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Distribution of mineral elements within the crown of Scots pine (*Pinus silvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.)

INTRODUCTION

Of the many factors affecting the flower formation in pine and spruce mineral nutrition appears to merit a special attention. There is no doubt that various mineral elements have an effect on flower initiation and consequently on seed production, and there are several fertilizer studies indicating this. Sweet and Will (1965) have found in a field experiment with Pinus radiata that suppressed trees have had a lower nitrogen content in the needles and these trees produced only male flowers. Vogl (1969) suggests that the accumulation of phosphorus in the buds may be of importance for the stimulation of flowering in spruce. The detailed studies of Giertych and Forward (1966) conducted on red pine (*Pinus resinosa* Ait.) have shown a distinct differentiation within the crown of a tree as regards fertility and the distribution of female and male flowers. They obtained a highly significant effect of the fertilisation with ammonium nitrate both on the total number of flowers and on the ratio of female flowers to male flowers, which was substancially increased. The authors suggested that the initiation of male flowers is taking place under a nitrogen deficit and female flowers in conditions of nitrogen abundance. These suggestions were further supported by fertilizer studies on Scots pine grafts (Giertych 1970).

These studies led to the present investigation. It was attempted to establish the concentration of the basic mineral elements in various organs (buds, one-year old stems, young needles, 2-year old needles) and in various positions within the crown of the tree, in order to establish the conditions as regards mineral nutrition under which flower buds are being initiated.

MATERIAL AND METHODS

For the mineral analyses samples of shoots were collected in two consecutive years. In 1971 6 pine and 5 spruce trees from the Kórnik Arboretum were selected for the purpose. There are free standing trees

with relatively large regular crowns. At the time the DBH for the pines was from 20 to 34 cm and for spruce from 53 to 76 cm. In 1972 samples were collected from 16 pines and 16 spruces. The pines grow in Kórnik in an area adjacent to the Kórnik Arboretum and their mean age is 30 years, DBH 17.7 cm and height 10 m. The spruces grow in the experimental forest Zwierzyniec, and their mean age is 90 years, DBH 43.6 cm and height 27 m. The trees selected in 1972 grow in stands at a certain density thus the crowns of these trees are relatively smaller.

The shoots have been sampled both years at the same time, that is for spruce from the 28th of June to lst of July and for pines from the 5th to 7th July. In 1971 samples were taken from 7 positions in the crown that is from the apex and from the external and internal upper, middle and lower crown. In 1972 the samples were taken only from 5 positions, that is from the apex and from the internal and external upper and lower crown.

From the shoots collected for mineral analyses use was made of the following tissues: old needles, needles of the current season, shoot apex with buds and the current year stem without buds. After separating the material it was dried at 105°C and stored in envelopes till the time of mineral analyses. These were made for nitrogen, phosphorus, potassium, calcium and sodium. In the first series (collections of 1971) sodium was not analysed for and in some samples of bud tissues there proved to be insufficient material so that not all the phosphorus analyses were made.

Nitrogen was analysed by the Kieldahl method (P i p e r 1957), phosphorus by the modified method of Kuttner and Lichtenstein (F i n k 1963) and the metallic elements with the help of a flame photometer (H u m p h r i e s 1956).

All the results of the chemical analyses have been treated statistically with the help of the variance analysis. The analyses were made separately for each element, organ, species and series and then jointly for each element but across all the other experimental variants.

One should also explain that all the trees from which the samples were collected have been previously treated by various combinations of N, P and K fertilizers (applying to individual major roots in the first series and to individual trees in the second series). However the variance analyses have not shown any major effects of the fertilizer applications on the concentration of these elements in the studied tissues, and thus for the purposes of the present investigation the fertilizer variants can be considered as additional replicates. Within each experimental replicate there were included all the fertilizer variants used.

RESULTS

1. CONCENTRATION OF THE BASIC MINERAL ELEMENTS IN VARIOUS ORGANS

In table 1 the concentration of nitrogen, phosphorus, potassium, calcium and sodium is given for the dry weight of the studied organs in the pine and spruce of the two, 1971 and 1972, series. These are average values over the replicates, fertilizer variants and positions within the crown.

Nitrogen. The mean nitrogen concentration over all the organs is the same for the two experimental series, however in pine it was higher in 1972 and in spruce higher in 1971 there being a significant interaction between series and species. The differences between the various organs though significant are not very great and the sequence of organs with an increasing nitrogen concentration is different for each series and species.

The tissues of pine have decidedly higher nitrogen concentrations than the tissues of spruce, and this difference was greater in 1972 than in 1971.

Phosphorus. Because of incompletness of the data for buds and stems the joint variance analysis has been made only for the needles. It showed that the needles of the current season have higher phosphorus concentrations than older needles. This is evident in both series but more so in 1972 than in 1971. Generally in 1972 the needles of both species have had a higher concentration of this element, than those collected a year earlier.

The 1972 data, which is also complete for buds and stems, has shown that similarily as with the needles the tissues of pine always have higher concentrations of phosphorus that the tissues of spruce.

Potassium. The concentration of potassium in the various organs is more or less the same for the two experimental series and for the two species. There was however a distinctly significant interaction between organs and species, caused by the fact that in pine the concentration of potassium in the current year needles is relatively high while in spruce it is relatively low.

Calcium. The concentration of calcium is the same for both series, however there are significant differences between species. Tissues of spruce have much higher concentrations of this element. The highest concentration of calcium is to be found in older needles. The lowest value of the calcium concentration in pine is to be found in the needles of the current season and in spruce in the stems.

Sodium. Analyses for the concentration of sodium in various tissues have been made only in the sample from the 1972 series. Spruce appears

Table 1

Concentrations of mineral elements in tissues of pine and spruce

Element	Species	Year	Old needles	Young needles	Stems	Buds
N	Pine	1971	1.61	1.81	1.43	1.85
		1972	1.81	2.10	1.73	1.61
	Spruce	1971	1.37	1.41	1.41	1.42
		1972	1.34	1.48	1.13	1.32
P	Pine	1971	1.114	0.219		
		1972	0.205	0.370	0.295	0.324
	Spruce	1971	0.129	0.207		
		1972	0.140	0.264	0.219	0.236
K	Pine	1971	0.442	0.744	0.701	0.586
		1972	0.399	0.813	0.858	0.546
	Spruce	1971	0.581	0.646	0.912	0.641
		1972	0.308	0.569	1.044	0.596
Ca	Pine	1971	0.521	0.220	0.243	0.336
		1972	0.511	0.170	0.244	0.232
	Spruce	1971	0.797	0.437	0.318	0.636
		1972	1.004	0.402	0.315	0.591
Na	Pine	1971				
		1972	0.018	0.018	0.019	0.014
	Spruce	1971				
		1972	0.008	0.027	0.020	0.029

to have somewhat higher concentrations of sodium than pine in all organs except old needles, which in spruce have a very low concentration of this element. Buds of pine, relative to other tissues of this species, have a low concentration of sodium, while the buds of spruce are characterized by high sodium concentrations.

2. DIFFERENCES IN CONCENTRATIONS OF MINERAL ELEMENTS IN VARIOUS POSITIONS WITHIN THE CROWN

The results of chemical analyses made on material collected in various zones of the crown are presented schematically in Fig. 1. As was mentioned above in the first experimental series 7 zones of the crown were sampled while in the second only five, thus on the joint figure only the average data for the five zones is presented. Each value shown in Figure 1 is an average over the 2 experimental series, 4 different organs, 8 different fertilizer treatments and 2 replicates.

The variance analyses have shown that the differences between the zones of the crown are highly significant, and we are obtaining a definite pattern of distribution of mineral elements in the crown, this pattern being identical for all the studied tissues. There are two models according to which the concentration of mineral elements is distributed in the crown. The concentration of nitrogen, phosphorus, potassium and sodium

in both species and the concentration of calcium in pine increase towards the inside of the crown and down the crown, while the concentration of calcium in spruce has an opposite pattern, it increases up the crown and towards the outside of it. The joint variance analyses made separately for each element have shown a highly significant differentiation between

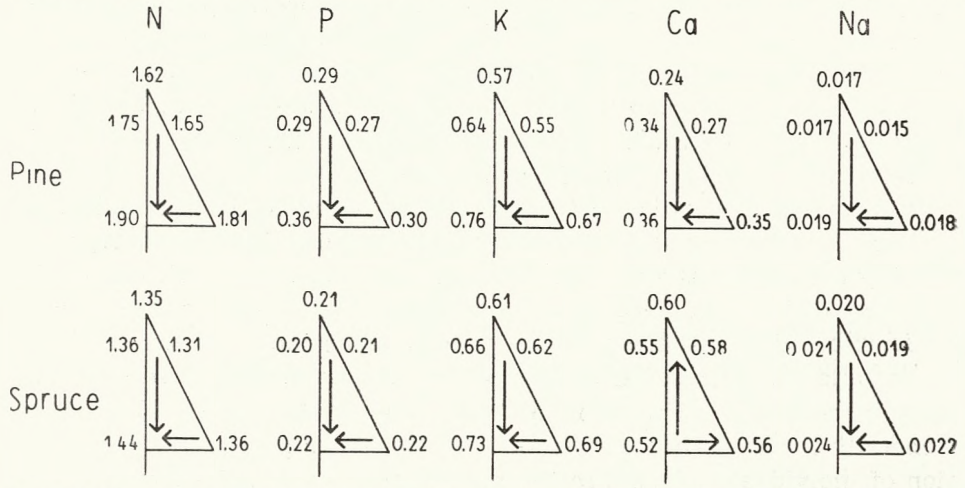

Fig. 1. Concentration of mineral elements in various parts of pine and spruce crowns. The values are averages from two experimental series, 4 tissues (old and new needles, stems, buds), 8 fertilizer treatments and 2 replicates. The averages for P and Na are based on less complete data (see Table 1)

the positions within the crown, always according to the pattern described above. In the case of calcium there was very strong interaction between crown zones and species.

The differentiation of concentrations of elements within the crown of pines is greater than within the crown of spruce, and as a result in the individual variance analyses the pine gave more frequently significant results than did the spruce data.

DISCUSSION

From the results of the study reported above of greatest interest is the vertical and horizontal differentiation of mineral concentrations within the crowns of the trees, and this appears to be true for 4 different tissues. The pattern is least obvious for the buds, but this could have been caused by the fact that we had insufficient quantities of material, and as a result the analyses made on too small samples were not as accurate.

Generally the lower concentration of mineral elements in the upper and outside parts of the crown could be explained by the greater vege-

tative growth in these crown regions which could result in a greater dilution of the mineral elements in celluloze, the major component of dry weight. Only the distribution of calcium would require some additional explanation, particularily in pine. It is the pattern in spruce that has to be considered as the typical one, since it is a common observation that the pattern of distribution of calcium is usually opposite to that of potassium. Since the differences in the size of needles and shoots between the outside and internal zones of the crown are much greater for pine than for spruce, one can suspect that the process of dilution of mineral elements effected by growth and celluloze increase has dominated any inverse relations between potassium and calcium.

Concerning the variation in the mineral concentration in various organs within the crown of the tree there exists a rich literature, particularily concerning the foliage. However the results of individual studies are very diverse and frequently contradictory. The reasons for this are various, but the most common one appears to be the time of sampling in relation to the vegetative season, when as a result of changes in the growth rate the concentrations of mineral elements change substancially. Generally it has been observed that in coniferous species the concentration of individual elements in the needles increases up the crown (Leyton 1948, Wehrmann 1957, Ovington and Madgwick 1958, Lavender and Carmichael 1966, Fornes 1969, Morrison 1972). This is true particularily for N, P, K and possibly Mg in the autumn. On the other hand the concentration of calcium in the needles tends to increase down the crown (Leyton 1948, Lavender and Carmichael 1966, Fornes 1969, Morrison 1972). Sometimes an absence of any regularity in the distribution of concentrations was observed (Strebel 1961, Fornes 1969). Fiedler and Müller (1973) point out for example that the distribution of potassium concentration within the crown of a tree will depend on the level of potassium nutrition. In our material at no time was there any significant interaction between the position in the crown and the fertilizer treatments.

The results of this investigation in general do not confirm the results obtained by other authors. They are only in agreement with the observation of Fraser (1966) who has found that vegetative buds from the lower parts of *Picea mariana* B.S.P. crowns are smaller and have higher concentrations of mineral elements.

The results obtained in the present study concern material collected at the time of intensive vegetative growth and bud setting including the initiation of flower buds. The observed pattern of variation suggests that female flowers, normally developing on the outer crown, are being initiated in conditions where mineral supply may be limiting, while male flowers, usually forming in the inner crown, are being initiated in conditions of mineral abundance. The frequently observed positive effect of

fertilisation on female flowering and the sometimes negative effect on male flowering may find an explanation in the distribution of mineral elements within the crown as reported in this paper.

The interaction between series and species for nitrogen may partly explain why 1973 was a better flowering year for pine and a poorer year for spruce than 1972.

SUMMARY

In order to establish the nutritive conditions under which flowering buds are being initiated it was decided to analyse the concentrations of mineral elements in the needles, buds and stems of different crown parts. Sample shoots have been collected for analysis in early July of 1971 and 1972, from 6 pines and 5 spruces in the former year and from 16 pines and 16 spruces in the latter.

Generally all the results are consistent for the two series. The studied species differ substancially in the concentration of mineral elements. In pine there are higher concentrations of N and P and lower of Ca than in spruce. Potassium concentration is more or less the same in both species. There are differences between sampled tissues as well as interactions between tissues, species and series, but generally nitrogen concentration is highest in new needles, potassium in the stems and calcium in old needles.

There are highly significant differences in mineral concentrations between crown parts. Concentration of N, P, K in both species and Ca in pine increase down the crown and towards the trunk, while the concentration of Ca in spruce has an opposite pattern. The observed distribution suggests that female flowers are being initiated in conditions of limiting mineral supply and male flowers in conditions of abundant nutrients. This can explain the frequently observed positive offect of fertilizers on female flowering and the sometimes negative effect on male flowering.

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Rozmieszczenie składników mineralnych w koronie sosny (Pinus silvestris L.) i świerka (Picea abies (L.) Karst.)

Streszczenie

W celu poznania warunków, w jakich zawiązują się pączki kwiatowe postanowiono przeanalizować zawartość składników mineralnych w igłach, pączkach i pędach w górnej i dolnej części korony drzewa. Próbki gałązek do analiz mineralnych pozyskano na przełomie czerwca i lipca; w 1971 r. z 6 sosen i 5 świerków, a w 1972 r. z 16 sosen i 16 świerków.

Na ogół wszystkie otrzymane wyniki powtarzają się w obu seriach doświadczalnych. Pod względem stężenia makroelementów w tkankach, badane gatunki drzew różnią się zasadniczo między sobą. W tkankach sosny stwierdzono wyższe stężenia N i P, a niższe stężenia Ca niż u świerka. Koncentracja K jest mniej więcej równa u obu gatunków. Istotnie różnią się między sobą badane organy, a ponadto istnieje wzajemna współzależność między organami a gatunkami czy seriami doświadczalnymi. Ogólnie jednak z badanych organów azot występuje w najwyższym stężeniu w igłach bieżącego przyrostu, potas w pędach, a wapń w igłach zeszłorocznych.

Stwierdzono jednokierunkową zmienność stężenia pierwiastków w tkankach wynikającą z miejsca zbioru próbki w koronie drzewa. Koncentracja N, P, K oraz Ca u sosny rośnie w dół korony i do wewnątrz, a Ca u świerka odwrotnie, tzn. w kierunku wierzchołka korony i na zewnątrz. Zaobserwowany kierunek zmienności sugeruje, że kwiaty żeńskie powstają w warunkach limitującego zaopatrzenia mineralnego, a kwiaty męskie w warunkach nadmiaru soli.

ХЕНРЫК ФОВЕР

Размещение минеральных элементов в кроне сосны (Pinus silvestris L.) и ели (Picea abies (L.) Karst.)

Резюме

В целях выяснения условий заложения цветочны почек, было решено проанализировать содержание минеральных элементов в хвое, почках и побегах верхней и нижней части кроны деревьев. Образцы веток для анализа были взяты на стыке июня и июля; в 1971 году они взяты с 6 сосен и 5 елей, а в 1972 году — с 16 сосен и 16 елей.

В целом в обеих опытных сериах все полученные результаты совпадают. По концентрации макроэлементов в тканях сосна и ель существенно различаются между собой. В тканях сосны установлена более высокая концентрация азота и фосфора и более низкая концентрация кальция, чем у ели. Концентрация калия более или менее одинакова у обоих видов. Существенно отличаются друг от друга изученные органы; кроме того, имеется взаимозависимость между органами и видами или опытными сериами. Из изученных органов самое высокое содержание азота обнаружено в хвое текущего года, калия — в побегах, кольция — в хвое прошлых лет.

Установлена односторонная изменчивость концентрации элементов в тканях, определяемая местоположением взятого образца в кроне дерева. Концентрация азота, фосфора, калия и кальция у сосны растет по направлению к низу кроны и вовнутрь ее, а концентрация кальция у ели изменяется в противоположном направлении, т.е. возрастает к верху кроны и к ее внешней стороне. Наблюдаемое направление изменчивости позволяет предположить, что женские цветки формируются в условиях ограниченного снабжения минеральными элементами, а мужские цветки — в условиях избытка солей.