Factors Limiting Tree Growth on Peat Soils

An Investigation into the nutrient status of two peatland plantations

R. E. PARKER,
Department of Botany, The Queen's University of Belfast.

A good deal has been said and written already about the potentialities and the limitations of both soil analyses and foliage analyses in the diagnosis of nutrient deficiencies of forest stands. (e.g. Binns, 1962; Duchaufour, 1958; Leyton, 1958b; Tamm, 1956; Viro, 1961; and Wright, 1959). It is not my object here to add to this discussion but to give an account of the investigation of two peatland plantations by means of a method which included the determination of the nutrient content of both soil and foliage samples.

Objects.

Among the plantations established on peat soils in Northern Ireland between the late nineteen-twenties and the early nineteen-fifties there are many in which tree growth, either in whole or in part, has been unsatisfactory. Some of the younger stands which were planted on very poor land just before the introduction of ploughing are more or less uniformly retarded and may be regarded as 'in check'. The older stands were generally planted on rather better land and have been more successful. Within them the areas of retarded growth occur only as patches within compartments, the growth of which has otherwise been satisfactory. Such stands have already been briefly described (Parker 1957, and 1962). In these older stands the trees show a very wide range of growth rate. In terms of present tree height there is often a ten-fold difference between the largest and the smallest trees. These large differences may be regarded as resulting from parallel differences in soil fertility and despite the complication of competing vegetation it was considered probable that these fertility differences could be interpreted simply in terms of nutrient supply. It would appear that on sites in this condition the locally unsatisfactory tree growth results from one or more nutrient deficiencies which have arisen directly as a result of site differences present at the time of planting; in other words, that the trees are acting as simple indicators of site fertility. In some of the peatland plantations where growth for several decades has been generally satisfactory there is now evidence of a fall in growth rate, particularly in those parts where growth in the past has been best. It was thought that this fall might be due to a significant reduction in site fertility brought about by the trees themselves: that on sites in this condition the larger trees are now reacting to their own past depletion of their rooting zone in respect of one or more nutrients.
The first and main object of this investigation was to test the hypothesis that the trees growing on these peat soils are subject to one or more nutrient deficiencies and to identify the deficient element or elements. The second object was to test the hypothesis that there are significant differences between the nutrient relationships of the two kinds of site described above; in particular that the fall in growth rate of the larger trees is indicative of the onset of further nutrient deficiency resulting from impoverishment of the site by the trees themselves.

Sites.

Two sites were selected for investigation; one, which will be referred to as Site 4/60, was thought to be typical of the first condition defined above; the other, which will be referred to as Site 5/60, was thought to be typical of the second condition. Both are located within Springwell Forest, which lies about 6 miles from Coleraine, astride the Coleraine-Limavady Road, in Co. Derry.

Site 4/60—Site 4/60 carries a crop of Sitka spruce which was planted in 1939. The site is flat and peat-covered to depths ranging from 9 inches to 4 feet 6 inches. In the course of the investigation a number of indistinct steps were found in the peat surface. These suggest that the site has at one time been subjected to some peat cutting. The area of the single patch which shows markedly poor growth, i.e. on which the trees have not yet closed canopy, is about 2,000 square yards. The smallest trees stand amongst tall Calluna which despite its age is still dense and accompanied only by a little Molinia and a fragmentary ground layer of mosses. Beneath the trees which are just closing canopy the Calluna is being killed out, the Molinia is more conspicuous, and mounds of Sphagnum are accumulating. The smallest trees which have been brashed have beneath them a thick spongy carpet composed of several Hypnaceous mosses and scattered mounds of Sphagnum. Under the rather larger trees the moss carpet thins out and there is no Sphagnum, and under the largest trees the mosses are sparse or absent altogether. Tree heights at the time of sampling ranged from 105 to 1,248 cms. (3 ft. 6 ins. to 41 ft.).

Site 5/60—The plantation selected as Site 5/60 had already been under observation for several years and two permanent belt transects had been established within it to facilitate the study of vegetation changes. It carries a crop of Sitka spruce which was planted in 1933. The site has an overall slight slope to the E.S.E. but the gradient is not uniform. Peat depth ranges from 9 inches to about 5 feet. Two small patches on which the tree canopy is not yet closed, with a total area of about 120 square yards, were included in the area sampled. The vegetation on the site varies with tree size much as that on Site 4/60 but differs in that the moss carpet extends further beneath the larger trees. There is good evidence that this extension has taken place recently in response to increased light intensity resulting from heavy needle cast.
Methods.

Following the recommendations of C. O. Tamm who found the nutrient content of Norway spruce needles to fluctuate least in late autumn and winter (Tamm 1955), sampling was carried out during the last few days of November and the first few days of December, 1960. The procedure used was the same on both sites. Trees were selected to cover as evenly as possible the whole height range present. 40 trees were selected on Site 4/60 and 21 trees on Site 5/60. In those parts of the stands where the canopy was closed only dominant or codominant trees were considered eligible for selection, and trees seen to have double or broken leading shoots were excluded.* For each tree the following measurements were made and samples taken:—

1. The peat depth was measured with a probe at several points within the crown spread of the tree and a mean value, to the nearest three inches, recorded.
2. A brief description of the vegetation beneath the larger trees or in the immediate vicinity of the smaller ones was recorded.
3. Two cylindrical samples, each about 250 mls. volume were taken of peat beneath the tree. These samples were taken from immediately beneath the soil surface and did not include needle litter or living vegetation.
4. The tree was marked at breast height (4 ft. 3 ins. from the soil surface) and then felled, care being taken that the leading shoot and the uppermost lateral branches were neither damaged nor soiled.
5. The total length of the felled stem was measured and the height of the stump surface above the ground added to obtain total tree height.
6. The length of the leading shoot was measured and the shoot was then carefully removed in a labelled polythene bag. (The needles from the leading shoot were to be analysed for plant nutrients and the results used in the diagnosis of nutrient deficiencies, following the recommendations of Leyton and Armson (1955).)
7. The uppermost lateral shoots were treated similarly. (The needles from the uppermost laterals were also collected in case they should also be required for analysis.)
8. The distances between adjacent branch whorls were then measured for as far back from the uppermost whorl as they could be reliably recognized.
9. From those stems capable of providing one a section about 2 inches long was taken at breast height. For the smallest trees a similar section was taken from the butt. (Cover photograph).

The shoots taken were oven-dried at 100° C. the next day and the needles removed. An enlarged record of the size and shape of a random sample of the needles from each leading shoot was made by placing them on a glass plate in the film carrier of a photographic enlarger and printing their enlarged shadows (at about × 3 linear) on bromide paper. The girths of the stem sections were measured. All needle samples were then ground to pass a 1 mm. sieve in a ‘Casella’ grain mill. The peat samples were stored at about 10° C. for a few days. One

* The twenty-first tree on Site 5/60 was intended to replace one which on felling proved to have a double leading shoot, but as samples taken from all trees were later analysed the data for the 21 trees have been included in the results.
of each pair was then used for the determination of pH; a spear-type glass electrode and reference electrode were inserted into the peat as collected and the value read directly from the scale of a ‘Pye General Purpose’ pH meter. The other was oven-dried at 100°C in a forced draught oven and milled to pass a 1 mm. sieve. The leading-shoot needle samples were analysed for their total content of nitrogen, phosphorus, potassium, calcium, magnesium, sodium and managanese. After the results of the needle analyses had been examined the peat samples were analysed for their total content of N, P, K, and Ca. N was determined by the semi-micro Kjeldahl method. The remaining elements were determined using a solution prepared by mixed-acid digestion. P was determined by the molybdenum-blue method using stannous chloride as the reducing agent. Both Na and K were determined by means of an ‘EEL’ flame photometer. Ca was determined by compleximetric titration with EDTA using murexide as the indicator; Mg by the titan-yellow method; and the Mn by the periodate method. During the summer of 1961 further observations were made on the relationship between tree size and vegetation type on Site 4/60.

Results.

Tree height was taken as a measure of overall tree growth and the relationships between this quantity and the other recorded variables were examined. On Site 4/60 the relationship between tree height and length of current leading shoot was strikingly linear (Plate 1).

The equation for the regression line of height on length of leading shoot (in cms.) is $Y = 12.66X + 93.8$, with a correlation coefficient ($r$) of .94. This relationship is consistent with the hypothesis that the planted trees have responded and are still responding consistently to differences in site fertility within the area sampled. On Site 5/60 the corresponding relationship is less regular (Plate 2) but there is an obvious tendency for the height increments of the tallest trees to fall below those of the trees of intermediate size. The history of the height growth of each tree sampled was reconstructed for as far into the past as the measurements between branch whorls would allow. This was to 1948 for Site 4/60 and to 1945 for Site 5/60. The seven largest trees on Site 5/60 began to show a fall in height-growth rate in 1953. A comparison of height-growth increments in more recent years is complicated in that all but the most stunted trees on both sites showed a marked fall in increment for the years 1957 and 1958. Since 1958 however only this group of large trees on Site 5/60 has failed to show a recovery, and the mean height increment for this group in 1960 was less than that of the 7 next tallest trees on the same site. This evidence is consistent with the hypothesis that the environmental conditions of the larger trees on Site 5/60 have markedly deteriorated in recent years. There is a significant negative correlation between tree height and peat depth on Site 4/60 ($r = .754$, $P$ better than .001) but inspection of the actual dot diagram shows that the relationship owes more to the absence
PLATE 1. Leading shoots from the two groups of 20 sample trees taken on Springwell 4/60, the shoots arranged in each group in order of tree height; smallest tree towards the top of page.
of small trees from the shallow peat than to the absence of tall trees from the deeper peat, e.g., whereas there are no trees under 400 cms. (13 ft. 6 ins.) on peat of under 3 ft. 6 ins. deep there are 5 trees of over 900 cms. (30 ft.) on peat of over 2 ft. 6 ins. deep. Data for the 21 trees on Site 5/60 indicate no simple relationship between peat depth and tree height. Trees under 400 cms. occur on peats both 9 ins. and 5 ft. deep but the tallest trees are confined to peats between 2 ft. 3 ins. and 4 ft. 6 ins. deep.

Vegetation.

The vegetation accompanying the trees on Site 4/60 was examined in detail and classified into six 'types' to allow the relationship between vegetation and tree height to be examined. The six types were defined as follows:

**Type 'F'—**Tall *Calluna vulgaris* (c 4 ft.) forming a more or less complete canopy, accompanied by frequent but small tussocks of *Molinia caerulea*, and occasional small tussocks of *Eriophorum vaginatum*. Beneath the weaker parts of the *Calluna* canopy, occasional mounds of *Sphagnum* (*S. rubellum* and *S. plumulosum*) and an incomplete ground layer consisting of the pleurocarpous mosses listed under Type 'D'.

**Type 'E'—***Calluna* still present but tall and weak or already dead. *Molinia* more conspicuous and mounds of *Sphagnum* species larger and more frequent.

**Type 'D'—***Calluna* absent. Almost complete bryophyte cover consisting of a thick spongy carpet of several pleurocarpous mosses, the most abundant species being *Hypnum cupressiforme*, *Rhytidiadelphus loreus*, *Plagiothecium undulatum*, *Hylocomium splendens*, and *Pleurozium schreberi*, with cushions of *Dicranum scoparium*, and occasional hummocks or more numerous small patches of several *Sphagnum* species. (*S. palustre*, *S. recurvum* and *S. rubellum*). Small tussocks of *Molinia* locally frequent.

**Type 'C'—**Similar to Type 'D' but *Sphagnum* species absent and other mosses less luxuriant.

**Type 'B'—**Forest floor bare except for a few thin wefts of pleurocarpous mosses, the most abundant species being *Hypnum cupressiforme*, *Thuidium tamariscinum*, and *Eurhynchium praelongum*.

**Type 'A'—**Vegetation absent.

Nine plots fifteen feet square were selected within the area sampled as bearing vegetation of the types described above; two plots each of types C, D, and E; and one plot each of types A, B, and F. The heights of the 70 trees present on these plots were measured, and also the B.H. girths of all but the smallest. The data for these 70 trees were combined with those for the 40 trees taken as samples. A close relationship between tree size and vegetation type was found to exist, the six
PLATE 2. Leading shoots from the 20 sample trees taken on Springwell 5/60 arranged in order of tree height; smallest tree towards top of page.
types from 'F' to 'A' indicating progressively higher fertility levels. A summary of the data is given in Table I.

<table>
<thead>
<tr>
<th>Vegetation type</th>
<th>Mean Height (cms.)</th>
<th>Mean Girth (cms.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>'F'</td>
<td>182</td>
<td>-</td>
</tr>
<tr>
<td>'E'</td>
<td>370</td>
<td>20</td>
</tr>
<tr>
<td>'D'</td>
<td>569</td>
<td>30</td>
</tr>
<tr>
<td>'C'</td>
<td>715</td>
<td>35</td>
</tr>
<tr>
<td>'B'</td>
<td>903</td>
<td>41</td>
</tr>
<tr>
<td>'A'</td>
<td>1,153</td>
<td>52</td>
</tr>
</tbody>
</table>

**Foliage analysis.**

The relationships between tree heights and nutrient contents of the needles taken from the leading shoots were examined for both sites. Dot diagrams were prepared for the individual elements, and for those cases in which rectilinear relationships were suspected the regression of tree height (in metres) upon foliage nutrient content (as percentage dry weight) was calculated. For those in which a significant linear component was found the correlation coefficient was also calculated. (Figs. 1-4).

**Nitrogen**—There are strong positive relationships between tree height and total needle N on both sites. For Site 4/60 $r = .869$ and for Site 5/60 $r = .797$ with $P$ better than .001 on both. This fact considered alone suggests a deficiency of this element over the whole, or at least the greater part, of the range represented (Leyton 1957a). If this were so the actual levels of N in the foliage would be expected to be sub-optimal. Leyton has suggested, on the basis of work with Sitka spruce on heathland sites in England (Leyton 1954 and 1958a, etc.), that the optimum value for this species lies between 1.5 and 1.6%. This suggestion appears to rest on the results of two experiments. In one the higher N levels were obtained by 'scalping' the surrounding heath vegetation, a type of disturbance which in some instances had an inimical effect on the trees' water relations. In the other supra-optimal concentrations of N in the foliage were not definitely established. This estimate may therefore be low. Recent work by Ingesstadt (1959) indicates that the optimum for Norway spruce is at about 2.0%, and that of Tamm (1956) that it is rather higher than this. In the present investigation all but the three highest values for Site 4/60 were less than 1.6%, so the case for the existence of N deficiency on both sites is well established.

**Phosphorus**—There are also strong positive relationships between needle P and tree height on both sites. For Site 4/60 $r = .701$ and for Site 5/60 $r = .680$ with $P$ better than .001 for both. Considered alone this would suggest that growth on both sites was limited not only by N but also by P supply. Leyton has suggested that the optimum level
of P for Sitka spruce is 0.14% (1957) but as Ingestadt (1959) observes, this value was obtained as a result of an experiment in which supra-optimal concentrations were not definitely established, and it may therefore be too low. Wright (1959) has reported growth responses of Sitka spruce with heavy application of G.M.P. up to a foliar P content of 0.0165% in one experiment (Glentrool 9 P.52) and 0.0212% in another (Watten 2 P.51) but these responses might have been due to increased availability of N, as the N levels are only 1.45% and 1.52% respectively. Ingestadt (1959), on the results of water-culture work with Norway spruce seedlings has suggested a value of 0.2% as the

Fig. 1. Springwell 4/60: Relationships between tree heights (in metres) and the N, P, K and Ca contents (as % dry wt.) of needles from leading shoots.
optimum for P. In the present investigation the mean value for Site 4/60 was 0.158% and for Site 5/60 it was 0.125%, with maximum values of more than 0.3% and 0.2% respectively, so the height range over which P is limiting current growth on these sites remains problematical. It is of some interest to note that the smallest trees on Site 4/60, e.g. those below 300 cms. (10 ft.) tall, and almost confined to vegetation type 'F', have rather higher P levels than would be expected from the nature of the overall relationship between tree height and P for the site. This may well be an indication of the persistence of the effect of the P given at the time of planting in trees the growth of which has been greatly retarded by some other deficiency or other deficiencies.

Potassium—Although there is a significant linear component in the

![Springwell 4/60](image-url)

Fig. 2. Springwell 4/60: Relationships between tree heights (in metres) and the Mg, Na, and Mn contents (as % dry wt.) of needles from leading shoots.
relationship between needle K and tree height, considered on the data as a whole \((r = .553\) with \(P\) better than .001), it is clear that the relationship between these two variables is different in the two halves of the tree height range. If the taller 20 trees, i.e. above 600 cms. (20 ft.) are considered alone the relationship is negative, with \(r = -.424\) and \(P\) approximately .05, but if the 20 smaller trees are considered alone the relationship is more strongly linear and positive, with \(r = .785\) and \(P\) better than .001. Few estimates for optimum K content of Sitka spruce needles have been made. Leyton (1957) has suggested an optimum value of 1.5 for the N/K ratio. For the optimum

![Graph](image-url)
of 1.5% N indicated by the same experiment this means a K optimum of 1.0%. Ingestadt (1959) suggests a value for Norway spruce of 0.9%. The strongly linear positive relationship between K% and tree height over the lower half of the height range and the occurrence within this range of K contents less than 1.0% only in trees of less than 500 cms. (16 ft. 6 ins.) tall strongly suggests that K is limiting growth on this site for the trees which have not yet closed canopy and thus eliminated the bog vegetation beneath them. This is a condition which might have been anticipated from our knowledge of the distribution of K in the vegetation and peat of unplanted sites (Parker 1962). Those methods of diagnosing nutrient deficiencies which rely on demonstrating linear relationships between the nutrient level and growth assume relative constancy of soil fertility, at least between the time of

Fig. 4. Springwell 5/60: Relationships between tree heights (in metres) and the Mg, Na, and Mn contents (as dry wt.) of needles from leading shoots.
planting and of sampling. For peatland plantations of more than a few years old this is not justified. The negative relationship shown here by the larger trees and the relatively low levels of K (0.8% and less) in the foliage of a few of the largest trees, are surely due to the failure of the faster-growing trees to obtain adequate supplies of K after exhausting those concentrated in the living bog vegetation and surface peat (Binns 1962). Further and stronger evidence of the depletion of peat nutrients will be presented later in this paper. The values for K content on Site 5/60 give no significant indication of the existence of a similar situation on that site.

Calcium—On site 4/60 there is a significant negative relationship between tree height and needle Ca content, with r = .429 and P about .01. This, considered alone might suggest that the concentrations of Ca are supra-optimal throughout and that the growth of the smaller trees in particular is retarded by high Ca levels. The significance of different Ca levels in Norway spruce needles has recently been discussed by Ingestadt (1959). There is no well-defined optimum for this quantity but it would appear that maximum growth of the spruce is possible with foliage values of below 0.1% Ca. In the present investigation even the lowest values are greater than 0.1% so Ca deficiency appears unlikely even for the largest trees. Again, there is no well-defined upper level beyond which Ca is clearly toxic so it is not possible to say on the basis of existing evidence whether the Ca levels approaching 1.0%, recorded for some of the smallest trees, are the cause of their slow growth or the result of it. The Ca values recorded for site 5/60 range from just above 0.4% to almost 1.0% and although apparently supra-optimal their distribution with tree height does not suggest a negative relationship.

Magnesium—The results for Site 4/60 suggest the existence of a negative relationship between foliage Mg and tree height but the probability level of the correlation coefficient does not reach 0.1. Ingestadt (1959) suggests that the optimum concentration of Mg for spruce foliage is about 1.0%. Since all the values recorded for Site 4/60 and all but one on Site 5/60 lie above 0.9% a deficiency of this element seems unlikely. In addition to the trees grown in culture solutions with the highest concentration of Mg used (45 p.p.m.), Ingestadt found Mg levels in the foliage exceeding 0.2% only for trees supplied with the two lowest concentrations of K. It seems possible then that the supra-normal levels of Mg found here (approaching 2% and above) are the result of K deficiency. This suggestion is consistent with the fact that there is no relationship between tree height and Mg% for site 5/60.

Sodium and Manganese—The values for the Na content of the needles taken from both sites mostly lie below 0.3% but those for a few of the taller trees on each site are several times greater. Binns reports similar results (Binns 1959) and suggests that the much higher figures result from the presence of atmospheric NaCl intercepted by
the tops of the taller trees. Since the two sites described here lie only about seven miles from the sea this explanation may also apply here. Most of the Mn values for the two sites lie between 0.02% and 0.10% with no relationship between concentration and tree height. A small number of trees have values greatly exceeding 0.10% but the distribution of these values does not suggest their cause.

When more than one element shows a simple linear regression between its concentration in the plant and plant growth it is not safe to assume that the different elements which show his kind of relationship are acting independently. For example, it would not be safe, on the evidence of simple regression alone, to conclude that tree growth on Site 4/60 was limited simultaneously by deficiencies of N, P, and K and by excess of Ca and Mg. It is possible, and indeed probable, that the variation in one element is the result of variation in one or more of the others rather than a separate cause in itself. Leyton, who obtained significant positive correlations between growth of young Japanese larch and percentages of N, P, K, and Ca in the foliage (Leyton 1956) submitted his results to multiple regression analysis and wrote "... from the analysis of the multiple regression of height on these nutrient factors, it was found that only N, and to a lesser extent K, made significant contributions to the regression and that the apparent relation of growth to P and Ca arose out of significant internal relations between these and the significant nutrient factors." (Leyton 1957a p 40). Leyton was later able to obtain confirmation for his conclusions by means of fertilizer trials (Leyton 1957b). In the face of this a conclusion that P is limiting growth on the sites described here, in the absence of the results of multiple regression analysis, would be suspect. The negative correlations between Ca and Mg contents of the foliage and tree height might be accounted for in terms of simple dilution or as resulting from the deficiency of K, but the positive correlation between the values for N and for P (4/60 r = .785 and 5/60 r = .735) is quite another matter. No direct evidence of an internal process which would account for this relationship in spruce has been brought forward. Ingestadt (1960) has shown a 50% increase in P accompanying a 300% increase in N with Scots pine but Norway spruce (Ingestadt 1959) showed no sign of this effect. Van Goor (1953) has found evidence of a marked antagonism between N and P with Japanese larch seedlings. Leyton's own results (1957b) with Japanese larch show that with this species fertilization with N reduces the P uptake and in discussing this he allows of the possibility that the interaction takes place outside the tree. The results of Tamm (1956) with Norway spruce and our own with Sitka spruce (Parker 1962) show this same effect. The linear relationship between tree height and the P content of the foliage of the leading shoot is real enough and should be susceptible to a casual explanation. In the absence of independent experimental evidence that increased availability of N, resulting in increased N content of the foliage, by some internal mechanism also
raises the P content, the most likely explanation of the results reported here would seem to be that the prime cause of the parallel variation lies outside the trees. Thus, the positive correlation between the concentrations of these two elements in the foliage of the trees on these peatland sites would seem to be due to the variation in an external factor which affects similarly the availability of N and P. The most likely factor is surely the rate of organic matter decomposition in the peat soils.

**Peat Analysis.**

The results presented so far have been relevant to the first object of this investigation. They have confirmed the existence of N deficiency and indicated also the existence of deficiencies in both P and K, but they have failed to show any marked differences between the sites which would account for the falling growth rate of the larger trees on Site 5/60. Evidence for this comes from an examination of the relationship between tree height and the present nutrient content of the peat in which they are rooted. (Figs. 5 & 6).

**Nitrogen**—For site 4/60 there is a strong positive relationship between peat N and tree height (Omitting the data for the two trees on 9 ins. peat, the peat samples for which were found to contain a high % of insoluble mineral material, $r = .75$ with $P$ better than .001). The values for the smaller trees lie at about 2% N and for the larger trees at about 2.5% N. The values for Site 5/60 show greater variation overall, there is some indication of a negative relationship but this does not reach significance. These results show however that the smallest trees on Site 5/60 are growing on peat with a very similar N content to that beneath the smallest trees on the other site, but that most of the larger trees are growing on peat with an N content considerably less than this.

**Phosphorous**—For Site 4/60 there is a strong positive relationship between peat P and tree height ($r = .75$ with $P$ better than .001). The values for the smaller trees lie at about 0.075% P and for the largest they rise to twice this value. The distribution of values for Site 5/60 suggests a negative relationship but the significance level is again not reached. The peat beneath the smallest trees on both sites shows similar concentrations of P but the P contents of the peats taken from beneath the taller trees on the two sites differ widely.

**Potassium**—As for N and P the relationship between the K content of the peat and tree height on Site 4/60 is positive and significant (omitting the data for the two trees also omitted from the N calculations $r = .37$ with $P$ about .02). The K values for Site 5/60 vary little about their mean of 0.030% and show no relationship with height. Many of the smaller trees on Site 4/60 are growing on peat with about this K content but the mean value of K for the site is 0.044%.

**Calcium**—The relationship of the peat Ca with tree height on Site
4/60, like that of the foliage Ca, is negative ($r = -0.56$ with $P$ better than .001). On Site 5/60 there is no regular relationship between these

---

**Fig. 5.** Springwell 4/60 and 5/60: Relationships between tree heights (in metres) and the N and P contents of the peat on which they are growing. (Points 4/60, Circles 5/60). Points ringed by broken line not included in calculations.
Factors Limiting Tree Growth on Peat Soils

quantities although the absolute values for peat Ca are generally much higher.

The positive relationships shown to exist for Site 4/60, between the tree heights and the amounts of N, P, and K in the peat on which they are growing, show that the original pattern of soil fertility on

SPRINGWELL 4/60 & 5/60

\[
y = 93.1x + 117 \\
r = 0.37
\]

\[
y = 933 - 1030x \\
r = -0.56
\]

Fig. 6. Springwell 4/60 and 5/60: Relationships between tree heights (in metres) and the K and Ca contents of the peat on which they are growing. Points ringed by broken line not included in calculations.
the site has not been markerly affected by tree growth. Those parts of
the site which before planting were richest in N, P, and K have grown
the largest trees and are still richest in these elements. The situation
on Site 5/60 is quite different. The positive relationship which must
formerly have existed between tree growth rate and the nutrient (N, P,
and K) content of the underlying peat has gone and there are now
indications even of a negative relationship. The largest trees here,
although currently bearing foliage relatively rich in these nutrients, are
growing on peat containing as little of these elements as the least fertile
parts of the other site, or less of them. This must surely be an indica-
tion of the extent to which the peat beneath the trees has been depleted.
The other marked difference between the two sites is in the Ca content
of their peats. Although the values for Site 5/60 are much greater than
those for the other site the importance of this difference in relation to
the fertility of the site and to its change with time is far from clear.

Discussion.

The analysis of the needles from the leading shoots of the trees on
these two sites provided a good deal of information concerning the
present nutrient status of the trees and in particular provided the basis
for the diagnosis of several nutrient deficiencies affecting growth. But
it failed to reveal the major differences between the two sites in terms
of nutrient content of the peat beneath the larger trees. These only
came to light when the nutrient content of the peat itself was examined.
There are three hypotheses which would account for this. It is possible
that despite the low nutrient levels indicated by our analysis for Site
5/60 the trees are not affected by nutrient deficiency. Either nutrient
supply is maintained at these levels or our technique, by excluding the
needle litter and the actual surface peat, has failed to reflect the
effective nutrient level of the soil. The third possibility is that although
nutrient uptake is now inadequate to maintain past growth rates this
deficiency is not significantly reflected in the nutrient content of the
current foliage. In view of the fall in growth rate of these trees the
third hypothesis seems the most likely, especially since the elements
likely to be deficient are all known to be mobile within the tree. This
hypothesis is consistent too with the history of heavy needle cast.

Two points of practical importance emerge. It is clear that foliage
analysis alone should not be relied upon for the diagnosis of nutrient
deficiencies in stands with a falling growth rate, and even if the growth
rate is not falling foliage analysis cannot be expected to indicate
incipient deficiencies resulting from the depletion of the soil by tree
growth. It would appear that although more laborious the combined
approach by means of both foliage and soil analyses is capable of
providing a clearer understanding of the nutrient relations of the stand
and of indicating more reliably the soil amendments required.

Forest soil development has apparently proceeded differently on
the two sites investigated and we might examine the available data for
the cause of this difference. The plantation on Site 5/60 is 6 years older than that on Site 4/60 and it might be that the difference in development is more apparent than real, i.e. that the stands are following very similar courses of development but that Site 5/60 has developed further. There is some evidence to support this in the fall in growth rate of the few largest trees on Site 4/60 (Plate 1), and for one nutrient element at least in the negative relationship between the height and foliage K content of the larger trees, and the low level of significance of the relationship between tree height and peat K on this site. These sites also differ greatly in the Ca content of their peats and it is possible that the higher Ca content of the peat of Site 5/60 has been one of the factors determining the rate of microbial activity and of peat decomposition on this site. (There is also a small but highly significant difference in mean peat pH between the two sites; Site 4/60 pH 3.20 and Site 5/60 pH 3.59 with $t = 5.5$ and $P$ better than .001).

Prolonged microbial action on fibrous organic matter with a wide C/N ratio normally results in the formation of a more amorphous residue with lower C/N and C/P ratios. It is of interest to note that prolonged microbial activity combined with the absorptive action of the roots of the larger trees on Site 5/60 has resulted, after a period of about 30 years, in the formation of a highly colloidal residue which contains percentages of N, P, and K (per unit dry weight) no higher than the material from which it was formed, and probably less.

Acknowledgments.

The very numerous chemical analyses in this investigation were carried out by Mr. I. T. Hamilton and I gratefully acknowledge his invaluable assistance. The sampling and field measurement was done by a team which included several of my colleagues and several members of the staff of the N.I. Forestry Division; thanks are due to those who took part. Thanks are also due to Mr. W. J. Bryan, the forester at Springwell Forest, who first drew my attention to the sites investigated, and to the Chief Forest Officer for N.I. (Mr. K. F. Parkin) who gave permission for the sample trees to be felled. This investigation forms part of the work carried out by staff and students of the Botany Department, Q.U.B. which has been supported financially by the Forestry Department of the N.I. Ministry of Agriculture.

Summary.

The application of the technique of foliage analysis to two representative peatland plantations in Northern Ireland has permitted the firm diagnosis of N deficiencies and the less firm diagnosis of deficiencies in P and K. It is suggested that the correlation between the N and P contents of the tree foliage and between these and tree height, over the whole tree height range, arises because the availability of these two elements is determined by the rate of microbial decomposition of
organic matter in the peat soil, and that the rate of this decomposition is the main factor limiting tree growth on these sites. The results for K are consistent with the hypothesis that at the time of planting a high proportion of the site K is contained within the living bog vegetation. The analysis of the peat soils has indicated the marked depletion of peat nutrients (N, P, and K) by tree growth associated with a current fall in growth rate of the larger trees on one site. The peat on this site has a much higher Ca content; the possible significance of this is discussed.

References.


Alder on Peatland and its role in Afforestation

D. N. McVEAN,

The Nature Conservancy, Aviemore, Scotland.

The only experimental plantings of alder on acid peat which I have come across have been on the Forestry Commission experimental forest at Inchnacardoch, near Fort Augustus in the Great Glen of Scotland. This is a fairly extensive area of blanket peat mostly over one metre in depth and lying around 150-300 metres above sea level. The alders were planted about 30 years ago, the species used being *A. glutinosa*, *A. incana*, *A. viridis* and *A. oregona*. None of these was a great success; all failed without the application of a few ounces of basic slag, and when I saw them in 1953 the best trees, *A. incana*, were those which had been given a top dressing of ditch cleanings from the A1 horizon in addition to slag; these had reached a height of four metres. The best *A. glutinosa* was only 1-2 metres high with sparse foliage and extensive die-back and the two other species had failed completely even where slag had been applied.

At the present day I think I am right in saying that alder, mostly *incana* and Oregon alder, is used for amenity purposes in small flushed areas along roadsides, where it forms thickets a few metres tall.

Between 1949 and 1952 I had gone into the ecology of *A. glutinosa* in some detail and it seemed to me that one should be able to do better than this. I therefore included alder in a programme for investigating the possibilities of establishing native trees by direct sowing on shallow blanket peat at Beinn Eighe in Ross-shire. The results of the alder trials have been published in the Journal of Ecology as Part VII of a series on the ecology of the species (McVean, 1959).