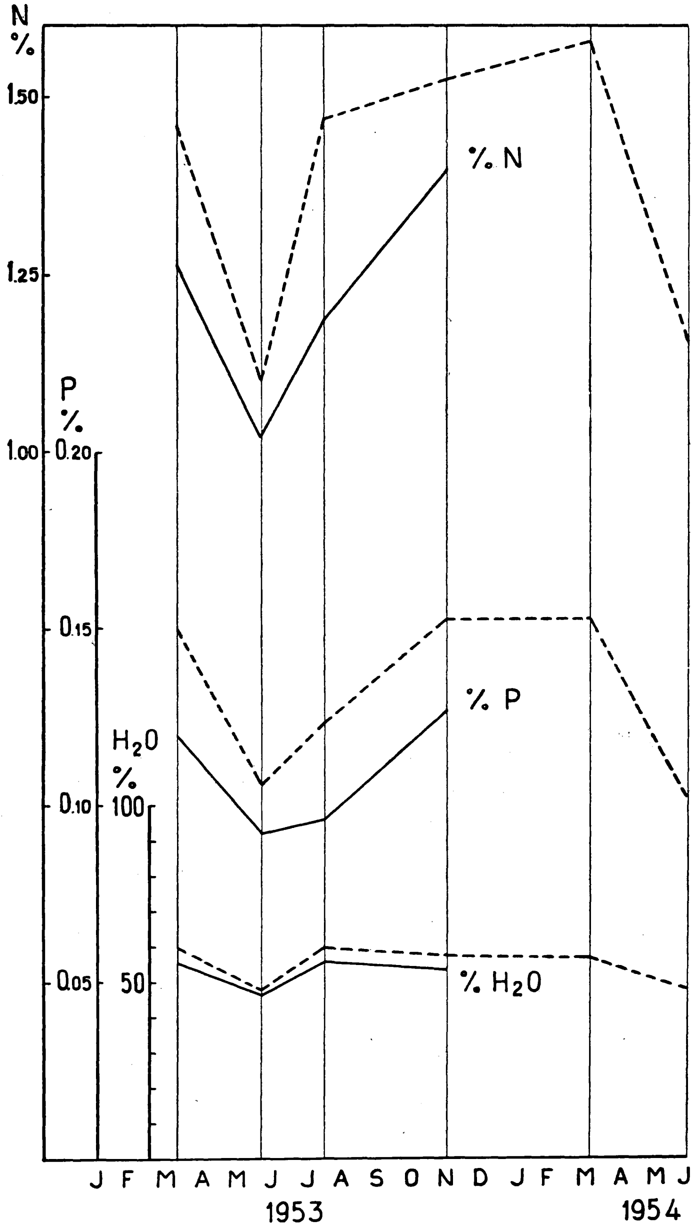

Fig. 5. Seasonal trends in dry weight percentages of nitrogen and phosphorus, and fresh weight percentage of water in pine needles from a single branch (c in Table V). Solid line: 1950 needles. Broken line: 1952 needles.

Årstidsvariation i halten av kväve och fosfor (% torrvikt) och vatten (% friskvikt) i tallbarr från samma gren (c i tab. V). Heldragen linje: 1950 års barr. Streckad linje: 1952 års barr.

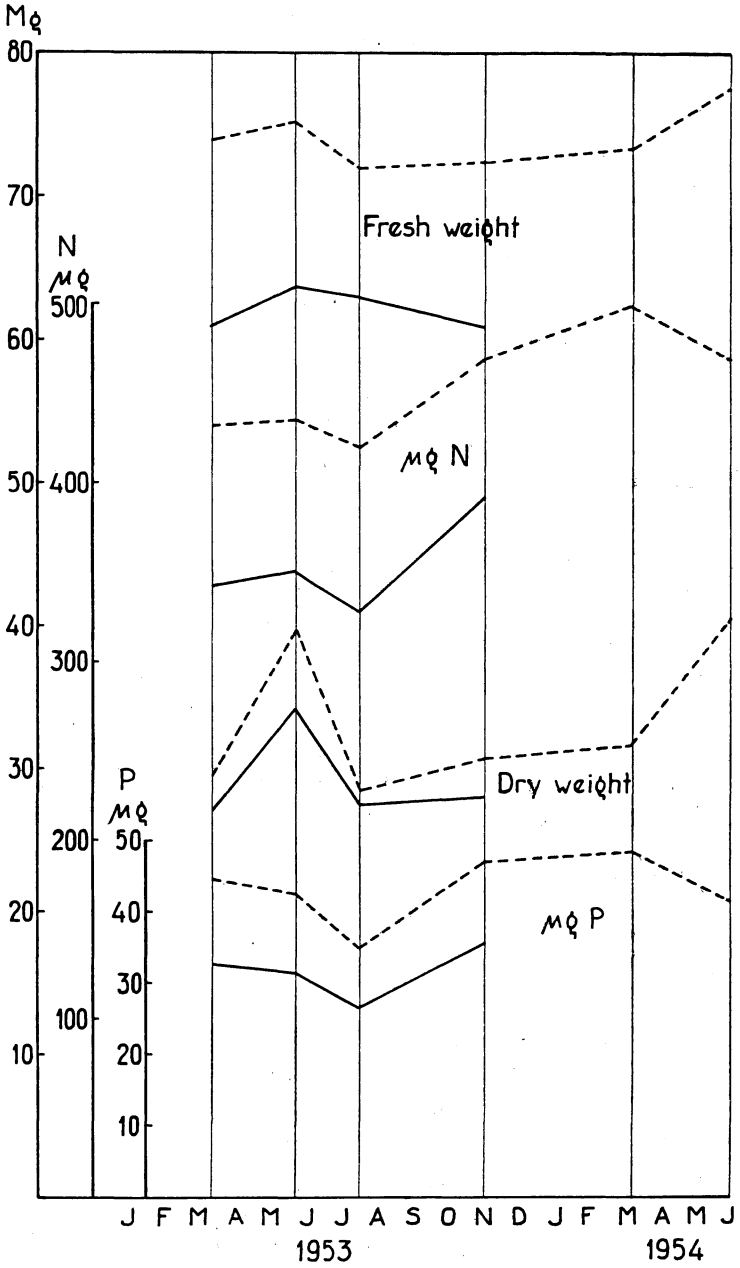

Fig. 6. Seasonal trends in fresh and dry weight in mgs per pair of pine needles, and the content of nitrogen and phosphorus per pair of needles (in μgs). Data for branch c in Table V. Legend as in Fig. 5.

Årstidsvariationen i barrvikt (frisk- och torrvikt, i mg) hos tall, samt totalinnehåll per barrpar av kväve och fosfor i μg). Värden för gren c i tab. V. Beteckningar som i fig. 5.

of the samples has been carried out by measurements of the needle length. The result were as follows:

	Branch *b*	Branch *c*	Branch *e*
March 26, 1953	46.4 mm	54.3±0.4 mm	51.0 mm
November 17, 1953	46.7 mm	54.4±0.4 mm	50.6 mm

Estimated from these three pairs of measurements (on 1952 needles), the average difference in needle length between two samples from the same branch would be 0.3 mm or 0.5 per cent of the average length. No serious error seems likely from this variation, even if the weight difference corresponding to the length difference found should be 1.6 per cent (the simple assumption that diameter increases at a rate corresponding to that of length yields approximately the same result as a more complicated calculation based upon Figs. 10 and 11 in TIRÉN 1927).

According to these data, no great random errors can be expected between different samples of needles from the same branches, collected as in this investigation. On the contrary the values appear to be much more reliable than those based upon collections of one or a few branches at each sampling, as in the earlier series. This conclusion is probably true, but it must be pointed out that the removal of a part of the needles from a shoot may change the composition of the rest. In fact this was one of the reasons why whole branches and not individual needles were sampled in the first two series. Yet the good agreement between Fig. 5 and the earlier curves (Figs. 1 and 3) shows that this error cannot be very serious. It may contribute to the fact that the needle weight and composition are not the same in March 1954 as in March 1953, but the error in the changes from one sampling to another must be rather small and without influence upon our conclusions.

The results of the investigation on pine needles from pre-selected branches are presented in Table V. Due to abscission of needles there are no data for some of the segments at the later samplings, and therefore no average figures for all five branches can be computed. In Figs. 5 and 6 the data for branch *c* have been plotted—in the absence of averages for all branches—but these diagram should be considered as representative examples of the changes in needle properties rather than as the sum of the information available in Table V.

We find in Fig. 5 the same types of curves as in Figs. 1 to 4: a pronounced minimum in nitrogen and phosphorus concentration in the needles during early summer, and a maximum in late autumn and winter. The percentage of water follows a similar trend. Fig. 5 thus presents relatively little new information but corroborates our previous findings. From Fig. 6, however, it is clear that the observed minimum in *nutrient percentage* in the beginning of June is mainly caused by an *increase in dry matter content* of the needles during spring, followed by a decrease during June and July. The *absolute content* of nitrogen and phosphorus is relatively constant during the spring, but there is some evidence of a slight decrease in nitrogen and a somewhat greater decrease in phosphorus content from the beginning of June to the end of July. During late summer and autumn the nutrient content per needle increases. The fresh weight of the needles is much more constant than the dry weight. The dry weight of the needles, as well as their nutrient content, is higher in March 1954 than in March 1953. In the normal course of development the percentages of most nutrient decrease with increasing needle age (se Table I and II), while nothing is known about the dry weight in this respect. The higher nutrient content in March 1954 than one year before, which recurs in the case of spruce (p. 17), may be explained in different ways: 1) The sampling in March 1954 was made 6 days earlier than in 1953; the spring of 1953 was also much earlier than that of 1954 (average temperature of March 1953 +3.2° C in Stockholm, and +0.8° C in March 1954). Both these circumstances tend to lower the nutrient percentages of the 1953 samples. 2) The summer of 1953 seems to have been extremely favourable for forest growth all over Sweden. It may well be possible that the climatic conditions during this summer have favoured nitrogen uptake by the trees. If so, the difference between the two years in needle composition corresponds to a real difference in nitrogen nutrition. 3) There is also some possibility that the nutrient percentages of the needles are abnormally increased on account of the reduced number of needles of the shoot segments sampled, or of damage in connection with the sampling. At present it is not possible to evaluate the precise role of these three factors.

In addition to these results we may gather from Table V that there are considerable differences between needles from different branches in all properties studied. The variation in nitrogen percentage is however less than the variation in needle weight. There is also considerable variation in the weight of the needles from the same shoot but on different annual segments. Generally the needles from 1951 weigh less than those from 1950 and 1952. The needles from the weak side-branch *d* constitute the sole exception; they grew smaller and smaller each year. It may also be remarked that there is no sign of a sudden decrease in nutrient content of senescent needles. As only healthy green needles were collected, it is possible that some downward translocation does occur from yellowing or browning needles, but many needles are apparently abscised when green or yellowish green. It may therefore be anticipated that pine litter (and spruce litter, as shown below) varies in chemical composition with the season. Seasonal variation in the composition of conifer litter has also been reported by Lindberg & Norming (Norway spruce) and Owen (Sitka spruce).

Collections from March 1953 to June 1954. Spruce.

The sample tree was a spruce 7.5 m high and about 30 years old, growing near the two pines in Table V. Two similar branches facing south and southeast respectively were selected for sampling. They were both about one metre above ground and fairly sun-exposed. The spruce was growing in the northwestern margin of a small opening in the park-meadow.

On each occasion a number of needles (usually about 20) were picked, weighed fresh and dry, and analyzed for nitrogen, as in the pine investigation. Owing to the small amount of each sample available, they were not ground. Usually the dried needles were divided into two equal parts, which were used directly for the nitrogen determinations. The analytical error has been somewhat greater than for pine, where aliquots of ground and well mixed samples were analyzed. The difference between duplicate determinations was 0.027 per cent N, corresponding to a standard deviation of the mean of two duplicates equal to 0.017 per cent N.

As in the case of pine we have tried to check the homogeneity of the material. Table VI presents figures for the average length of all samples of 1952 needles. The value from June 11, 1954, is rather different from all other values. It consisted of the last 9 needles remaining on the shoot segment, and is evidently not comparable with the other samples. Figures concerning this sample have therefore been put in brackets in Table VI, and are excluded from the diagrams. The standard deviation of the 10 remaining length figures in Table VI is 0.16 mm or 1.26 per cent of the needle length, if samples from the same branch are compared. This would correspond to a considerable variation in weight (4 per cent, if the assumption is made that diameter increases at the same rate as length). Judging from the good agreement between independent sets of data (two branches with three or more needle generations each), the variability is overestimated by length determinations. This is probably because needle length and weight vary with location on the shoot. On account of this variation a fairly large estimate is obtained for the standard deviation of needle samples collected at random. However, the needles have not been sampled at random, but in a systematic arrangement from all sides and parts of the shoot.

In another attempt to test the reliability of the figures in Table VI all needles from 1949 (branch *a*) were weighed individually. The standard deviations of the means for each sample are found in Table VI, and they average 2.5 per cent of the needle dry weight. This estimate of the error appears more adequate than that deduced from the length measurements (even if it may also be too high for the same reason). Yet the length measurements are valuable, because they exclude the occurrence of more important systematic differences in needle size during the course of the investigation.

Changes in needle weight and composition due to removal of certain needles are of course possible in spruce as well as in pine, but there is no evidence in favour of such a hypothesis. In any case it seems unlikely that differences between two consecutive samplings will be notably affected by this source of error.

In Table VI and Fig. 8 we again find an increase of needle dry weight during spring, and a decrease during summer. Pine and spruce thus behave in a very similar way. The changes in dry weight result in a reverse change in nitrogen percentage (Fig. 7), but in addition to this "apparent" decrease in nitrogen content there is also a real decrease in the absolute content of nitrogen during spring or early summer (before June 6—11). During the late summer and autumn of 1953 nitrogen content per needle increased, and a higher level of nitrogen was attained during the winter of 1953—1954 than that found in March 1953. As in the case of pine (see p. 15) the causes of this difference are not known, but it may be mentioned that year-old needles from the spruce in Table IV contained 1.20 per cent nitrogen in November 1952, and 1.44 per cent in November 1953.

The data in Tables I to VI also present information about problems other than those directly connected with seasonal variation in needle composition. As these question will be discussed in more detail in another paper, only a few remarks are necessary here.

In table I pine branches facing south and north have been analyzed separately. No consistent difference in composition was found between south-exposed and north-exposed needles. During their first summer the needles seem to develop faster on the more sun-exposed side, to judge from their lower percentages of nutrients in July. The behaviour of the spruce in Table VI, which has been sampled in the same way, is different from that of the pine: the needles attain a higher percentage of all studied nutrients when south-exposed. The differences are as follows (for 9 pairs of 1950 needles and one pair of 1951 needles, the latter from 19. XI. 1952): 0.09±0.01 per cent N, 0.017±0.004 per cent P, 0.10±0.02 per cent K, and 0.14±0.06 per cent Ca.

As mentioned before, differences also occur in needle composition between similarly located branches (more data will be presented in a paper in preparation). Table III compares analytical data for 8 pairs of pine branches. As a rule one branch in each pair faced SW. and one SE., but both were taken from the upper part of the crown of a well exposed tree. The average differences are 4 per cent of the nitrogen value, 3 per cent of the phosphorus value, and 6 and 12 per cent respectively in the case of potassium and calcium.

Table II presents data for four pairs of similar spruce branches. The average differences within pairs of values (1949 needles) are 4 per cent of the nitrogen value, 2 per cent of the phosphorus value, and 11 and 12 per cent respectively in the case of potassium and calcium. Of course four sets of data are too few to give a reliable estimate of the variability.

We note a relatively high variability in calcium content between different branches, while the more mobile elements nitrogen and phosphorus—in this case at least—show less variation. The consequence for the present investigation is that the calcium and perhaps also the potassium curves in Figs. 1 to 4 are less accurate than the nitrogen and phosphorus ones.

Discussion

The most remarkable result of the present investigation seems to be the discovery of great seasonal variations in the dry weight of conifer needles. The obvious explanation would be that large amounts of photosynthates are formed during the spring and stored in the needles until they are translocated downwards during summer. The period of dry weight decrease—to judge from the present data from the beginning of June to the end of July—coincides

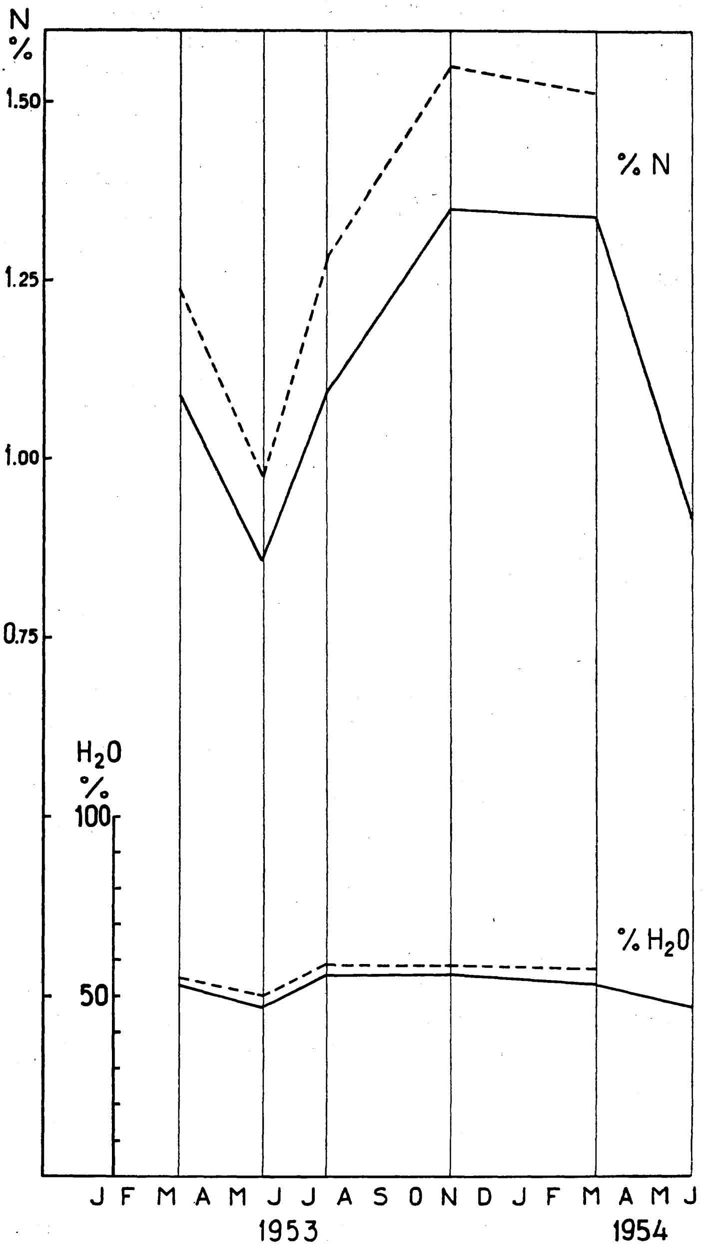

Fig. 7. Seasonal trends in dry weight percentage of nitrogen, and fresh weight percentage of water in spruce needles. Averages of the data for two similar branches in Table VI. Legend as in Fig. 5.

Årstidsvariationen i halten av kväve (% torrvikt) och vatten (% friskvikt) i granbarr. Medeltal av värden för två grenar i tab. VI. Beteckningar som i fig. 5.

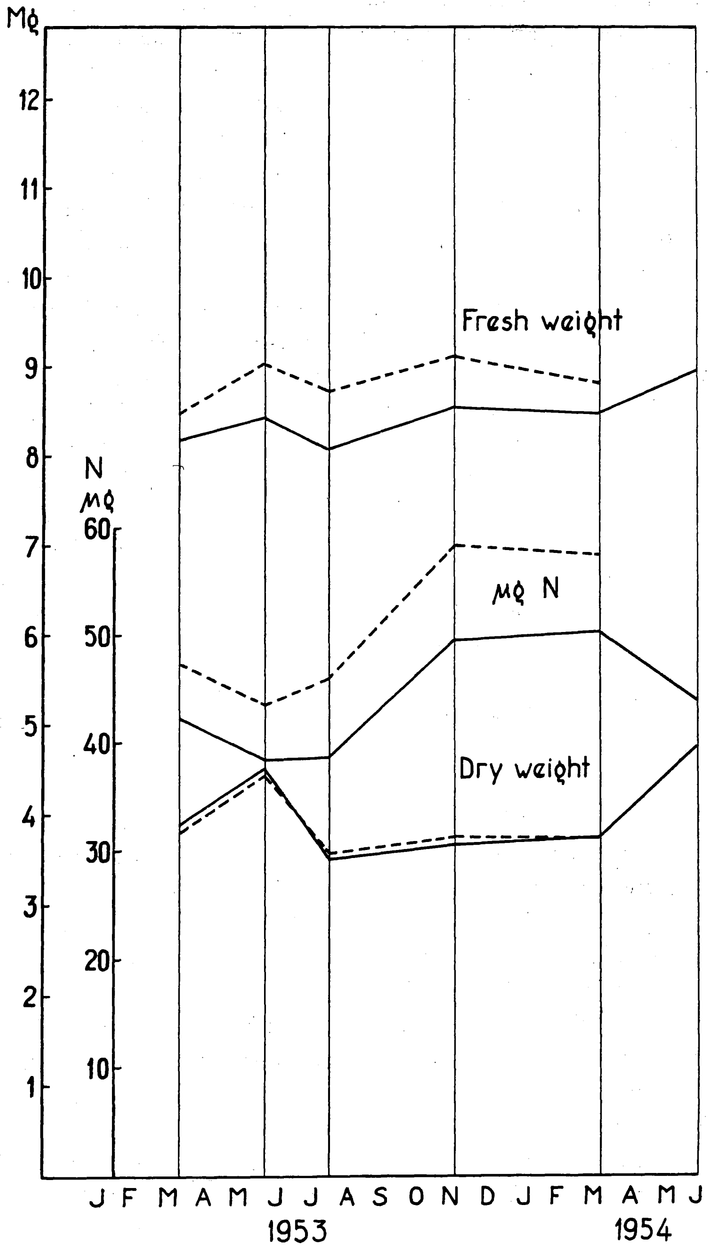

Fig. 8. Seasonal trends in fresh and dry weight (in mgs) of spruce needles, and the content of nitrogen per needle (in μgs). Averages for two similar branches in Table VI. Legend as in Fig. 5.

Årstidsvariationen i barrvikt (friskvikt och torrvikt, i mg) hos granbarr, samt totalinnehållet av kväve per barr (i μg). Medeltal av värdena för två grenar i tab. VI. Beteckningar som i fig. 5.

more or less with the most active growth of the young shoots and their needles, and also with the formation of the new growth ring in the wood. There is thus hardly any doubt that the photosynthates of the needles are used for this growth. Some of the mobile nutrients are also translocated out of the needles, presumably for the same purpose. In spruce this loss corresponds to 10.5±0.8 per cent of the needle nitrogen (average of 10 differences between March and June in Table VI). It is not quite clear whether there is also such a loss of nitrogen from the pine needles, but according to Table V and Fig. 6 an even greater part of the phosphorus content is withdrawn from the pine needles between March and the end of July. There may be some difference between pine and spruce regarding the time of the nutrient minimum. This difference may have something to do with the faster development of the spruce needles on the new shoots (cf. the data for the young needles in Tables V and VI).

The conifer needles thus act not only as photosynthesizing organs, but also as reserve stores for photosynthates and, to some extent, for nutrients. Some 20 per cent of the dry weight of pine and spruce needles in early summer is later withdrawn; this corresponds to a considerable part of the dry matter contained in the new needles. In pine there are usually two or three older needle generations which may contribute, and in spruce there may be six, seven or more living needle generations. Judging from the curves presented, considerable storage of photosynthates also occurs in old needles. In young actively growing trees the importance of the contributions from the older needles is somewhat reduced owing to an increase in the amount of needles from year to year; but in other cases the carbohydrates stored in the older needles may well correspond to about half the amount contained in the young needles. The rest of their dry matter, as well as the dry matter needed for other growth and for respiration, then corresponds to the amounts stored in places other than the needles, to the photosynthates of the growing needles themselves, and to photosynthates formed in the old needles but immediately translocated downwards.

It is rather curious that the author has been unable to find any description of the seasonal variation in needle dry weight in the literature. Even in the case of the corresponding variation in the percentages of nutrients, which is easier to measure, the scarce literature data are somewhat confusing. One of the reasons is probably that many investigators have studied only the composition of the current issue of needle, which in general lacks the summer minimum in nutrient percentage (cf. Figs. 1 and 2). This is the case with SATTLER (1929). AALTONEN (1950) has also concentrated on the current needle issue, but reports some data on the composition of 1- to 2- year-old spruce needles (l.c. Table 2). He demonstrates a nitrogen trend of the same type as that obtained by the present author, although with less difference between maximum and minimum. The irregular variation of his figures suggests that sampling errors must have been rather great, and conclusions cannot be drawn with any certainty about the seasonal trends of most other elements. AALTONEN himself suggests the occurrence of autumn maxima and spring minima in the case of ash, silica, and calcium. These constituents are exactly those for which little or no downward translocation would be expected, and a minimum in their content probably means a maximum in dry weight. AALTONEN (l.c. Fig. 3) also reports a curious variation in aluminium content of spruce needles, similar to that of ash, silica, and calcium, but much stronger. These seems, however, to be something wrong with the scale of the cited diagram, because 3 per cent Al_2O_3 in spruce needles does not sound very likely; moreover it is not consistent with the ash contents reported by AALTONEN.

CHANDLER (1939) analyzed three consecutive needle issues of white pine from June 1 to October 1 for calcium, but unfortunately no data are given from the spring, when a decrease in calcium percentage may have occurred. Recently WHITE (1954) has got curves for the N, P, and K content of the current season's pine needles, wich are similar to those in Fig. 1.

HAGEM (1947) studied the changes in dry matter content of conifer seedlings during eleven winters in Bergen, western Norway. He found significant increases in dry matter during all winters, even if the darkest months sometimes showed a constant level or a very slight decrease. The seedlings maintain a positive balance of photosynthesis over respiration during most of the year. The winter climate in middle Sweden is much colder than in Bergen, but there seems to be no reason why photosynthesis in full-grown trees should not start as soon as temperature rises sufficiently above zero, always supposing that the water deficit of the needles is not too great. HAGEM also found a rapid downward translocation of photosynthates in autumn, when root growth is intense, while most of the increase in dry weight during the winter and early spring remained in the needles.

PREISING (see GUTTENBERG 1928) studied the seasonal changes in content of dextrose, saccharose and starch in the needles of *Pinus cembra*, and found them small in comparison with those in the leaves of *Hedera helix* and *Ilex aquifolium*. GUTTENBERG concludes that either there is a rapid downward translocation of the photosynthates of *Pinus cembra* all through the year, or that a part of the photosynthetic products is not carbohydrate. The last hypothesis would agree best with the results from the present investigation, but it is of course also possible that *Pinus cembra* differs in its physiology from *Pinus silvestris* and *Picea Abies*.

When the information presented here in Figs. 1 to 8 is used for practical purposes, *e.g.*, to determine the suitable period for needle sampling, we must remember that the details of the seasonal trends are very incompletely known, due to the long intervals between collections. Moreover, they may vary according to climate and in different years depending upon weather conditions. Edaphic conditions, particularly deficiency of a nutrient in the soil, may affect the trend of this and other elements. We have, however, found only very small changes in needle composition during late autumn and winter in three different years, and in both pine and spruce. There seems little reason to doubt the general validity of this result. Needle samples collected during this period will thus be properly comparable, and observed differences between well-exposed needles of the same age can be considered as expressions of physiological differences other than the incidental balance between photosynthesis and downward translocation. As it is often desirable to note the ground vegetation and take soil samples at the same time as needle samples, late autumn is a better season than winter in most parts of Sweden. In south Sweden sampling may start at the end of October, in middle Sweden about two weeks earlier, and in north Sweden still earlier, the exact time depending on latitude and altitude.

In this connection we may discuss the choice of some other basis than dry weight for our needle analysis data. Dry weight changes may affect results in different ways. The weather during the period before sampling may influence photosynthesis and thereby dry weight. These effects are however less in late autumn than in summer. Rain may leach soluble substances from the leaves. Respiration during the time from sampling to air-dry condition may result in dry weight losses.

The fresh weight is considerably more constant over the year than the dry weight (Figs. 6 and 8). Fresh weight is, however, even more dependent on weather conditions than dry weight, and therefore cannot be recommended as a basis. Other investigators have suggested to the author the use of water-saturated fresh weight instead. This would eliminate both the variation in water content due to weather conditions, and the occurrence of starch (which takes approximately the same place as an equal weight of water). It would then be necessary to determine the water-saturated weight on separate aliquots from the fresh samples, because preliminary experiments have shown considerable dry weight losses (1 to 10 per cent) of living pine and spruce needles stored upon moist filter paper during 48 hours at room temperature. Part of this loss is due to respiration (about 2 per cent of the dry weight in other experiments), but leaching phenomena may also be involved. A standardization of the drying conditions seems highly desirable, as indicated by these results. Recently WHITE (1954) has found still greater respiration losses in drying pine needles.

If the "water-saturated fresh weight" were thus used as our basis, the variation due to dry weight variations could be eliminated. Yet variations in the absolute content of nutrients also occur during the year. It would be advisable to avoid these changes by sampling in autumn or winter, but in that case calculations on the basis of dry weight will give results satisfactory for most purposes. As will be shown in another paper in this series, differences between different years are considerable; thus the nutrient status of a certain stand can only be evaluated with rather moderate accuracy.

For special purposes it may be practical to calculate the nutrient content per needle (LEYTON 1954 a, Table 6) or per unit length of the needles (MÜLLER 1934). As needle weight and diameter vary with the vigour of the tree, very good correlations may obtain between nutrient content and growth, but many factors other than nutrition may be involved.

Further and more detailed studies of seasonal variation in composition in conifers seems desirable from different viewpoints. The chemical nature of the stored photosynthates should then be studied, as well as their distribution in different organs. This might help to explain why evergreen conifers do not endure attacks by leaf-eating insects as well as deciduous trees. The reason may well be that the insects—which often appear in early summer—not only destroy the photosynthesizing organs but also, in conifers, consume much of the substance necessary for growth. The observation by GÄUMANN (1928, 1935) regarding the small reserves of "food" in conifer wood as compared with those in beech wood may also have something to do with this problem.

The detailed course of the seasonal variation in composition of the needles would also be worth studying, preferably in connection with meteorological observations. Judging from the data presented here the increase in dry weight of the needles starts in early spring, before what is commonly considered as the start of the vegetation period (cf. LANGLET 1936). If it is true that the downward translocation of photosynthetic products is slow in early spring, the rate of increase in dry matter of the needles may be a measure of the photosynthesis during this period. It would also be possible to compare the photosynthetic ability of needles of different age and position, which might offer a valuable check on results obtained by other methods, *e.g.*, by short-term experiments with excised branches.

Summary

1) The contents of nitrogen, phosphorus and potassium in needles of pine and spruce show a cyclic variation over the year, if expressed as dry weight percentages. A sharp minimum occurs in early summer, while a maximum obtains in late autumn and winter. Needles of different age (except the current summer's needles) behave very similarly in this respect, though the contents of these elements also show a decrease with age.

2) The variation in nutrient percentages is to a large extent caused by a variation in dry weight of the needles. It is concluded that photosynthetic

products are stored in the needles during spring and translocated downward during summer, when the tree is actively growing. Yet a certain translocation of nutrients also occurs, downward during spring and/or summer, and in the opposite direction during autumn.

3) Collection of needle samples in order to determine the nutrient status of a tree or a stand is best made when the nutrient contents of the needles are most constant, *i.e.*, in late autumn or winter. If the samples are taken during late autumn, there seems little reason to express the nutrient contents otherwise than as per cent dry weight, at least at the present stage of investigation.

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Sammanfattning

Studier över skogens näringsförhållanden

Inledning

Under denna rubrik är det vår avsikt att publicera ett antal arbeten, som alla handlar om den svenska skogens och de svenska skogsträdens näringsekologi och näringsfysiologi.

Vår kunskap är ännu otillräcklig om växtnäringsämnenas roll som begränsande faktorer för skogsproduktionen. Det har i försök visats att på vissa lokaler kan skogens tillväxt ökas betydligt, ibland t. o. m. flerdubblas, genom tillförsel av växtnäringsämnen (t. e. Mitchell & Chandler 1939, Malmström 1952, 1953). Jämförande undersökningar har dessutom påvisat ett nära samband mellan skogsproduktionen och förrådet av vissa näringsämnen eller mineral i marken, under förutsättning att jämförelsen gäller lokaler med likartat klimat och likartad vattenförsörjning (se t. ex. O. Tamm 1937, Viro 1951). Å andra sidan förefaller det som om vattenfaktorn — direkt eller på indirekt väg — bestämmer skogstyp och skogsväxt inom stora delar av Nordsverige, där underlagets (moränens) sammansättning är tämligen ensartad men fuktighetsförhållandena växlar med höjden över havet, lutningen, väderstrecket, underlagets kornstorlek, etc. (se O. TAMM & WADMAN 1945, MALMSTRÖM 1949). Det är sålunda klart att såväl hydrologien som underlagets geologiska och mineralogiska beskaffenhet är viktiga för skogen, men samspelet mellan dessa bägge komplex av faktorer gör det svårt att finna markegenskaper som står i ett direkt och enkelt förhållande till skogsproduktionen, annat än i vissa begränsade fall. Man kan visserligen tänka sig att analysera humuslagret i stället för underlaget, men att döma av den stora spridning inom varje skogstyp som MALMSTRÖM (1949) har funnit beträffande ett flertal humuslager-egenskaper, torde det vara ganska litet att vinna på den vägen. Ser man saken ur fysiologisk synpunkt finns det dessutom åtminstone två skäl som gör det tvivelaktigt om det överhuvud taget går att få fram en strikt korrelation mellan markegenskaper och skogsproduktion: 1) Beståndets näringstillstånd och förrådet av mer eller mindre lättillgänglig näring i marken är bägge variabla storheter, och det är långtifrån säkert att deras variation alltid går parallellt. 2) Det är mycket svårt att avgöra vilka markegenskaper som är av omedelbar betydelse för träden. Näringsupptagning genom rötter (eller mykorrhiza) och extraktion med kemiska lösningsmedel är vitt skilda företeelser.

Trots att vi sålunda måste betrakta skogens näringstillstånd och möjligheterna att påverka detta som ett av de för närvarande viktigaste forskningsområdena när det gäller skoglig grundforskning, saknas det sålunda en enkel metod att bestämma ett skogsbestånds näringstillstånd. Även om möjligheten finns att göra gödslingsförsök, föreligger det ett stort behov av en snabbare, bekvämare och billigare metod.

Bladanalys är en tänkbar väg att bestämma näringstillståndet i skogen mera direkt än med markanalysmetoder (MITCHELL & CHANDLER 1939, TAMM 1951 a). Fördenskull togs metoden upp till prövning vid Skogsforskningsinstitutets avdelning för botanik och marklära år 1949. Alltifrån början har vi i dessa undersökningar lagt huvudvikten vid trädens näringsfysiologi och -ekologi. Liksom LUNDEGÅRDH (1945) anser vi en god fysiologisk grundval vara en förutsättning för ett effektivt utnyttjande av denna metod. De negativa slutsatser som AALTONEN (1950) dragit ur sina jämförande bladanalysundersökningar har snarast styrkt oss i denna uppfattning. Det centrala problemet i våra undersökningar är sambandet mellan den inre näringsnivån i träden (framför allt i blad och barr) och deras tillväxt. Detta samband måste studeras för varje trädslag och för vart och ett av de växtnäringsämnen som kan ha betydelse i sammanhanget. Dessutom är relationen mellan inre näringsnivå och tillväxt olika vid brist och överskott på näringsämnet. Eftersom förekomsten av näringsbrist, och fastställandet därav, är det som i allra första hand intresserar oss, har vi börjat arbetet med att undersöka koncentrationen av olika näringsämnen i björkblad från lokaler med påvisad eller sannolik näringsbrist (TAMM 1951 a, b). Liknande undersökningar pågår även för tall och gran. En orienterande undersökning över sammansättningen hos blad och barr från »normala» bestånd har också utförts. En preliminär rapport över de hittills vunna resultaten framlades vid den internat. botaniska kongressen i Paris (TAMM 1955). En utförligare redogörelse kommer senare i denna serie.

Innan man kan börja använda en fysiologisk metod som bladanalys i större skala, måste man känna till något om hur näringshalten hos bladen (eller de andra organ man studerar) varierar icke blott med trädens näringstillstånd utan även med andra faktorer. I denna uppsatsserie kommer en del av dessa variationer i näringshalt hos blad och barr att beskrivas, antingen i samband med provtagningsmetodiken, eller — om variationen i fråga kan anses ha allmänt fysiologiskt eller ekologiskt intresse — i särskilda uppsatser. Det första arbetet i serien handlar just om en sådan variation, nämligen årstidsvariationen i sammansättningen hos tall- och granbarr. Tidigare har motsvarande variation hos björkblad beskrivits (TAMM 1951 c).

I samband med arbetet på bladanalysmetoden har en rad gödslingsförsök utförts, och resultaten av dessa försök, eller i varje fall av en del av dem, kommer också att framläggas i denna serie. Skogens näringsförhållanden kommer sålunda att granskas även från andra synpunkter än dem som enbart har med blad- och barranalys att göra. I seriens andra uppsats redogöres sålunda för ett gödslingsförsök med radioaktivt fosfat.

I arbetet på att utreda skogens näringstillstånd möter man en rad ganska komplicerade fysiologiska problem, som det är svårt och ofta omöjligt att studera i naturliga bestånd. Det gäller särskilt samspelen mellan näringsfaktorerna inbördes, och mellan dessa och andra tillväxtfaktorer. Dessa problem kommer därför även att tas upp i det arbete med näringsfysiologien hos skogsträdsplantor, som pågår på avdelningen (INGESTAD, TAMM & INGESTAD, ej publ.) och som kommer att framläggas i annat sammanhang.

I. Årstidsvariationen i näringsinnehållet hos tall- och granbarr

Experimentell del

Den föreliggande undersökningen avsåg från början endast att fastställa vilken årstid som var mest lämplig för att insamla barrprov, avsedda för kemisk analys. Prov insamlades därför under olika årstider från april 1950 till april 1951 från en tall och en gran, bägge växande i Roslagen. Tallen växte i ett sedan länge övergivet grustag, medan granen stod i en löväng. Vid varje provtagning togs en eller (oftast) två kvistar från varje träd; de olika barrårgångarna analyserades sedan var för sig. De viktigaste resultaten återges grafiskt i fig. 1 och 2. Som synes visar halterna av alla undersökta ämnen (utom kalcium i granbarr) tydliga minima på försommaren. De högsta halterna påträffas under senhöst och vinter. Alla barrårgångar utom den yngsta visar samma förlopp, även om halterna av de olika ämnena ändrar sig från årgång till årgång: kväve, fosfor och kalium sjunker med stigande ålder, medan kalcium förhåller sig tvärtom. Då årstidskurvor av denna typ ej kunde påträffas i litteraturen, ansågs det lämpligt att insamla ytterligare en provserie, vilket skedde från april 1951 till november 1952. I stort sett stämmer resultaten från den nya serien (Fig. 3 och 4) med de förut erhållna, men något kalcium-minimum erhölls icke denna gång.

Växlingarna i näringshalt hos barren kan uppenbarligen bero antingen på ändringar i barrens näringsinnehåll, eller på ändringar i deras torrvikt (eller ev. på bägge dessa orsaker). För att utröna hur det förhöll sig härmed insamlades en tredje provserie, från mars 1953 till juni 1954. Denna gång skördades vid varje provtagning en del av barren från i förväg utmärkta skott, fem tallskott med vardera omkring tre barrårgångar, samt två granskott där 3—5 barrårgångar togs med. Barrens friskvikt och torrvikt bestämdes sedan, varjämte de flesta proven analyserades på kväve och några dessutom på fosfor. De viktigaste resultaten återges i fig. 5—8.

Som synes i dessa figurer kan större delen av nedgången i näringshalt hos tall- och granbarr under våren förklaras med en samtidig ökning av barrens torrvikt. En viss borttransport av kväve förefaller dessutom att ske, åtminstone hos gran. Det rör sig om ungefär 10 % av barrens kväveinnehåll, medan upplagringen och den senare borttransporten av assimilat kan uppgå till 20 % av barrens torrvikt. Att döma av de visserligen fåtaliga fosforbestämningarna sker det också en borttransport av fosfor ur tallbarren under våren och sommaren.

Diskussion

Det mest anmärkningsvärda resultatet av denna undersökning är upptäckten av stora säsongvariationer i barrtorrvikt hos våra skogsträd. Uppenbarligen bildas det stora mängder assimilat i barren under våren, som icke transporteras bort förrän under sommaren, när de unga skotten och den nya årsringen växer ut. Även växtnäringsämnen som kan tas i bruk för andra organ tycks kunna lagras i barren. Eftersom det i regel finns flera äldre barrårgångar samtidigt, kan det nog vara en rätt betydande del av trädets disponibla assimilat- och näringsförråd som lagras i barren. Detta förhållande rymmer kanske en del av förklaringen till att barrträden ej lika bra som lövträden uthärdar kalätning av insekter. Icke minst ur denna synpunkt vore det av intresse med nya och mera detaljerade undersökningar. Det är också tänkbart att man skulle kunna utnyttja torrviktsändringarna i barren under våren för att bestämma intensiteten i fotosyntesen under denna årstid och dennas beroende av en rad såväl yttre som inre faktorer. Det vill nämligen synas som om den nedåtgående transporten vore svag under våren, åtminstone den tidiga våren (jfr HAGEM 1947).

Sammanfattning

1) I tall och gran varierar barrens halter av kväve, fosfor och kalium (uttryckta i % torrvikt) regelbundet med årstiden, och visar ett utpräglat minimum på försommaren och ett maximum under senhöst och vinter. Barr av olika ålder förhåller sig likartat, med undantag för den allra yngsta barrårgången.

2) Variationen i näringshalter beror till stor del på en variation i barrens torrvikter, vilka är högre på försommaren än under resten av året, tydligen beroende

på tillfällig upplagring av assimilat. Det förekommer dock även en viss transport av växtnäringsämnen såväl till som från de utvuxna barren. Transport från barren äger rum under vår och/eller sommar, till barren under hösten.

3) Barrprov för att bestämma näringstillståndet hos ett träd eller ett bestånd insamlas bäst när barrens näringshalter håller sig mest konstanta, d. v. s. under senhöst och vinter, varvid senhösten av praktiska skäl är att föredra framför vintern.

TABLES

TABELLER

Table I. The dry weight percentages of nitrogen, phosphorus, potassium, and calcium in pine needles collected at different seasons from April 1950 to April 1951. The sample tree was a pine 3.5 m high and 13 years old (in 1950), growing in an old gravel pit. On each occasion two branches were collected from about 1.5 to 2 m above ground. One branch was always taken on the south side of the tree, and one on the north side.

Issue of needles	Element	Exposure of branch	Date of sampling						
			30. IV.	29. V.	9. VII.	9. VIII.	2. X.	23. I.	17. IV.
1950	N	South	—	—	1.64	1.47	1.64	1.61	1.44
		North	—	—	1.94	1.42	1.58	1.56	1.47
	P	South	—	—	0.24	0.19	0.20	0.18	0.19
		North	—	—	0.27	0.18	0.18	0.19	0.17
	K	South	—	—	0.90	0.98	0.92	0.95	0.76
		North	—	—	1.07	0.92	0.93	0.94	0.85
	Ca	South	—	—	0.24	0.22	0.25	0.29	0.34
		North	—	—	0.25	0.22	0.26	0.36	0.28
1949	N	South	1.52	1.16	1.00	1.14	1.54	1.46	1.30
		North	1.52	1.20	1.02	1.12	1.43	1.44	1.38
	P	South	0.16	0.12	0.10	0.12	0.16	0.16	0.18
		North	0.17	0.13	0.11	0.11	0.14	0.16	0.14
	K	South	0.79	0.63	0.49	0.69	0.88	0.90	0.70
		North	0.78	0.62	0.53	0.70	0.88	0.84	0.81
	Ca	South	0.42	0.30	0.34	0.50	0.56	0.55	0.62
		North	0.43	0.31	0.38	0.48	0.57	0.58	0.54
1948	N	South	1.28	1.00	0.88	1.08	1.33	1.32	1.28
		North	1.35	1.02	0.91	1.03	1.36	1.34	1.32
	P	South	0.13	0.11	0.10	0.11	0.14	0.14	0.14
		North	0.13	0.11	0.10	0.11	0.15	0.14	0.15
	K	South	0.67	0.59	0.50	0.60	0.76	0.72	0.74
		North	0.64	0.54	0.51	0.62	0.82	0.75	0.64
	Ca	South	0.61	0.40	0.55	0.69	0.67	0.74	0.72
		North	0.69	0.48	0.46	0.67	0.78	0.74	0.67
1947	N	South	1.24	1.01	—	0.95	—	—	—
		North	1.22	0.97	0.85	0.93	—	—	—
	P	South	0.13	0.10	—	—	—	—	—
		North	0.12	0.12	—	—	—	—	—
	K	South	0.61	0.52	—	—	—	—	—
		North	0.60	0.59	—	—	—	—	—
	Ca	South	0.73	0.67	—	—	—	—	—
		North	0.82	0.63	—	—	—	—	—

Table II. The dry weight percentages of nitrogen, phosphorus, potassium, and calcium in spruce needles collected at different seasons from April 1950 to April 1951. On the 1st, 3rd and 4th occasion one branch was collected; on the other occasions two similar branches were taken and analyzed separately. The sample tree was a spruce 7.5 m high and about 25 years old, growing in a small opening in a park meadow. Branches were taken from about 2 m above ground on the north side of the tree.

Issue of needles	Element	Date of sampling						
		30. IV.	29. V.	9. VII.	6. VIII.	2. X.	23. I.	17. IV.
1950	N	—	—	1.06	1.06	1.06 1.24	1.24 1.28	1.13 1.14
	P	—	—	0.139	0.122	0.140 0.137	0.130 0.137	0.108 0.117
	K	—	—	0.77	0.78	0.73 0.92	0.70 0.90	0.69 0.83
	Ca	—	—	0.34	0.43	0.46 0.42	0.40 0.51	0.46 0.49
1949	N	1.12	0.82 0.89	0.82	1.00	1.16 1.14	1.17 1.21	1.07 1.03
	P	0.107	0.076 0.076	0.074	0,089	0.121 0.118	0.120 0.122	0.099 0.103
	K	0.60	0.53 0.42	0.51	0.59	0.75 0.76	0.66 0.79	0.62 0.60
	Ca	0.44	0.47 0.57	0.86	0.92	1.02 0.88	0.88 0.99	0.94 0.97
1948	N	0.96	0.80 0.80	0.72	0.88	1.07 1.02	1.06 1.04	0.97 0.94
	P	0.086	0.071 0.072	0.068	0.079	0.108 0.102	0.111 0.115	0.091 0.099
	K	0.61	0.46 0.50	0.42	0.50	0.61 0.65	0.57 0.67	0.53 0.52
	Ca	0.78	0.63 0.87	1.11	1.03	1.30 1.16	1.20 1.15	1.13 1.30
1947	N	0.88	0.74 0.74	0.67	0.86	—	1.04 1.01	0.90 0.91
	P	0.087	0.071 0.071	0.066	0.083	—	0.110 0.109	0.091 0.092
	K	0.51	0.43 0.48	0.42	0.48	—	0.52 0.61	0.47 0.50
	Ca	1.24	0.98 1.00	1.35	1.40	—	1.57 1.47	1.42 1.48
1946	N	0.88	0.73 0.68	0.66	0.75	—	0.90 0.92	—
1945	N	0.78	0.67 0.64	—	—	—	—	—

Table III. The dry weight percentages of nitrogen, phosphorus, potassium, calcium, silica, and ash in pine needles collected at different seasons from April 1951 to November 1952. As a rule two similar branches were taken on each occasion (one from 17.IV. 1951, and three from 21.IV. 1952). Sun-exposed branches from the upper part of the crown were collected from a pine, 6 m high and about 20 years old, growing in the same park meadow as the spruce in Table II.

Issue of needles	Determination	Date of sampling									
		17. IV.	24. VI.	16.VII.	19. X.	24. XI.	28 XII.	21. III.	21. IV.	4. VII.	19. XI.
1951	N	—	—	2.03	—	—	—	—	1.72 1.86 1.64	1.61 1.50	1.68 1.78
	P	—	—	0.248	—	—	—	—	0.161 0.161	0.121 0.118	0.149 0.171
	K	—	—	0.87	—	—	—	—	0.56 0.62	0.52 0.52	0.65 0.73
	Ca	—	—	0.16	—	—	—	—	0.30 0.31	0.48 0.42	0.58 0.68
	SiO_2	—	—	0.02	—	—	—	—	0.11 0.08	0.03 0.07	0.05 0.05
	Ash	—	—	2.64	—	—	—	—	2.48 2.48	2.63 2.47	3.07 3.49
1950	N	1.66	1.50 1.40	1.52 1.44	1.78 1.88	1.72 1.74	1.67 1.74	1.67 1.74	1.57 1.65 1.56	1.46 1.42	—
	P	0.168	0.118 0.116	0.118 0.116	0.154 0.166	0.168 0.159	0.149 0.154	0.148 0.152	0.141 0.141	0.110 0.112	—
	K	0.67	0.47 0.46	0.53 0.50	0.68 0.73	0.68 0.71	0.63 0.60	0.58 0.66	0.50 0.56	0.43 0.43	—
	Ca	0.27	0.34 0.31	0.42 0.33	0.50 0.56	0.48 0.54	0.50 0.62	0.50 0.52	0.48 0.50	0.53 0.58	—
	SiO_2	0.08	0.02 0.03	0.08 0.04	0.05 0.08	0.07 0.04	0.06 0.03	0.03 0.05	0.12 0.12	0.04 0.08	—
	Ash	2.50	2.12 2.10	2.44 2.18	3.05 3.23	2.98 3.02	2.86 3.15	2.86 3.03	2.73 2.83	2.54 2.68	—

Table IV. The dry weight percentages of nitrogen, phosphorus, potassium, calcium, silica, and ash in spruce needles collected at different seasons from April 1951 to November 1952. At each sampling two branches were collected, one exposed toward the south and one toward the north. The sample tree was a spruce 8.5 m high and about 25 years old, growing in an open stand of mostly lower hardwoods in the same park meadow as the spruce in Table II.

Issue of needles	Determination	Exposure	Date of sampling									
			17. IV.	24. VI.	16.VII.	19. X.	24. XI.	28.XII.	21. III.	21. IV.	4.VIII.	19. XI.
1951	N	South	—	—	—	—	—	—	—	1.27	1.12	1.24
		North	—	—	—	—	—	—	—	1.06	0.96	1.16
	P	South	—	—	—	—	—	—	—	0.141	0.102	0.130
		North	—	—	—	—	—	—	—	0.109	0.093	0.120
	K	South	—	—	—	—	—	—	—	0.63	0.57	0.76
		North	—	—	—	—	—	—	—	0.53	0.47	0.66
	Ca	South	—	—	—	—	—	—	—	0.98	1.03	1.23
		North	—	—	—	—	—	—	—	0.78	1.00	1.14
	SiO_2	South	—	—	—	—	—	—	—	0.45	0.69	0.86
		North	—	—	—	—	—	—	—	0.36	0.52	0.67
	Ash	South	—	—	—	—	—	—	—	4.20	4.31	5.19
		North	—	—	—	—	—	—	—	3.31	3.69	4.58
1950	N	South	1.33	1.00	1.12	1.34	1.37	1.31	1.40	1.09	1.02	—
		North	1.20	0.96	1.04	1.26	1.29	1.26	1.22	1.01	0.94	—
	P	South	0.128	0.087	0.102	0.154	0.136	0.125	0.143	0.137	0.085	—
		North	0.112	0.081	0.082	0.123	0.121	0.126	0.104	0.103	0.082	—
	K	South	0.59	0.50	0.58	0.81	0.68	0.72	0.70	0.53	0.39	—
		North	0.51	0.36	0.47	0.60	0.63	0.59	0.56	0.50	0.37	—
	Ca	South	0.87	0.80	1.26	1.67	1.56	1.41	1.77	1.58	1.49	—
		North	0.78	0.89	1.00	1.28	1.38	1.53	1.45	1.26	1.48	—
	SiO_2	South	0.45	0.45	0.72	0.95	0.99	0.86	1.01	1.00	1.14	—
		North	0.36	0.47	0.55	0.71	0.73	0.73	0.69	0.73	0.96	—
	Ash	South	3.93	3.49	4.90	5.39	5.93	4.75	6.58	5.83	5.60	—
		North	3.38	3.41	3.26	5.19	5.27	4.72	5.21	4.50	5.20	—

Table V. The changes in weight and nutrient content of pine needles during different seasons from March 1953 to June 1954. Sample trees were two young pines growing in a park meadow.

Issue of needles	Determination	Branch	Date of sampling					
			26. III.	6. VI.	30. VII.	17. XI.	20. III.	11. VI.
1953	Fresh weight mg/ pair of needles	a	—	—	—	—	—	—
		b	—	—	36	37.6	37.1	38.0
		c	—	—	52	56.4	54.2	58.4
		d	—	—	24	25.8	25.1	25.2
		e	—	—	58	67.6	66.0	68.3
	Dry weight mg/ pair of needles	a	—	—	—	—	—	—
		b	—	—	10.9	15.2	15.3	19.6
		c	—	—	15.5	22.7	22.3	30.2
		d	—	—	7.6	10.5	10.4	12.9
		e	—	—	15.6	26.1	26.0	32.2
1952	Fresh weight mg/ pair of needles	a	80	84.4	81	85.5	82.1	85.1
		b	53	56.1	53	53.3	53.2	55.2
		c	74	75.3	72	72.6	73.5	77.8
		d	45	45.2	47	44.2	42.9	—
		e	75	77.6	80	74.2	79.4	81.9
	Dry weight mg/ pair of needles	a	33.4	44.6	33.3	37.1	35.9	44.5
		b	20.9	29.3	21.3	23.0	23.0	28.6
		c	29.6	39.7	28.5	30.9	31.7	40.6
		d	17.5	23.4	19.0	18.9	18.6	—
		e	29.9	40.2	31.7	30.5	33.7	40.3
	N % dry weight	a	1.32	0.98	1.36	1.50	1.48	1.18
		c	1.46	1.10	1.47	1.52	1.58	1.16
		d	1.36	1.08	1.31	1.42	1.39	—
		e	1.45	1.02	1.28	1.40	1.33	1.10
	P % dry weight	c	0.150	0.106	0.124	0.153	0.153	0.102
	N µg/pair of needles	a	442	435	454	558	532	524
		c	433	437	419	471	500	469
		d	238	253	249	268	259	—
		e	434	410	405	429	448	441
	P µg/pair of needles	c	44.4	42.1	35.5	47.3	48.5	41.6
1951	Fresh weight mg/ pair of needles	a	53	56.1	53	53.8	53.4	56.5
		b	45	42.2	40.5	42.1	41.4	43.6
		c	40.5	40.6	39	39.6	38.0	41.0
		d	41	43.9	44	41.9	39.9	—
		e	58	64.0	59	58.2	61.2	—
	Dry weight mg/ pair of needles	a	24.4	30.6	23.0	25.1	24.4	29.3
		b	18.3	22.6	17.3	18.7	18.9	21.7
		c	17.6	22.1	16.7	17.7	17.3	21.1
		d	18.2	23.5	17.8	18.7	18.8	—
		e	24.6	33.5	23.2	24.2	25.7	—
1950	Fresh weight mg/ pair of needles	a	77	77.2	78	77.3	71.6	—
		b	64	62.8	62	—	—	—
		c	61	63.8	63	60.8	—	—
		d	54	58.4	55	—	—	—
	Dry weight mg/ pair of needles	a	34.9	41.1	34.4	35.2	34.2	—
		b	28.6	32.9	25.9	—	—	—
		c	27.0	34.2	27.7	28.0	—	—
		d	24.1	31.1	24.0	—	—	—
	N % dry weight	a	1.29	1.00	1.21	1.35	1.39	—
		c	1.26	1.02	1.19	1.40	—	—
		d	1.34	1.04	1.16	—	—	—
	P % dry weight	c	0.120	0.092	0.096	0.127	—	—
	N µg/pair of needles	a	451	410	417	474	476	—
		c	342	351	329	392	—	—
		d	324	322	278	—	—	—
	P µg/pair of needles	c	32.3	31.5	26.7	35.6	—	—

Table VI. The changes in weight and nutrient content of spruce needles during different seasons from March 1953 to June 1954. The sample tree was a spruce growing in a park meadow.

Issue of needles	Determination	Branch	Date of sampling					
			26. III.	6. VI.	30. VII.	17. XI.	20. III.	11. VI.
1954	Fresh weight mg/needle	a	—	—	—	—	—	7.17
		b	—	—	—	—	—	7.70
	Dry weight mg/needle	a	—	—	—	—	—	1.21
		b	—	—	—	—	—	1.31
	Number of needles	a	—	—	—	—	—	44
		b	—	—	—	—	—	71
1953	Fresh weight mg/needle	a	—	7.59	7.4	8.31	8.37	9.51
		b	—	7.53	6.9	8.76	8.59	9.30
	Dry weight mg/needle	a	—	1.59	2.77	3.20	3.35	4.65
		b	—	1.52	2.80	3.26	3.33	4.55
	Number of needles	a	—	21	19	22	31	28
		b	—	17	18	23	31	35
1952	Fresh weight mg/needle	a	8.4	8.76	8.7	8.84	8.53	—
		b	8.6	9.30	8.8	9.38	9.11	(10.32)
	Dry weight mg/needle	a	3.78	4.29	3.51	3.66	3.60	—
		b	3.82	4.62	3.64	3.89	3.95	(5.41)
	N % dry weight	a	1.19	0.96	1.26	1.54	1.50	—
		b	1.29	0.98	1.30	1.56	1.53	(1.01)
	N μg/needle	a	45.0	41.4	44.4	56.3	54.0	—
		b	49.5	45.5	47.5	60.6	60.5	(54.6)
	Needle mean length, mm	a	12.36	12.36	12.66	12.54	12.28	—
		b	12.61	12.76	13.04	12.90	12.91	(13.39)
	Number of needles	a	23	15	15	16	18	—
		b	22	17	16	16	24	9
1951	Fresh weight mg/needle	a	8,3	8.44	7.8	8.16	8.27	9.08
		b	8.7	9.14	8.5	9.06	8.92	9.63
	Dry weight mg/needle	a	3,90	4.38	3.35	3.49	3.65	4.85
		b	4.10	4.85	3.77	3.80	3.91	5.20
	N % dry weight	a	1.18	0.90	1.20	1.47	1.40	0.94
		b	1.21	0.92	1.22	1.42	1.46	0.98
	N μg/needle	a	45.8	39.4	40.2	51.2	51.1	45.6
		b	49.5	44.6	46.0	54.0	57.2	50.9
	Number of needles	a	26	23	23	24	30	23
		b	17	18	13	16	31	31
1950	Fresh weight mg/needle	a	8.5	8.62	7.9	8.90	8.75	9.34
		b	7.9	8.25	8.3	8.27	8.16	8.55
	Dry weight mg/needle	a	4.00	4.56	3.67	3.81	3.89	4.91
		b	3.80	4.43	3.42	3.55	3.65	4.60
	N % dry weight	a	1.02	0.83	1.06	1.32	1.29	0.89
		b	1.15	0.88	1.12	1.38	1.38	0.94
	N μg/needle	a	41.1	38.1	39.1	50.4	50.2	44.6
		b	43.7	39.0	38.4	48.9	50.6	43.0
	Number of needles	a	24	29	24	26	35	25
		b	28	20	18	24	30	35
1949	Fresh weight mg/needle	a	8.1	8.36	8.3	8.16	7.92	8.84
		b	—	—	—	—	—	—
	Dry weight mg/needle	a	3.98 ± 0.09	4.59 ± 0.17	3.71 ± 0.12	3.64 ± 0.09	3.60 ± 0.07	4.74 ± 0.07
		b	—	—	—	—	—	—
	Number of needles	a	16	20	20	21	33	20
		b	—	—	—	—	—	—