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THE GROWTH AND COMPOSITION OF NATURAL STANDS OF BIRCH

2. THE UPTAKE OF MINERAL NUTRIENTS

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INTRODUCTION

Data of the dry weights and production of dry matter for individual trees and natural stands of birch growing on fen peat have been published in a previous paper (Ovington and Madgwick [9]). The birch woodlands form a series ranging in age from 6 to 55 years and by analysing the sample trees of *Betula verrucosa* it has been possible to determine the incorporation of certain chemical elements within the tree stands. The amounts of sodium, potassium, calcium, magnesium, phosphorus and nitrogen in trees of differing ages have been calculated and estimates made of the gross and annual nutrient uptake by the plantations.

METHODS

Two birch trees of approximately average size were felled in each of the nine woodlands. Six additional trees, giving a representative range of sizes for the stand, were sampled in the youngest of the woodlands in order to determine the variation between trees within the plot. A large sample of the leaves and branches as well as samples of the boles, taken at two-metre intervals along the tree trunks, were collected from each tree and oven dried at 80°C. When dry, the samples were ground in a Christy and Norris mill to pass through a sieve with round holes of 0.4 mm diameter and then stored for chemical analysis.

Nitrogen was determined by the micro-Kjeldahl method. To determine the other elements the wet-ashing procedure, as described by Piper [10], was followed using nitric, perchloric and sulphuric acids. The sodium and po-

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tassium contents of the resultant acid solution were measured with a flame photometer, calcium by the versenate technique, magnesium by the titan yellow and phosphorus by the molybdate-blue methods. The results obtained were combined with the dry weight data to estimate the amounts of the various elements in the trees and tree stands.

The peat soils in four plots were sampled by taking five cores of 10 cm diameter to a depth of 50 cm in each plot. The soil samples were dried and analysed as for the tree samples.

CHEMICAL COMPOSITION AS A PERCENTAGE OF THE DRY WEIGHT

Some variation in chemical composition occurs within the leaves, branches, bole and roots of individual trees. The percentage values given in Fig. 1 have been calculated to be representative of the

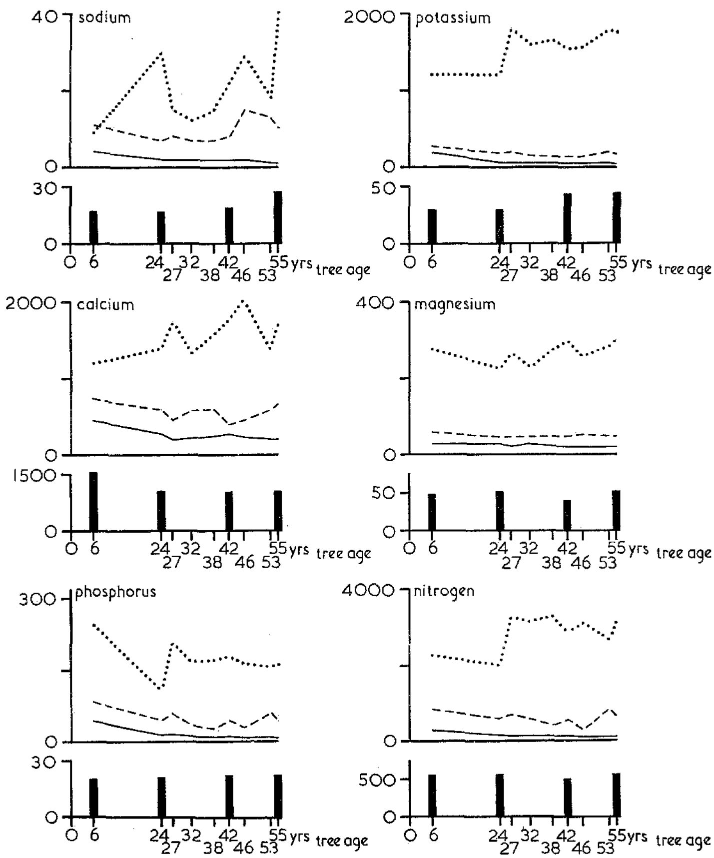

Fig. 1. The composition (mg/100 g O.D.) of the peat soil (histograms) and birch trees (leaves ......, live branches ------, bole ———).

whole of each respective part of the trees. The average percentages of all six elements decrease in the order leaves, branches and bole with the roots being broadly comparable in nutrient content to the branch or bole material. Nitrogen, potassium and calcium together represent about 93 per cent of the total weight of all six elements. The relative proportions of the various elements differ considerably for different parts of the trees, for example, the percentage of nitrogen in the leaves is almost double that of potassium or calcium whilst in the boles the percentage of calcium is nearly twice that of nitrogen and four times that of potassium (Table I).

TABLE I

The average nutrient content of sample trees as percentages of the oven-dry weight

Nutrient	Leaves	Branches	Boles	Roots
Sodium	0.02	0.01	0.002	0.01
Potassium	1.56	0.18	0.07	0.09
Calcium	1.57	0.56	0.25	0.35
Magnesium	0.27	0.05	0.02	0.03
Phosphorus	0.17	0.05	0.01	0.02
Nitrogen	2.85	0.60	0.14	0.41

The average percentages of nutrients in the leaves, branches, bole or roots vary considerably for different sample trees but frequently there appears to be some relationship to tree age or height. For instance, the leaves of the trees from the older plots generally have greater percentages of sodium, potassium, calcium, magnesium and nitrogen but smaller values of phosphorus than the leaves of the younger sample trees. The average concentrations of all six elements tend to be smaller in the older boles but for the living branches there is an initial period of decreasing concentration of nutrients in the juvenile stages followed by an increase in the more mature trees.

Although soils from only four of the nine plots were sampled, it seems clear that the differences in the percentages of the elements for sample trees cannot be attributed to differences in the soil conditions of the plots. The decreasing concentration of nutrients within the tree boles is almost certainly related to the different chemical compositions of bark, sapwood and heartwood and to the change with age in the proportions of these in the boles (Wright and Will [16]). Comparable changes have been recorded up individual trunks, thus samples from the young distal two metres of bole consistently contain higher concentrations of nutrients than samples from the older and lower part of the stem with a larger proportion of heartwood. The initial decrease in the percentages of the elements in the branches may result from the increasing average size of the branches as the trees age. The differences in the nutrient content of the leaves from the various trees are probably caused by a variety of factors. Leyton [4] has demonstrated that differences occur in the nutrient content of spruce, pine or larch needles depending on tree size within a stand. Comparisons of the leaves of the eight trees representing the size range in the younger plot have shown that the concentrations of potassium, phosphorus and nitrogen in the leaves are negatively correlated with tree height whilst sodium, calcium and magnesium are positively correlated (Table II), but for sodium and nitrogen the correlation is not significant at the 5 per cent level. Since the less vigorous trees in a plot are likely to be supressed and die, the average trees are being selected from a progressively smaller group of faster growing trees and this could cause a gradual change in average leaf composition. However, this does not appear to have any significant effect on the change of leaf composition as the stands mature, for potassium decreases with height within a plot but increases with height between plots.

TABLE II

Correlation coefficients between tree height and percentage composition

Nutrient	For the average trees from the nine plots			For the eight sample trees from the 6 yr. old plot		
	Leaves	Branches	Boles	Leaves	Branches	Boles
Sodium	+0.594	+0.439	—0.866 **	+0.477	—0.550	—0.532
Potassium	+0.731 *	—0.637	—0.809 **	—0.730 *	—0.171	—0.073
Calcium	+0.701 *	—0.446	—0.818 **	+0.752 *	—0.809 *	—0.601
Magnesium	+0.333	—0.461	—0.883 **	+0.922 **	—0.274	—0.678
Phosphorus	—0.446	—0.525	—0.826 **	—0.727 *	—0.316	—0.548
Nitrogen	+0.526	—0.378	—0.877 **	—0.118	—0.599	—0.627

* Significant at 5% level.
** Significant at 1% level.

THE AMOUNT OF NUTRIENTS IN AVERAGE TREES

As the trees become older, increasing amounts of nutrients are incorporated within them (Table III). This increase occurs prima-

TABLE III

The mineral content (g) of average trees									
	Tree age yrs.								
	6	24	27	32	38	42	46	53	55
Sodium									
Leaves	0.001	0.14	0.08	0.05	0.07	0.17	0.60	0.41	1.13
Live branches	0.004	0.17	0.27	0.16	0.51	0.52	3.50	3.90	3.19
Bole	0.004	0.15	0.52	0.22	0.75	0.79	2.21	2.03	2.19
Total	0.009	0.46	0.87	0.43	1.33	1.48	6.31	6.34	6.51
Roots	0.004	0.26	—	—	—	4.73	—	—	4.69
Dead branches	0.001	0.02	0.04	0.04	0.18	0.31	0.41	0.27	0.18
Potassium									
Leaves	0.16	5.6	9.8	5.8	7.3	12.3	32.6	39.2	49.2
Live branches	0.10	4.3	7.1	3.7	9.8	9.7	31.1	58.6	52.7
Bole	0.18	5.8	18.4	7.3	21.7	22.8	64.9	69.6	73.8
Total	0.44	15.7	35.3	16.8	38.8	44.8	128.6	167.4	175.7
Roots	0.03	3.1	—	—	—	13.8	—	—	52.0
Dead branches	< 0.01	0.1	0.2	0.3	0.9	1.8	1.1	1.8	0.5
Calcium									
Leaves	0.16	6.5	9.4	4.8	7.0	14.1	42.5	30.6	48.2
Live branches	0.26	13.9	16.3	12.9	43.4	27.4	104.2	177.1	204.0
Bole	0.36	26.4	56.2	28.0	97.8	118.1	324.9	289.7	312.8
Total	0.78	46.8	81.9	45.7	148.2	159.6	471.6	497.4	565.0
Roots	0.10	15.9	—	—	—	59.4	—	—	175.5
Dead branches	0.03	1.8	1.2	3.0	14.3	16.1	16.0	11.1	10.8
Magnesium									
Leaves	0.04	1.1	1.5	0.8	1.2	2.4	5.4	6.3	8.5
Live branches	0.02	1.1	1.7	1.1	3.5	3.3	12.1	14.6	14.8
Bole	0.02	2.5	5.7	3.3	8.9	8.8	26.0	25.9	30.1
Total	0.08	4.7	8.9	5.2	13.6	14.5	43.5	46.8	53.4
Roots	0.01	0.9	—	—	—	7.4	—	—	16.0
Dead branches	< 0.01	0.1	0.1	0.2	0.5	0.8	0.7	0.6	0.4
Phosphorus									
Leaves	0.03	0.5	1.1	0.6	0.8	1.4	3.5	3.5	4.6
Live branches	0.03	1.1	2.1	0.8	2.1	3.0	6.9	18.1	13.3
Bole	0.04	1.2	4.1	1.4	3.4	4.6	10.4	12.0	12.4
Total	0.10	2.8	7.3	2.8	6.3	9.0	20.8	33.6	30.3
Roots	0.01	1.0	—	—	—	3.0	—	—	8.3
Dead branches	< 0.01	< 0.1	< 0.1	0.1	0.3	0.4	0.2	0.5	0.2
Nitrogen									
Leaves	0.29	9.4	17.7	11.5	14.4	22.7	64.9	59.0	88.5
Live branches	0.29	13.7	24.6	12.9	29.6	38.1	67.9	243.5	190.6
Bole	0.26	14.7	37.5	16.4	48.4	55.0	138.4	161.9	165.2
Total	0.84	37.8	79.8	40.8	92.4	115.8	271.2	464.4	444.3
Roots	0.11	17.9	—	—	—	73.4	—	—	173.1
Dead branches	0.01	1.5	0.6	1.5	7.7	7.7	4.9	7.5	3.9

rily as a result of the large increase in dry weight for the percentages of nutrients in the boles, for instance, decrease with greater age. After 55 years growth, the surviving birch trees on average contain 11.4 g of sodium, 228 g of potassium, 751 g of calcium, 70 g of magnesium, 39 g of phosphorus and 621 g of nitrogen. These elements are not distributed equally between the component parts of the trees and the distribution depends on both the dry weight and the average percentages of the elements in the tree parts. Thus, the canopy of the oldest birch tree is only a fifth of the dry weight of the living shoot but contains about two thirds

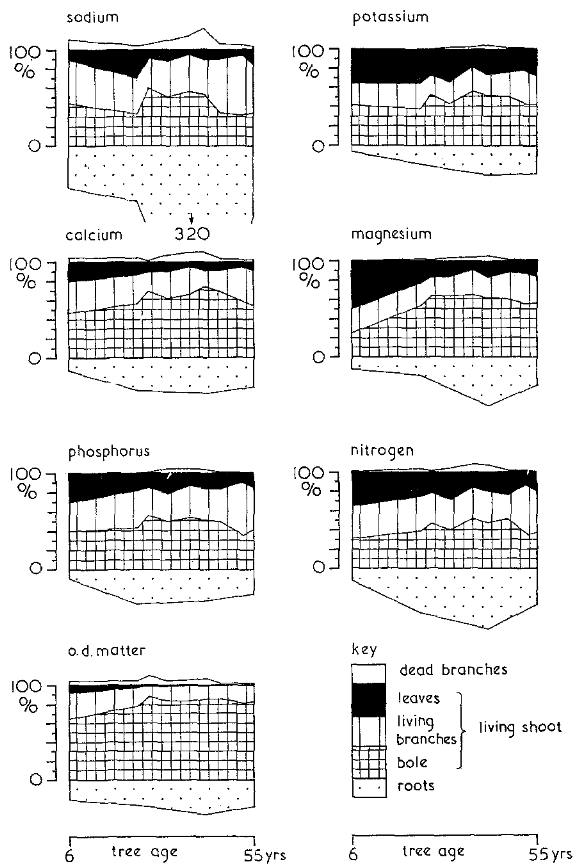

Fig. 2. The distribution of dry matter, sodium, potassium, calcium, magnesium, phosphorus, and nitrogen in birch trees of different ages. Expressed as percentages of the weight of the living shoot.

of the weights of nutrients in the shoot. In particular, the leaves contain relatively large amounts of nutrients for their weight for although they only represent 2 per cent of the dry weight, they contain 5 to 30 per cent of the sodium, 19 to 36 per cent of the potassium, 5 to 21 per cent of the calcium, 9 to 50 per cent of the magnesium, 10 to 30 per cent of the phosphorus and 13 to 35 per cent of the nitrogen in the living shoot. Similarly, the branches contain about 18 per cent of the dry matter, but in most cases, higher proportions of each of the elements, *i.e.* 31 to 62 per cent of the sodium, 20 to 35 per cent of the potassium, 17 to 36 per cent of the calcium, 19 to 31 per cent of the magnesium, 29 to 54 per cent of the phosphorus and 25 to 52 per cent of the nitrogen. In contrast, although the bole represents about 80 per cent of the dry weight of the living shoot, it only contains 32 to 60 per cent of the sodium, 37 to 56 per cent of the potassium, 46 to 74 per cent of the calcium, 25 to 65 per cent of the magnesium, 36 to 56 per cent of the phosphorus and 31 to 52 per cent of the nitrogen.

On the whole, the tree canopy contains a greater weight of nutrients than the bole and the bole more than the root system, except for sodium and nitrogen, which occur in relatively large amounts in the tree roots. Although the total nutrient content of all the different parts of the trees tends to increase with age, the leaves contain a decreasing proportion of the nutrients since, because of the annual leaf fall, the build-up of leaf material per tree is not so rapid as that of branch, bole or root matter (Fig. 2).

THE AMOUNT OF NUTRIENTS IN TREE STANDS

The amounts of nutrients contained in all the living trees comprising each woodland have been estimated by multiplying the weights of nutrients in the average trees by the number of trees per hectare (Table IV). The increase in the total quantities of the six elements with greater tree age closely parallels changes in dry weight. For example, the amounts of the nutrients in the tree boles become steadily greater as the woodlands become older, but the nutrient content of the tree leaves increases very rapidly between 6 to 24 years of age as a leaf mass develops but afterwards only increases slightly since the leaf weight within the woodland canopy becomes relatively constant up to 55 years of age. From about 32

TABLE IV

The mineral content of tree stands (kg/ha)									
	Tree age yrs.								
	6	24	27	32	38	42	46	53	55
Sodium									
Leaves	0.01	0.7	0.2	0.2	0.1	0.2	0.4	0.4	1.0
Live branches	0.04	0.8	0.7	0.7	0.8	0.7	2.6	4.0	2.8
Boles	0.04	0.7	1.3	0.9	1.1	1.1	1.6	2.1	1.9
Total	0.09	2.2	2.2	1.8	2.0	2.0	4.6	6.5	5.7
Roots	0.04	1.3	—	—	—	6.3	—	—	4.1
Dead branches	0.01	0.1	0.1	0.2	0.3	0.4	0.3	0.3	0.2
Potassium									
Leaves	1.6	28	24	25	11	16	24	40	43
Live branches	1.0	21	18	15	15	13	23	60	46
Boles	1.8	29	46	31	32	31	48	71	65
Total	4.4	78	88	71	58	60	95	171	154
Roots	0.3	15	—	—	—	18	—	—	46
Dead branches	< 0.1	< 1	< 1	1	1	2	1	2	< 1
Calcium									
Leaves	1.6	32	23	20	10	19	31	31	42
Live branches	2.7	69	40	54	65	37	77	181	180
Boles	3.8	132	139	118	147	158	240	295	275
Total	8.1	233	202	192	222	214	348	507	497
Roots	1.1	79	—	—	—	80	—	—	154
Dead branches	0.3	9	3	13	21	22	12	11	10
Magnesium									
Leaves	0.4	5	4	4	2	3	4	6	7
Live branches	0.2	6	4	5	5	4	9	15	13
Boles	0.3	13	14	14	13	12	19	26	26
Total	0.9	24	22	23	20	19	32	47	46
Roots	0.1	4	—	—	—	10	—	—	14
Dead branches	< 0.1	< 1	< 1	1	1	1	1	1	< 1
Phosphorus									
Leaves	0.3	3	3	3	1	2	3	4	4
Live branches	0.3	5	5	3	3	4	5	18	12
Boles	0.4	6	10	6	5	6	8	12	11
Total	1.0	14	18	12	9	12	16	34	27
Roots	0.1	5	—	—	—	4	—	—	7
Dead branches	< 0.1	< 1	< 1	< 1	< 1	< 1	< 1	1	< 1
Nitrogen									
Leaves	3.1	47	44	49	22	30	48	60	78
Live branches	3.1	68	61	54	44	51	50	248	168
Boles	2.7	73	93	69	73	74	102	165	145
Total	8.9	188	198	172	139	155	200	473	391
Roots	1.2	89	—	—	—	98	—	—	152
Dead branches	0.1	7	2	6	12	10	4	8	3

to 42 years the total nutrient content of the living trees does not vary greatly and may even decline slightly because a temporary reduction in leaf weight at this stage compensates for any increase in the accumulation of nutrients within the living tree boles. After 42 years of age there is a renewed accumulation of nutrients within the stand as a whole so that the trees of the oldest woodland contain, as kilograms per hectare, 10 of sodium, 200 of potassium, 661 of calcium, 60 of magnesium, 34 of phosphorus and 546 of nitrogen after 55 years. The average annual incorporation of sodium, potassium, calcium, magnesium, phosphorus and nitrogen within the trees, throughout the fifty-five years, amounts to 0.2, 3.6, 12.0, 1.1, 0.6 and 9.9 kilograms per hectare respectively but this only applies to the summer period for in autumn when the leaves have been shed the values would be reduced.

THE NUTRIENT CYCLE

The nutrient content of the tree stock does not represent the gross uptake of nutrients by the tree since some trees will have died and some of the nutrients taken up by the surviving trees will have been returned to the soil in various ways. Consequently, the gross uptake of nutrients by the trees has been calculated from the estimates of total dry-matter production. During the period from 6 to 55 years when the canopies have closed and dry-matter production is high, the gross annual uptake of nutrients by the trees, excluding roots, is relatively constant averaging 0.6, 28, 44, 5.6, 4.1 and 56 kilograms per hectare for sodium, potassium, calcium, magnesium, phosphorus and nitrogen respectively. Leaf fall returns to the soil about half of the nutrient uptake and this is further augmented by branches falling from the trees and the death of weaker trees to give an average annual return, as kilograms per hectare, of 0.5 for sodium, 25 for potassium, 34 for calcium, 4.7 for magnesium, 3.6 for phosphorus and 48 for nitrogen. These values are only slightly less than the annual uptake of the various elements and the difference between the two sets of figures represents the annual increase of nutrients within the tree mass during the period. Decomposition of dead tree material occurs fairly rapidly on the base rich peat and the fallen birch leaves rarely persist for more than a year so that the annual return of nutrients in the litter fall is approximately equal to the amount of nutrients released yearly by decomposition of organic matter derived from the trees. The estimates of nutrient return to the soil will be underestimates for they do not include nutrients washed out of the birch canopies by precipitation (Madgwick and Ovington [5]) and the release of nutrients by the annual decay of root material from living trees. Comparable nutrient cycles may occur between the ground flora and the soil but this is not likely to be of great importance in the birch stands for the ground vegetation in such dense woodlands is absent or poorly developed.

DISCUSSION

Holme Fen is located in the Fenland region, one of the most intensively cultivated areas of Britain characterised by high agricultural productivity once the peat soils are effectively drained. Consequently, there are only small areas of semi-natural vegetation left in the Fens but Kassas [2 3] has described the natural tree and bush colonization of nearby Chippenham Fen and gives the dry weight of the Molinia-Phragmites community there as approx. 3,550 kilograms per hectare. The birch stands would attain this weight about 7 to 8 years after colonisation but the average nutrient content of the trees is probably much less than that of the herbaceous flora so that it would take about 20 years before the nutrient content of the trees equalled that of the herbaceous vegetation type. Compared with other tree species (Ovington [7 8]), the birch stands do not contain very large amounts of plant nutrients but the total quantity of nutrients contained in the trees after fifty-five years does represent a significant retention of nutrients. The amounts retained are relatively small when compared with the gross uptake by the trees and, of the total uptake, about 77 per cent of the sodium, 87 per cent of the potassium, 74 per cent of the calcium, 81 per cent of the magnesium, 85 per cent of the phosphorus and 84 per cent of the nitrogen have been returned to the soil after 55 years. The woodland community is therefore characterised by a large interchange of nutrients between the trees and soil.

With the need for more intensive forest management increased attention is being paid to the possibilities of applying artificial fertilizers to replace the nutrients removed when a tree crop is harvested. Viro [15] and Tamm [13 14] have demonstrated that the application of fertilizers to birch woodlands may increase the nutrient content of the leaves and improve tree growth. The fertilizer-application experiments of Tamm were, however, located on peats much poorer in mineral nutrients than the fen peat and the nutrient content of the birch leaves at Holme Fen tends to be greater than those from the unfertilized plots in Tamm's experiment. The nutrient content of the leaves of the Holme Fen birch trees is comparable to that of birch growing on base rich mineral soil in the same general climatic region (Ovington [6]). The potassium, magnesium and calcium values for the leaf material lie within Ingestad's [1] 90 per cent of control growth range and phosphorus and nitrogen above the 50 per cent level for seedlings grown in nutrient solutions. It seems unlikely that nutrient deficiency of the soil is limiting the growth of the birch on the fen peat and the nutrient uptake must be approaching the maximum for the species in that region. Waterlogging as a result of failure to maintain the drains may have reduced productivity and consequently total nutrient uptake at certain stages of growth.

In recent years increased interest has been aroused in determining the effects of nutrient uptake by forest stands on soil-forming processes (Remezov [11], Rennie [12]). There is no evidence that the establishment and growth of the birch stands has caused any reduction of soil fertility but such effects would be long term and would need to be measured in terms of the breakdown of the peat and the general circulation of nutrients within the woodland ecosystem.

SUMMARY

Sample trees up to 55 years of age from nine natural woodlands of birch at Holme Fen Nature Reserve were analysed for sodium, potassium, calcium, magnesium, phosphorus, and nitrogen. Data are given of the amounts of these elements in the leaves, branches, boles, and in some cases of roots for the sample trees and the stock of the tree stands. The average annual uptake of nutrients and the return of nutrients to the soil as the woodlands mature are estimated.

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