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GROWTH OF A SITKA SPRUCE PLANTATION: SPATIAL DISTRIBUTION AND SEASONAL FLUCTUATIONS OF LENGTHS, WEIGHTS AND CARBOHYDRATE CONCENTRATIONS OF FINE ROOTS

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SUMMARY

As part of an investigation into the primary production of a forest the activity of fine roots was estimated by taking weekly soil cores from 24 May to 27 September in the 11 year of growth of a plantation of *Picea sitchensis*. Distinct maxima were found in 1) starch and soluble carbohydrate concentration in the root, mid-June, 2) root weight/soil volume, early July, and 3) root length/soil volume, late July with a second maximum in early September. However, root concentrations in the soil were the same at the end as at the start of the period and it is suggested that the fine root system of the forest had reached a dynamic equilibrium.

The growth of the fine root system, from mid-May to late July is described as a continuous process; there is no indication that root activity ceases during the period of shoot elongation.

Two populations of fine roots were found in the forest. In the surface horizons of the soil roots classified with a diameter < 0.5 mm have a greater mean diameter, more root tips per unit length and are present in greater concentrations than in the peat and mineral soil below. Higher concentrations of root were found both in regions of soil which had been disturbed by preplanting cultivation and in regions close to the tree trunk.

INTRODUCTION

To understand the processes in the edaphic environment that contribute to, and influence primary production accurate estimates of weights and lengths of fine roots are essential.

These organs frequently have a short life and Coleman[3] has stressed the need to measure fluctuations with a better than annual sampling frequency if reliable estimates are to be made of root growth and mortality and so of organic matter input to decomposer cycles. Newman[16] illustrated the importance of accurate estimates of root length per unit of ground surface area, L_A. An underestimate will over emphasise the role of the rhizosphere resistance in water movement through the plant compared with that of the whole plant resistance.

Laboratory studies[25] have shown that conifer root growth can be influenced by many environmental factors and not unexpectedly considerable variation has been found in the amounts of fine roots in different forests. In some instances this has been correlated with obvious biological or environmental factors. Kalela[8] demonstrated a trend of increasing root amount with age of forest; Paavilainen[17] showed the large influence which nutrient supply may have on root amount in forests. There are many indications that root growth in conifers can be distinctly periodic. In North Temperate regions increment appears to be confined to the summer months although there are conflicting reports as to whether there are one or more periods of activity[13] and also how this periodicity is related to the supply of photosynthate[9 12].

Variation in root amount has not always been found to be related to biological or environmental gradients. The hypothesis that spatial variation in the amount of fine root in a forest would be significant and would have functional importance related to environmental variation has been implicit in a number of studies but has not been verified. Large variation within stands is a frequent finding of forest root studies particularly when root weight per unit of ground surface area, W_A, is estimated. Bowen[2] excavated duplicate soil monoliths in three plantations of *Pinus radiata* D. Don of the same age and fertilizer regime but at different positions on a soil catena and found as much variation within sites as between them. Using a coring technique Reynolds[21] found percentage standard errors of 30 per cent for W_A and between 15 and 20 per cent for L_A in a 35 yr stand of *Pseudotsuga taxifolia* (Poir.) Britt. Despite such large variation he concluded that the amount of root in a core could not be related to core position relative to the edge of crowns or tree trunks or with any obvious environmental gradient within the stand. One exception was that high concentrations of roots were found near to tree trunks with high stem flow rates. A lack of correlation between the distance of a sample position from a tree trunk and the total amount of root it contains has been found by others[15 23] although such a gradient has been found when the roots of an individual tree were traced[10].

Root amount in a coniferous forest may vary with age, with season and certainly with some environmental conditions. Spatial variation in the horizontal plane is complex and not well understood though in the vertical plane it seems more consistent. Concentrations are greatest near to the surface though on mineral soil the humous layer has been shown to have lower concentrations than the topmost inorganic layer[6] and vertical distribution may be influenced by cultivation before planting[28].

The object of this work was to quantify the distribution and growth activity of fine roots in a young plantation during a period when parallel measurements were made of above ground production and fluctuations in the above ground environment; these latter investigations will be reported in detail elsewhere in the literature. In measuring root activity we wished to establish the patterns, if any, of spatial and temporal variation in W_A, L_A and soluble carbohydrate and starch concentrations as a necessary part in a programme to i) compare the growth of different meristems of the tree, and ii) investigate the effects which complex ploughing and planting techniques used in forest establishment may have on root function.

Because window techniques give inconsistent estimates of root activity[22] and because estimates of W_A and carbohydrate concentrations were also required a coring technique was selected. This was operated with a stratified sampling system adapted to the spatial variation in soil structure found in the cultivated plantation.

SITE

A forest laboratory was established in the Rivox section of the Forestry Commission's Greskine Forest (Nat. Grid Ref. NT 016045) during 1972. The area is classified in the hyperoceanic subsection of the extremely humid southern boreal and lower oroboreal thermal and moisture climatic type[1], annual rainfall *c.* 1800 mm.

Nine ha were designated as a study area for forest ecology and production processes. The area is on a uniform south facing slope of 6°, 355 m above sea level.

CROP ESTABLISHMENT

Prior to planting the vegetation was predominantly *Molinia caerulae* (L.) Moench with occasional patches of *Vaccinium myrtillus* L. growing on blanket peat which was 0.25–1.50 m deep according to topography (Table 1). Following the Forestry Commission standard practice for sites which are typically waterlogged for much of the year[19] the land was ploughed at 1.5 m intervals with furrows running down the slope. A single mouldboard Cuthbertson plough[26] was used which threw up a ribbon of peat and inverted turf (Fig. 1), with a small amount of mineral soil where the plough penetrated the A horizon. Drains 0.5 m deep were cut across the direction of ploughing at intervals of *c*, 30 m.

The area was planted in 1962 with a British Columbian Coastal provenance of *Picea sitchensis* (Bong.) Carr. Failed plants were replaced in 1964. Seedlings were spaced at 1.5 m intervals along the edge of the inverted ribbon nearest to the ditch with their roots planted into the turf sandwich (Fig. 1).

TABLE 1

Soil description for the experimental site, Rivox block, Greskine Forest, Dumfriesshire, Scotland

Series:	Dochroyle
Association:	Ettrick
Land Use Capability:	5WC
Parent Material:	Till derived from Ordovician and Silurian greywackes and shales
Classification:	Peaty Gley

Horizons								
	Length (cms)	Colour	Consistence	Texture	Structure	Stones	Mottles	Orga conte
L & F	31–26							
0	26–0	Black (5YR 2/1)	Amorphous peat					
$A_{2}g$	0–11	Dark greyish brown (10YR 4/2)	Slightly plastic	Fine sandy loam	Moderate, medium angular and sub-angular blocky	Frequent rounded and sub-rounded	Frequent and brown diffuse staining	Low
A/Bg	11–23	Very dark greyish brown (10YR 3/2)	Slightly plastic Gleyed	Fine sandy loam	Moderate, medium angular and sub-angular blocky	Frequent rounded and sub-rounded	Occasional ochreous mottles and diffuse brown staining	Low
$B_{3}g$	23–37	Dark greyish brown (10YR 4/2) and brown (10YR 4/3)	Plastic strongly Gleyed	Fine sandy loam	Massive	Abundant	none	Low
Cg	37+	Dark greyish brown (10YR 4/2)	Plastic strongly Gleyed	Fine sandy loam	Massive	Abundant with occasional boulder	none	Low

Figures in brackets refer to Munsell's colour reference charts.

By the time this investigation was made the trees had closed canopy, none of the original flora remained alive and the ground was covered with a layer of needles.

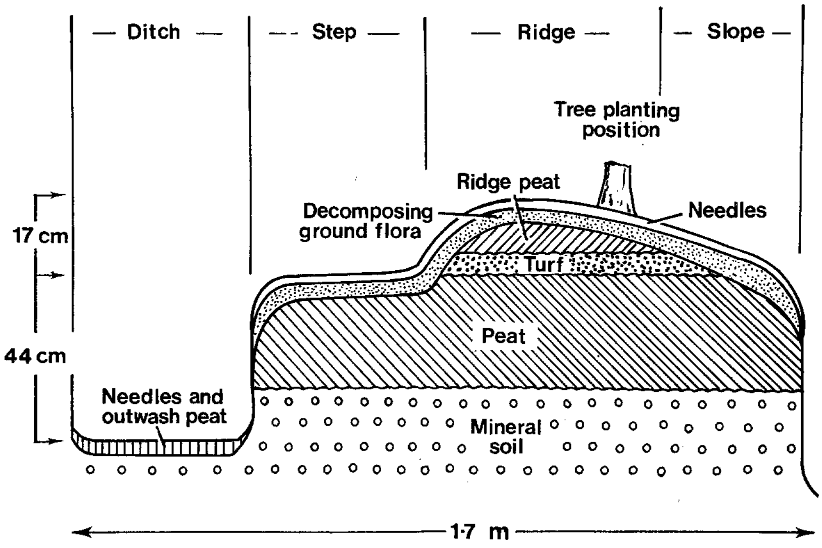

Fig 1. Schematic arrangement of soil horizons at the experimental site, Greskine Forest, Dumfriesshire, Scotland.

METHODS

Root sampling

Because preliminary investigations indicated that very few fine roots penetrated the A horizons the corer was specifically designed to cut through organic horizons (Fig. 2). It is a narrow cylinder with a sharp cutting edge and was hammered into position with an electric hammer (Kango Electric Hammers Ltd., London) fitted with a concrete tamping bit from which the rubber grommet had been removed. The bit then formed a closed cylinder giving a good transference of power. This arrangement overcame three problems of particular importance at this site: 1) the tendency of large diameter corers to 'bounce' in the peat particularly against thick roots, 2) the tendency of the core, on occasion to fall out of a large diameter corer during extraction perhaps because of the dry nature of the peat combined with the loosening of the peat structure due to 'bounce', 3) the restricted access in the thicket stage plantation where closely interwoven branches prohibit the free movement to manually hammer a corer.

An intact row of trees separated from drains or timber extraction routes by at least two rows was selected and from within it a 10 m × 1.7 m plot was marked out. This included 6 trees of the row and extended across the planting unit of ditch, slope, ridge and step (Fig. 1).

Each week from 24 May to 27 September 1973 four transects were made across the row of trees; an incomplete sample was obtained for 17 May. Four cores made up a transect one placed centrally in each of the zones, ditch, slope,

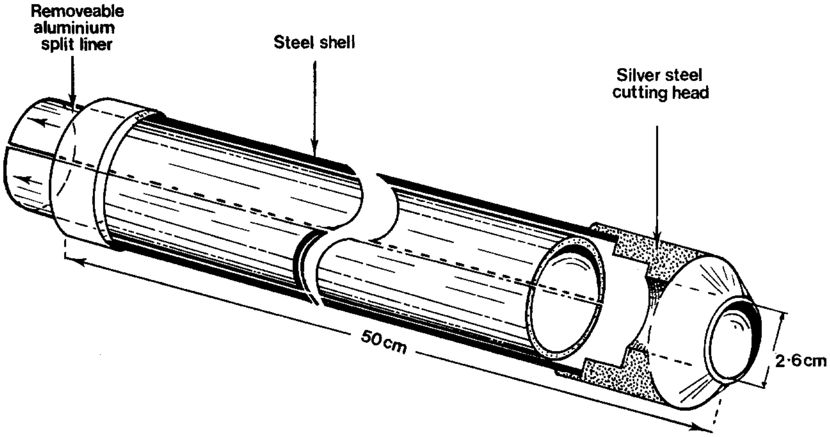

Fig. 2. Soil sample corer.

ridge and step, Fig. 1, so that a weekly sample comprised 16 cores in all. A stratified random system was designed for the placement of each transect across the planting unit. An arbitrary decision was taken that no core should be extracted closer than 0.1 m to the site of any other extraction and the 10 m length of the plot was marked off at 0.1 m intervals. These points were classified into quadrant intervals between the trees. One quadrant included the tree, one was midway between trees and two were intermediate zones, one on each side of midway. Each quadrant typically contained 3 or 4 possible transect positions and one sample transect was made in a zone of each type each week with the exact position being selected by random numbers. Approximately 1 per cent of the total volume of material was removed from the plot during the investigation.

The corer was driven in to its full extent unless stopped by a very large root or the occasional stone when another attempt was made. In the majority of cases penetration to the mineral soil was achieved. Some cores with incomplete horizon complements resulted from the premature arrestment of the corer but this was not a serious problem.

After extraction the cores were separated into their constituent horizons, the lengths of each were measured, and the samples were immersed in liquid nitrogen and taken to storage in a deep freeze. The samples were washed manually over 500 μ sieves in a gentle stream of water, care being taken to avoid both damaging the root and forcing small fragments through the sieves. Inspection of the contents of the sink traps showed that sample loss was minimal. After washing, the contents of the sieves were transferred to water filled trays where the roots were separated from the remaining debris. Dead roots, recognised as those being black and shrivelled, were discarded at this stage. Live roots were categorised as <0.5, 0.5–<1.0, 1.0–<2.0 and + 2.0 mm in diameter. In the following text these categories will be referenced as <0.5, 0.5–1.0, 1.0–2.0 and + 2.0 respectively.

Length was measured by arranging roots linearly in a glass petri dish over graph paper. Root tips of several samples were enumerated at this stage. The samples were dried at 70°C to a constant weight.

Frequency distributions of root diameters were made on samples independent of the main sequence. Roots were extracted and washed in the normal way and sub-samples were placed in a petri dish and examined with a binocular microscope. The diameters measured, 200 per sub-sample, were selected by random manipulation of the microscope stage and the graticule eyepiece.

Chemical analyses

Starch was extracted from root samples with perchloric acid and measured colorimetrically after forming the blue complex with iodine[18]. Starch was used as standard and sample extracts and standards were treated similarly at the colouring up stage. Soluble carbohydrates were measured, following water extraction, with anthrone reagent as the colouring agent and glucose as the standard[5].

Soil samples were air dried and total N, P and K were estimated following a modified Kjeldahl digest[4]; the NH_4-ion and P were determined colorimetrically, K by flame emission. Exchangeable Ca, Mg and K were estimated following extraction in neutral *N* NH_4 acetate; Ca and Mg by atomic absorption and K by flame emission.

ANALYSIS

It is implicit in this work that there is a distinct population of fine' roots *i.e.* that a classification can be made of roots of small diameter. Less than 6 per cent of the root in the cores by length was of diameter >1.0 mm. The frequency distribution of root diameters up to a diameter of 1.0 mm is shown in Fig. 3 and this supports a classification of 'fine' roots as those of less than 1.0 mm diameter. The intermediate classifications of <0.5 and 0.5–1.0 are also used in the presentation of results in an attempt to interpret some aspects of the population dynamics of 'fine' roots.

Some 90 per cent of the total length of root contained in the cores was <0.5 and in the absence of automatic measuring devices it was necessary to evolve a technique for estimating the length of these smallest diameter roots by taking sub-samples. The total length of roots with diameters 0.5 mm and above was measured directly throughout.

A direct and total measurement of root length <0.5 was made for each soil horizon in each of the 16 cores for the samples taken on 24 May, 21 June, 2 August and 13 September. The data were examined for the feasibility of developing a system of regression equations of root length, y, on root weight, x, $y = bx$. This showed that roots from the needle, decomposition and turf horizons, Group I, were distinctly heavier per unit length of root than those from the peat and mineral horizons, Group II, and the data for each weekly sample was most effectively expressed by two separate regressions. There were also significant differences between these four samples for the b values of both Groups, see below, and for each remaining sample separate estimates

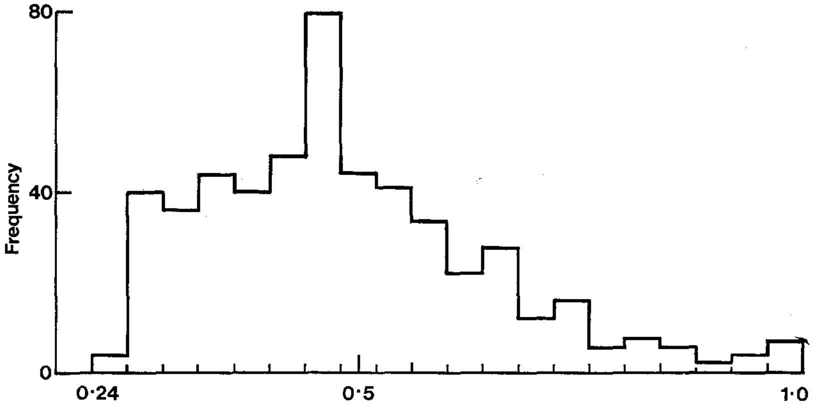

Fig. 3. Frequency distribution of the diameters of fine roots of *P. sitchensis* up to 1 mm diameter growing in the needle, decomposition and turf soil horizons, Group I.

of b were made for the two Groups by measuring the length and weight of sub-samples of 300–500 mm from each horizon. Total length of root<0.5 was estimated by applying this parameter to root weights.

RESULTS

Spatial variation in the concentration and total amount of root

Along the row of trees the greatest concentrations of fine roots, < 0.5 *i.e.* root length/total extracted soil volume, were adjacent to trees; smallest concentrations, some 33 per cent lower, occurred midway between trees (Table 2). In the intermediate zones there was a greater concentration of roots downhill on the south side of the tree than uphill.

Across the row the greatest concentrations were found in the ridge and slope sections. These were some 40 per cent higher than in the step region and 60 per cent higher than in the ditch (Table 3). It is suggested that these differences are not attributable to an increase in distance from the base of the tree, but reflect the different categories of soil horizon at each point on the planting unit (Fig. 4). The order of highest concentrations was the decomposition layer, the needle layer, the upturned peat and the inverted turf sandwich; the latter two are specific to the ridge and slope positions. The concentration of roots was substantially lower in the undisturbed peat, and

TABLE 2

(a) Length of root, <0.5 mm diameter per volume of soil at different positions along the row of trees. Mean values for all cores taken 17 May–27 September
(b) Matrix of significance of differences between the positions

	Zone midway between trees	Intermediate zone upslope, N, of tree	Zone around tree	Intermediate zone downslope, S, of tree
(a) Mean value mm/cm^3	18.0	20.4	27.7	24.8
(b) Matrix of significance of differences				
Intermediate zone upslope, N, of tree	NSD			
Zone around tree	***	*		
Intermediate zone downslope, S, of tree	**	*	NSD	

F = 7.14, NSD = No significant difference, * $p = 0.05$, ** $p = 0.01$, *** $p = 0.001$.

in the upper mineral horizons roots were absent from many samples. The decomposition layer of the ditch had lower concentrations than other decomposition layers, it was composed of outwash peat, needles and decaying *Polytrichum commune* Hedw. which had colonised the ditch surface prior to complete canopy closure.

From estimates of surface area and thickness of each of the soil horizons their contribution to the total length of fine root in the forest

TABLE 3

(a) Length of roots, <0.5 mm diameter per volume of soil at different positions across the planting unit. Mean values for all cores taken 17 May–27 September
(b) Matrix of significance of differences between the positions

	Ditch	Step	Ridge	Slope
(a) Mean value, mm/cm^3	11.5	16.9	28.2	28.4
(b) Matrix of significance of differences				
Step	**			
Ridge	***	***		
Slope	***	***	NSD	

F = 38.96, NSD = no significant difference, ** $p = 0.01$, *** $p = 0.001$.

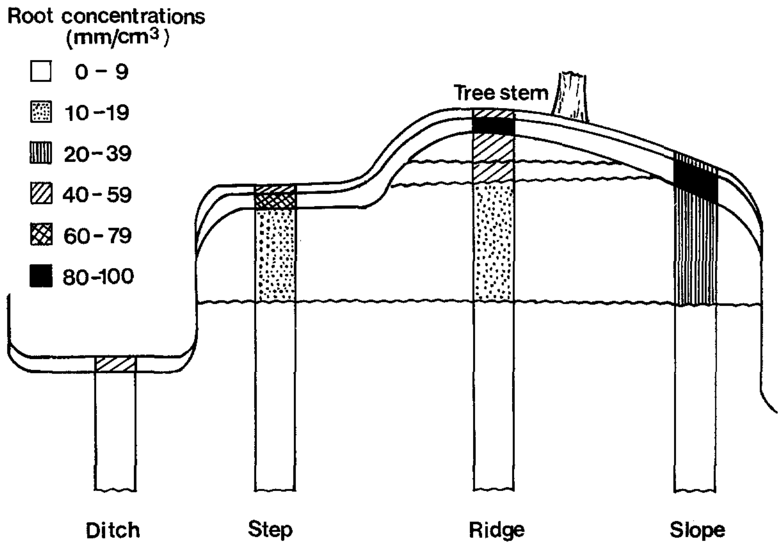

Fig. 4. Mean concentrations, 24 May–27 September, of fine roots < 0.5 mm diameter of *P. sitchensis* in different soil horizons in an 11th year plantation.

TABLE 4

Length of roots of <0.5 mm diameter in different soil horizons of an 11 yr plantation of Sitka spruce. Values in km/ha

Soil horizon	Position across the planting unit			
	Ditch	Step	Ridge	Slope
Needles	—	1007	1478	410
Decomposition	3710	5361	9024	3806
Ridge peat	—	—	14380	—
Turf	—	—	7476	—
Undisturbed peat	—	5770	7864	4796
Mineral	1100	577	486	290

Total length of roots = 67500 km/ha

— indicates a soil horizon not present in that position across the planting unit.

was calculated (Table 4). 70 per cent of the total length occurs within the needle, decomposition, turf and upturned peat horizons. Three quarters of this is in the ridge where the upturned sod was deposited during the pre-planting cultivation; the maximum depth of this section is 0.2 m. The concentration of roots in the upturned peat of the ridge is greater, 2.5:1.0 than that of the undisturbed peat immediately below it.

The ratio of root length:root weight

The weekly values of b (Fig. 5b), for roots < 0.5 demonstrate consistent variation between the two Groups of horizons. The values

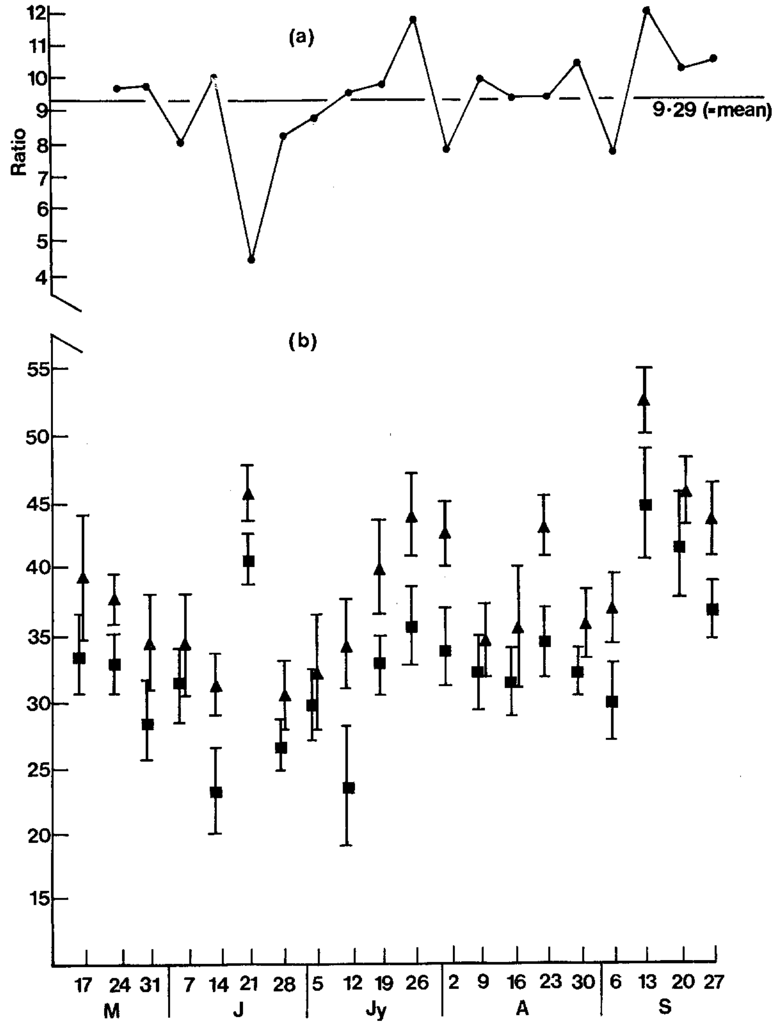

Fig. 5. Changes in the structure of the population of fine roots 24 May–27 September in an 11th year plantation of *P. sitchensis*; (a) ratio of length of root < 0.5 mm diameter: length of root 0.5–1.0 mm diameter, (b) length: weight ratios of roots < 0.5 mm diameter growing in needle, decomposition and turf horizons, ■, Group I, and peat and mineral horizons, ▲, Group II.

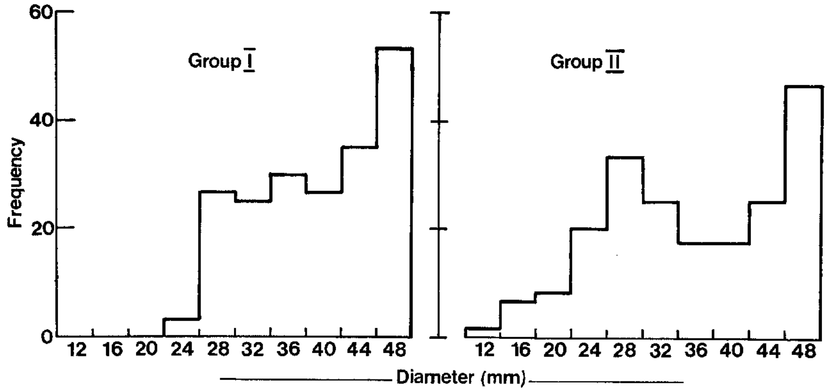

Fig. 6. Frequency distributions of the diameters of root < 0.5 mm diameter in two sets of soil horizons; Group I, needles, decomposition and turf; Group II, peat and mineral.

for Group I are always lower than those for Group II, *i.e.* the roots of Group I are heavier per unit length than those of Group II. An explanation for this is that Group II roots have a higher proportion of thinner roots within the arbitrary classification of < 0.5 mm (Fig. 6). The data from Fig. 6 translated into root volume for unit root length and expressed as a ratio is 1.15:1.0 Group I:Group II. This lies within the range of weekly ratios between the two Groups for the values of b; maximum = 1.45, minimum = 1.08, mean = 1.20.

In most instances the week to week variation of b can be seen as part of trends which extend over a number of weeks. The values for 21 June are an exception. This was the first sample to be washed from the soil and the most likely explanation for the large isolated increase in b is that there was mis-classification of roots between categories. The isolated increase in b at this date is parallelled by a very marked but isolated decrease in the ratio of roots in the two classifications < 0.5:0.5–1.0 (Fig. 5a), although the total amount of root in the two categories taken together does not fluctuate greatly about this time, (Fig. 7a). There was a change in personnel after this sample was processed.

The ratio, root length:root weight was calculated for 0.5–1.0 roots; this showed no distinct trends either between soil horizons or over the season.

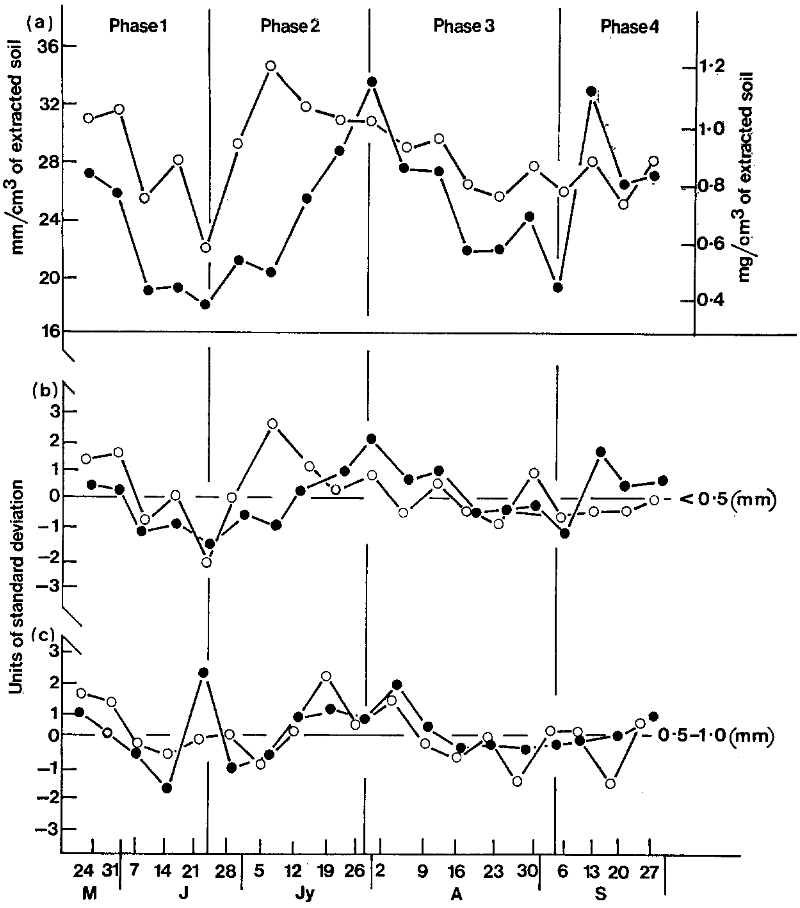

Fig. 7. Changes in the concentration of fine root amount in an 11th year plantation of *P. sitchensis*, (a) lengths ●, and weights o, of roots < 1.0 mm diameter, (b) and (c) Standardised deviations $(x-\bar{x})/s$ of lengths ●, and weights o, of roots < 0.5 and 0.5–1.0 mm diameter respectively.

Seasonal fluctuation in root amount

Fig. 7a shows the weekly values of mean concentration of roots < 1.0 in the 16 extracted cores. Four features are noted; i) over the period of measurement there is no net increase, ii) the major changes in weight/cm^3 and length/cm^3 are not synchronous, iii) change of weight/cm^3 and length/cm^3 take place at different rates, weight shows a rapid increase from 21 June to 5 July and a slow decline from then until the last sample, length has a more gradual increase from 21 June and a faster rate of decrease from its maximum value at 26 July, and iv) there is a second maximum in root length, 13 September, but not in root weight.

Weekly values of concentrations for the two sub-populations are expressed as standardised deviations from the mean values of the 21 weeks (Fig. 7b, < 0.5, Fig. 7c, 0.5–1.0). This technique allows the relative trends in development to be compared without reference to the absolute amount of root. Three features are noted; i) within each sub-population rates of change and time of maximum concentration are different for root length and weight, ii) there are differences in rates of change and times of maxima and minima between the two sub-populations, and iii) presentation as standardized deviations from the mean indicate the difficulty of resolving changes in concentration as 'significant' in the sense of the value at one week being different from the mean value of the series and illustrates the need to consider trends in the development of values.

Root tips

The number of tips/m of root, < 0.5, for Groups I and II were 244, 246 on 24 May; 168, 137 on 21 June; 163, 129 on 2 August and 161, 130 on 13 September. There were always more root tips per unit length in Group I than Group II horizons. The high values before the increase in length of roots suggest that the initials of the new root branching system are formed before extension takes place. The rather constant values after the period of net root extension and when there is a decrease in root amount suggest that whole segments of root die rather than just small extending tips or that new tip production balances tip death.

Seasonal fluctuation in carbohydrate concentration

Concentrations of starch and soluble carbohydrate fluctuated similarly in roots of Group I and II horizons (Figs. 8a and b) although point to point variation in time was greater for the Group II samples. Soluble carbohydrate concentrations were greater than those of starch; the maximum combined proportion of total dry weight was 32 per cent, 0.5–1.0 category, Group I early June. The maximum combined weight for the < 0.5 category was 14 per cent, Group I early June.

The major variations in root length and weight occur in the Group

I horizons and with this in mind the following points are noted on Fig. 8a. Soluble carbohydrate and starch concentrations are similar and fluctuate in a similar way for two of the categories of root 0.5–1.0 and +1.0. The most notable difference between them is the faster rate of decline and lower minimum in soluble carbohydrate for the 0.5–1.0 category over the period late June-early July. In the < 0.5 category the concentrations of both types of carbohydrate are lower and their fluctuations, though similar in pattern to the

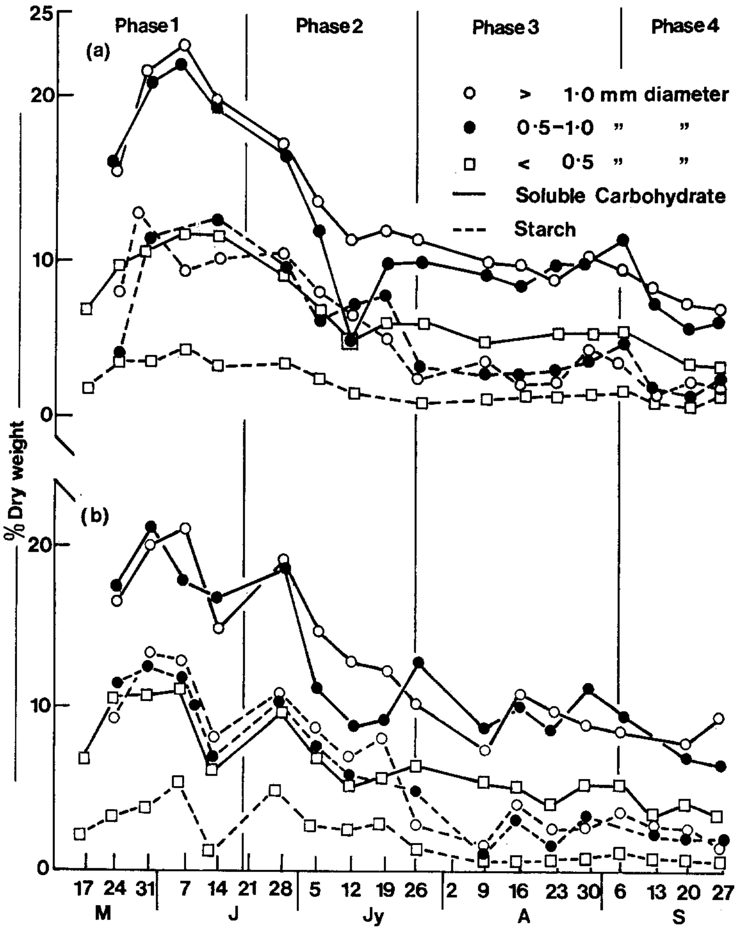

Fig. 8. Carbohydrate content of roots of *P. sitchensis* in an 11th year plantation in (*a*) the needle, decomposition and turf horizons, Group I, and (*b*) peat and mineral horizons, Group II.

thicker roots are less marked. It is suggested that the roots thicker than 0.5 mm act as 'storage' roots and will be described as such below.

THE GROWTH AND DEATH OF FINE ROOTS

It is envisaged that four processes influence the annual course of biomass fluctuations of fine roots; i) extension, ii) secondary thickening, iii) fluctuations of storage materials, and iv) death. These processes have not been measured independently but some indication of their different importance during the summer months can be inferred from the data.

Some of the recorded alterations in fine root amount or structure could be caused by more than one combination of fluctuations in the four processes, *e.g.* simultaneous loss in weight and length of fine roots could be the result of death, it could also be the result of root thickening which removes biomass from a classification as fine root. It is also possible that more than one process may proceed at one time with no net alteration to the amount of fine roots, *e.g.* root death and extension could both proceed at a fast rate. However the fluctuations in root weight and length and in the starch and soluble carbohydrate concentrations are large and sufficiently separate in time to suggest, as a hypothesis, that the development of the fine root system during summer months takes place in four phases during which different processes predominate.

Phase 1 Mid May-mid June. A period of fine root loss and accumulation of carbohydrate in the living root which remains. The formation of root branch initials takes place in the early part of this phase or prior to it. The loss in root weight and length is thought to indicate mortality rather than a period of secondary thickening or redistribution of material because rates of loss are similar for both < 0.5 and 0.5–1.0 categories and it is unlikely that secondary thickening would be so uniform as to effect this. Redistribution of material from the fine roots to other parts of the plant seems unlikely because starch concentration increased in all categories of root. There is an indication that the peak concentration of soluble carbohydrate in the 'storage' roots, 7 June Group I Fig. 8a, precedes that of starch, 14 June 0.5–1.0 and 28 June $+1.0$. This suggests the formation of starch reserves from previously translocated sugars, *i.e.*

that the translocation and starch formation rates are not identical. Maximum concentrations of starch plus soluble carbohydrate occurred 7–14 June for the 'storage' roots. Root tips/root length on 21 June was higher than that for later in the season.

Phase 2 Mid June-late July. There was a major increase in weight of fine root in the soil in the first two weeks of this period and a more gradual increase in root length. The greater part of both increases is due to increases in the < 0.5 category. During this period there was a major decline in both soluble carbohydrate and starch concentrations. This reduction in the 0.5–1.0 roots was greater than that in the $+1.0$; possibly because the 0.5–1.0 roots are 'physiologically closer' to the main site of synthesis of new root, the < 0.5 category.

Phase 3 Late July-late August. There was a maximum in the length of 0.5–1.0 roots at the start of this period which suggests that secondary thickening of the fine roots proceeds longer than extension. Over the whole of this phase there was a decline in both root length, 42 per cent and root weight, 23 per cent. This suggests root death but the decreases are not uniform which may indicate a preferential loss of < 0.5 category or a continuation of the thickening procedure.

Phase 4 Late August-late September. A period of lengthening of the < 0.5 roots with no concomitant increase either in root weight or in the length of 0.5–1.0. There is a small increase in soluble carbohydrate and starch concentrations in the 0.5–1.0 roots preceding and at the time of the extension. There was a less marked increase in these concentrations in the $+1.0$ roots which perhaps underlines the 'physiological closeness' of the 0.5–1.0 roots to the site of the new root formation.

DISCUSSION

Temporal and spatial variation in the quantity and structure of the fine root system of a forest has been demonstrated. What processes in the plant and environment cause this variation and what significance does it have for the growth of the forest?

Although the variation in root concentration during the summer months is large, maximum/minimum is 1.8 for lengths and 2.3 for weights the concentrations at the end of September were almost identical to those of mid-May suggesting that unless there is root growth during the winter period the fine root system of the 11 year old forest has reached some form of dynamic equilibrium and is not expanding its mean amount.

Within the season there are maxima in carbohydrate concentration, mid-June, root weight, early July and root length, late July. Work with conifer seedlings and young trees has shown similarly timed maxima in carbohydrate concentrations in both roots and above ground parts[9 11]. Loach and Little[12] described the production of photosynthate and its export to, and utilization by, roots in three overlapping phases; a) pre-budbreak export of photosynthate from the previous seasons' shoots to roots and other parts of the plant, b) diversion of export to the newly forming shoots once shoot elongation starts, and c) when shoot growth stops a resumption of export to other plant parts including roots. They suggested that this pattern is substantiated by ^{14}C uptake and distribution studies[7 24] and by direct observations of root growth[25] which indicated growth during a) and c) but not b).

An increase in root carbohydrate concentrations was found early in the summer and although maximum values were some three weeks after bud-break the large build up from mid-May onwards when the current year's shoots were small suggests that this was most probably the result of export from previous seasons' shoots. However, although root branch initials were present this was not a period of net root growth.

The period of shoot elongation in a forest cannot be so clearly defined as it can be for a seedling; shoots at different positions on the tree have their period of maximum increment at different times and their durations of growth also differ (Fig. 9). However, during the clear period of maximum shoot elongation there was a rapid increase in fine root weight/volume of soil and a gradual increase in root length, Phase 2. This increase in root weight may come from a continued translocation from the shoots during shoot elongation[27] and/or a re-translocation from the 'storage' roots. The minimum soluble carbohydrate concentration in the 'storage' roots was reached on 12 July, one week after the maximum of fine root weight. The minimum starch concentration was reached on 26 July, the time of maximum fine root length. The net decrease in root weight during the root extension period was small and may be the result of root

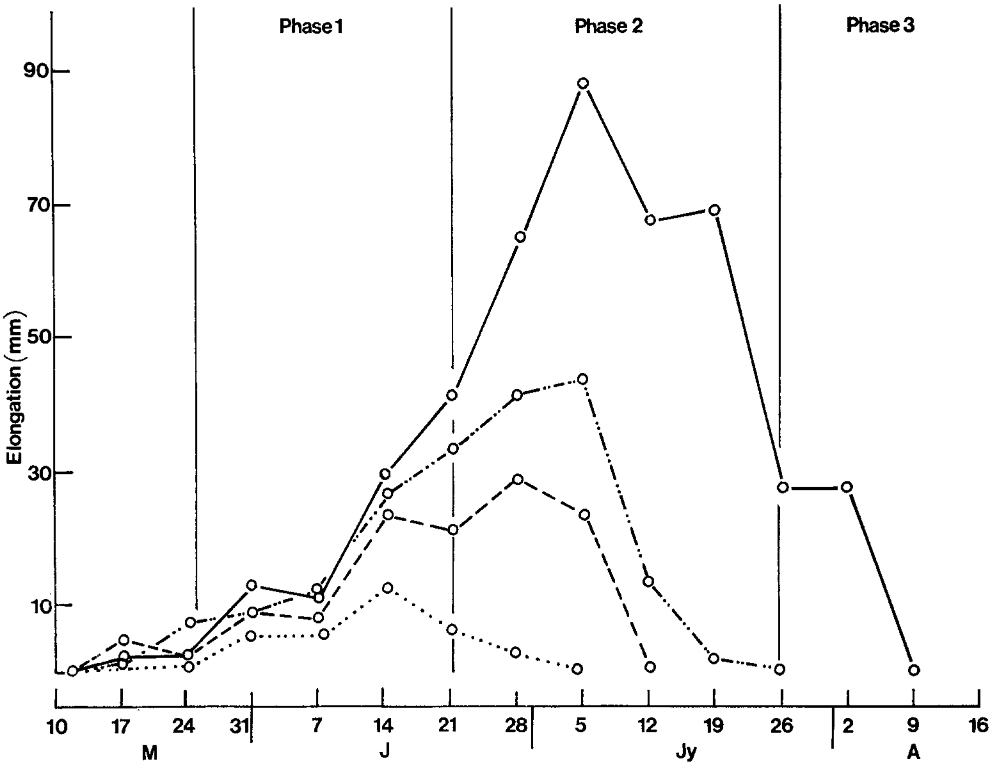

Fig. 9. Weekly shoot elongation increment at 4 positions on an 11th year *P. sitchensis* tree, Greskine Forest, Dumfriesshire. —— main apex; on branches arising at a series of whorls below the apex, – .. – 2 whorls below, – – 4 whorls below, ... 6 whorls below. Measurements were made weekly with a ruler from the growing apex to its point of connection with the preceding year's growth.

respiration during the period of active synthesis. The total weight of large diameter, +2.0 roots and of very large roots can not be estimated accurately by coring and therefore an attempt to balance carbohydrate loss from 'storage' roots against gain in weight and length of fine roots is not possible.

The period following shoot extension is not one of clear net gain in root length or weight save for the early September increase in length.

The population of fine roots in the forest was not spatially homogenous. In the needle, turf and decomposition horizons, Group I, there was a higher density of root than in the rest of the soil; these roots had more root tips per unit length and a greater weight per unit length which, it is suggested, is the result of a greater mean diameter. Three simplified hypotheses can be proposed to explain this pattern of root distribution and root structure.

1) A negative response in the lower horizons to anaerobic conditions developing at water saturation[20]. During the winter the soil water table rises at times to within 20 cm of the upper planting ridge and the lower organic horizons are inundated. In these conditions anaerobiosis could develop and kill roots with a predictably higher mortality rate in the lower horizons. However it must be noted that a) high water tables are not persistent on this site, and b) root activity is most likely confined to the summer months, the concentrations in September were almost identical to those of mid-May.

2) A positive response in root growth in the surface horizons to high nutrient conditions. No fertilizers were applied to this site at planting. Soil analysis (Table 5), indicates gradients in 'extractable' K, Ca, Mg, with high values in the surface horizons although no large gradients in total N, P, K, apart from high total K in the mineral horizons. Yeatman[28] demonstrated that the requirement for applied fertilizer in a plantation forest diminished as the extent of pre-planting cultivation increased. Comparison of the concen-

TABLE 5

Concentrations of mineral elements in soil horizons of an 11 year plantation of Sitka spruce, Greskine Forest, Dumfriesshire, Scotland

	Total			Extractable		
Soil horizons	N	P	K	K	Ca	Mg
	%a.d.s.	%a.d.s.	mg/100g	meq/100g a.d.s.		
Group I						
Needles	0.90	0.057	1.16	1.16	7.48	1.64
Decomposition	1.29	0.072	2.34	0.74	1.37	1.06
Turf	1.40	0.070	1.12	0.36	1.25	0.71
Group II						
Ridge peat	1.75	0.110	1.25	0.64	0.62	0.52
Undisturbed peat	1.23	0.081	1.96	0.33	1.04	0.36
Mineral	0.20	0.022	8.24	0.02	1.25	0.05

a.d.s. air dried soil

trations in ridge peat with those in the undisturbed peat give some indication of the consequences of cultivation. The concentration ratios, ridge peat: undisturbed peat are 2.3 root length, 1.6 extractable K, 1.4 extractable Mg, 1.4 total P, 1.4 total N though 0.6 for extractable Ca.

3) A positive response in the surface horizons to low water potentials in the summer (low potential = moist soil). Preliminary observations of soil moisture tensions indicate that as with other forests[29], the penetration of rainfall in summer is restricted to the surface horizons. Zahner[29] described the soil moisture dynamics in forest stands: 'When partially wet by a summer thunderstorm, a dry soil is depleted rapidly from the moist zone at the soil surface... whilst practically no water is removed from the dryer layers below the wetted front'.

The hypothesis which is advanced to explain the high concentration of roots in the surface regions of this forest is one of interaction between higher nutrient concentrations in the surface regions due perhaps to the deposition there of fresh plant materials with the higher amounts of water which reach these horizons during the period of active growth. McColl[14] emphasised the importance of the passage of wetting fronts through forest soils in causing the movement of ions and has shown that transport is dependent upon 1) total moisture flow and 2) conditions in the surface horizons.

TABLE 6

Estimates of fine root length for different forests

Species	Location	Soil type	Age (Years)	Root diameter	Fine Root length Km/tree	Source
Picea abies Karst	Finland	moraine gravel	130	0–5mm	10	Kalela 1950
Pinus sylvestris L.	Finland	sand	110	0–5mm	8	
Tsuga heterophyla	Canada	Chemainus silt loam	19–38	0–5mm	17	Eis 1974
Pseudotsuga menziesii	Canada	Chemainus silt loam	32–35	0–5mm	13	
Western Hemlock and Douglas Fir		shallow organic	90–105	0–5mm	6–9	
Picea sitchensis	Scotland	peaty gley	11	0–0.5mm	12	this study

If the pattern of rainfall is such that water movement is confined to the surface horizons then so too will be the uptake of nutrients by mass flow.

The mean value of L_A reported in this study is in excess of most values from previous work in forests (Table 6). However simple comparisons of fine root amount with a view to inferring possible differences in function is difficult for three reasons. 1) Root concentrations and root structure are variable during the year and single biomass estimates will always be uninformative as to the dynamics of the fine root population. 2) Many different methods of extraction, separation and classification have been used in forest root studies and these can produce different values of root from similar soil samples. 3) There is no standardisation of what should be considered as fine root. Moir and Batchelard[15] suggested that fine roots be considered as those with a diameter of <3 mm but this work does not support the use of any arbitrary diameter. If comparisons are to be made then the first need is to compare the structure of fine root populations at least in terms of the frequency distributions of root diameter.

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