

ROOT DISTRIBUTION AND THE CAUSE
OF ITS SPATIAL VARIABILITY IN
PSEUDOTSUGA TAXIFOLIA (POIR.) BRITT.

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SUMMARY

The roots of 36-year-old Douglas firs were sampled in a stratified random fashion with a Veihmeyer-type auger. The lengths of root were very variable as was the proportion of fine roots which were dead. From consideration of the possible causes of spatial variability, it was concluded that it was not due primarily to environmental variation, nor to position relative to the tree trunks and crowns except for concentrations adjacent to the trunks where stem flow is considerable. Cyclical initiation, extension and death of fine roots in a spatial pattern with cells perhaps as small as 30 cm diameter could explain the observations. A drought period might have caused more extensive death of fine roots on one of the three plots examined.

INTRODUCTION

The purpose of studying root distributions largely determines the method employed. The nature of the data collected ought to be that most relevant to the understanding of the specific root function being considered (ultimately, in the present case, to interpret the uptake of water by the plants). Uprooting or excavating single root systems examines to varying degrees the major root skeleton rather than the absorbing roots, and deals with the system of the individual investigated and not the interacting systems of all the plants. Examination of roots on the face of a trench has been very extensively and usefully employed, but the interpretation in terms of root function of the results of arduous mapping or counting of the visible cut roots is difficult. The location of the vertical face in a woodland soil poses problems of representativeness. In the present investigation, the soil was sampled with a volumetric core tool at random

to estimate the length of roots and its spatial variability. The method was outlined previously ¹¹ and has been successfully followed by McQueen ⁸.

SITE

The samples were taken from Bagley Wood near Oxford (Grid Ref. SP 508024) in a stand of P. 29 Douglas fir (*Pseudotsuga taxifolia* (Poir.) Britt.) on a 1 in 18 slope whose aspect was approximately south east. A square (side 15.23 m) was defined in this and subdivided into four plots (sides 7.62 m), samples for root distributions being taken in three of these on the dates in Table 1. The samples were from 0–15 cm in the mineral soil in plots B and C, and 0–15, 15–46, 46–77, 77–107 cm in D. From a crown projection map (Fig. 1) random co-ordinates of points on a 15-cm grid were classified into four zones by the ratio of the distance to the tree trunk under whose crown each fell to the crown radius along the same line (or the mean ratio of the distances to the trunks of trees between whose crowns it fell and the corresponding crown radii). 100% corresponds with the crown edge. By this means the areas of the zones in each plot were determined (see Table 1). The mean top height was 28.5 m and the stocking was 774 stems/ha with a basal area (the cross-sectional area of the tree stems at 1.3 m above ground level) of 30.1 m²/ha. There were scattered larch in the plantation: one occurred in plot A accounting for 15% of the basal area in the plot, and one in B accounting for 26% of the basal area. Five weeks prior to the third sampling date the plantation was thinned: 4 stems (including one of the larch trees), comprising 6.6% of the total basal area, were removed from the plots as shown in Figure 1. The stand had last been thinned several years before and all the stumps were dead. The site had previously carried oak: the remains of several oak stumps (40–60 cm diameter) were still visible. It had also at one time been a rabbit warren and old burrows were common, mostly in plot C. The ground vegetation was very sparse and not at all vigorous. All roots in the samples

TABLE 1
Douglas fir stand, Bagley Wood, Plot data, May 1964

Plot	Sampling date	Nos. random points	% areas of zones *				Basal area m ²	Numbers of stems
			0–50%	51–90%	91–110%	> 110%		
A	N.S.	135	12.6	31.1	30.4	25.9	0.23	5
B	23: 6:64	118	16.9	35.6	22.9	24.6	0.15	4
C	5: 8:64	122	6.6	36.1	27.0	30.3	0.13	3
D	19:10:65	122	13.1	35.2	24.6	27.1	0.19	6

* Zones based on distance from tree trunks as % crown radius. N.S. plot not sampled.

were taken to be Douglas fir although a small proportion were likely to have been larch or roots of the herbs.

The soil is developed in Pleistocene gravel which in the immediate vicinity of the plots is a coarse sand or sandy loam more than two metres thick with alternating layers of pale yellow soft sand and weakly cemented orange sand commonly associated with gravel. Vertical soil profiles showed that these latter horizons usually prevent Douglas fir roots extending below about 87 cm. However, these bands are not completely continuous and occasionally roots reach 140 cm often being localised in old root channels.

METHODS

The volumetric soil samplers used are of the form devised by Veihmeyer¹⁵. The narrowest part of the bore is the cutting edge (internal diameter 4.5 cm). The widest external diameter (6.8 cm) of the tool is well behind the cutting edge. The organic horizon contained no roots and was removed before the top 15 cm of mineral soil was sampled by pushing in by hand a short tube, 21 cm long. Deeper samples at the same point were taken with a longer tube inserted with a post hammer and extracted with a jack screw (W. H. Hinson, U.K. Forestry Commission). In this latter sampler the cutting edge was of hardened alloy ('EutecTrode 2') and was seated on a padding alloy ('EutecTrode 680'). This tool was used to sample 30.5 cm layers successively down to 106.5 cm. The sampling tools were able to cut through roots up to 0.6 cm diameter, and not more than 1 in 30 sampling points encountered roots too thick to cut.

Random sampling within zones beneath the tree crowns was adopted to ensure that some of the smaller but possibly important zones of the woodland were adequately sampled. Sampling on each plot was at ten random points in each of the following zones: 0-50%, 51-90%, 91-110% and greater than 110% of the crown radius. The distance from the tree trunk or trunks under or between whose crowns a sampling point fell was measured in the field and the corresponding crown radii. Around and immediately adjacent to the trunks of two random trees on each plot, ten samples per tree were taken where thicker roots were found to be absent, and a plan drawn of the base of the trunk and the sampling positions.

The organic material was separated mechanically from the mineral material by automatic washing and sieving². The roots and plant remains collect on a 16 mesh sieve (0.91-mm holes). Since many of the roots are finer than 0.5 mm diameter, there is an inevitable loss of root material. Tests with a 30-mesh sieve (0.57-mm holes) suggested that this would retain a third as much root again as the coarser strainer, but separate the fine sand less efficiently from the plant remains. Almost all the root fragments passing through the coarse mesh were less than 0.5 mm diameter and their average length was less than 5 mm. Tests using root fragments which had been drawn before being washed with soil in the apparatus, showed that root tips and fine straight fragments were not held by the coarse sieve.

The samples contained both living and dead roots. The criterion used for distinguishing 'living roots' was the presence of a white vascular strand, since Kramer⁶ has shown that even dead vasculated roots may take up water. This meant that each fragment was examined individually and often teased or dissected (grateful acknowledgement is made of Mr. E. A. S. Ogden's assistance). Examination in transmitted light proved inadequate for sorting: staining also proved ineffective. The ratio of the dry weight of dead to living roots was very variable (Fig. 3). Among the coarser roots there were frequently none which were dead. Among the fine roots dead ones often comprised more than half the oven-dry root weight in the superficial layer, but in the deeper horizons very rarely more than one third of the dry weight were dead roots. It was therefore impossible to apply a simple adjustment to the figures.

It was feasible to estimate lengths of roots from oven-dry weights, provided the roots were separated into size classes as shown in Table 2. Lengths of roots thicker than 2 mm diameter were individually measured.

TABLE 2

Dry weights of living roots (mg/cm) from plot D by diameter classes. Means of 2 random samples from each of 4 depths with standard errors (n = 8)

< 0.5 mm	0.5-1.0 mm	1-2 mm	> 2 mm
0.29 ± 0.019	0.58 ± 0.027	2.47 ± 0.304	0.68 ± 0.069

RESULTS

Throughout the data there is a distinct tendency for the frequency distribution of root lengths or weights to be skewed: there are usually a very few samples with large lengths or weights of root and relatively many samples with small amounts. A similar sampling distribution was reported by Hack³ in a very different situation, that of tomato plants grown in a glasshouse (see also McQueen⁸). One is immediately struck by the variability of the data: both weights and lengths have a range among the samples of about two orders of magnitude. Much of the discussion of the results will revolve around this variability. At present comment will be restricted to noting that the percent standard errors of the untransformed dry weights are more often larger than those of lengths (Table 3). The percent standard error for root lengths in ten random samples from any zone commonly lies between 15 and 20 per cent while that for weights averages about 30 per cent. Variability of root length tended to increase with depth. Due to this variability no significant differ-

ences in root lengths or weights can be demonstrated between zones or between depths in this stand. Perhaps as many as a hundred samples from each depth in each zone would be necessary to demonstrate significant differences. Angelo and Potter¹ were able to use dry weights for comparisons probably because of their standardised sampling procedure: 4 replicate samples were taken with a 2.2-cm diameter Veihmeyer tube at the corners of a 15-cm square 91 cm from the trunks of orchard trees (standard error 5.3% of the mean, 75 degrees of freedom).

TABLE 3
Percent Standard Errors. Douglas fir live-root weights and lengths.
Plot D. In parentheses-number of samples

Zone	Depth (cm)									
	0-15		15-46		46-77		77-107		0-107	
	Weight	Length	Weight	Length	Weight	Length	Weight	Length	Weight	Length
Tree base	15 (9)	11 (9)	—	—	—	—	—	—	—	—
	24 (6)	33 (6)								
	24 (7)	24 (7)								
0- 50%	95 (9)	16 (9)	51 (4)	28 (4)	40 (3)	39 (3)	18 (2)	25 (2)	20 (2)	19 (2)
51- 90%	11 (10)	13 (10)	85 (10)	16 (10)	49 (10)	20 (10)	31 (10)	27 (10)	56 (10)	16 (10)
91-110%	32 (9)	21 (9)	23 (8)	21 (9)	26 (10)	17 (10)	22 (10)	24 (10)	17 (9)	15 (8)
> 110%	37 (9)	15 (9)	84 (9)	12 (9)	21 (9)	20 (9)	31 (9)	28 (9)	17 (6)	15 (6)

From the above it should be noted that comparisons of mean root amounts between plots, zones or depths must be received with considerable caution. Summarised results are given in Tables 4 where perhaps the most striking feature is the considerable length of root in the soil, about a kilometre per square metre in the top 15 cm of soil and as much as 7 km in the top metre. These considerable lengths are associated with a fairly small weight of roots (about 200 g per kilometre) although the thicker and heavier roots near the base of the trunk are excluded. The differences between the plots might have been due to the month of sampling, to crop development (plot D was sampled the year after the other two), or to changes in technique during the execution of the study. However, inspection of the relative amounts of root in each zone in Table 4 suggests that none of these explanations is very likely.

TABLE 4

Douglas fir, Bagley Wood. Length (km/m³) and weight (kg/m³) of living roots of all diameters

Zone	Plot											
	Depth (cm) B		Depth (cm) C		Depth (cm) D							
	0-15		0-15		0-15		15-46		46-77		77-107	
	Length	Weight	Length	Weight	Length	Weight	Length	Weight	Length	Weight	Length	Weight
Stem base	0.31	—	0.28	—	1.06	0.09	—	—	—	—	—	—
0- 50%	0.28	0.92	0.39	0.21	2.28	0.09	4.25	0.43	3.29	0.19	2.20	0.12
51- 90%	0.43	0.11	0.70	0.09	1.66	0.09	2.31	0.22	1.85	1.96	1.77	0.16
91-110%	0.26	0.03	0.59	0.38	1.99	0.18	2.41	0.22	2.40	0.16	1.36	0.07
> 110%	0.48	0.04	0.38	0.07	1.65	0.15	1.64	0.69	1.10	0.06	0.94	0.07
Whole plot	0.37	0.21	0.55	0.17	1.81	0.13	2.41	0.37	1.97	0.76	1.50	0.11
Total 0-107 cm depth: 7.69 km/m ³ , 1.37 kg/m ³												

Depth sampling was not independent of horizontal sampling and it is noticeable in Table 4 that there is more consistency between depths in a zone than between zones. However, we may notice a tendency for greater root length to occur in the 15-46 cm horizon than in the lower horizons, but the top 15 cm of soil had almost twice the density of roots (weight or length of root per unit soil volume). In every zone the 77-107 cm horizon had the lowest concentration of roots but still, in this deep soil, about half the surface concentration.

Despite their proximity to one another, samples taken around a tree trunk contained as variable amounts of roots as the random sampling (see Table 3), but real differences occur between trees so that the root length in samples adjacent to the trunk of tree *I4* was significantly less than that around tree *II* (Fig. 1 and Table 5). The mean lengths of root in this region were relatively small in all three plots (Table 4). However, considering the individual samples, those with abundant rooting in some trees at least (*I8*, *25*), were juxtaposed. Certain trees (*8* and *I2*) appeared to have fairly uniformly small root amounts around the trunk base, while others (*e.g.* tree *II*) uniformly large amounts. There was no apparent rooting preference correlated with compass direction.

Mean values of root lengths within each zone tend to obscure a

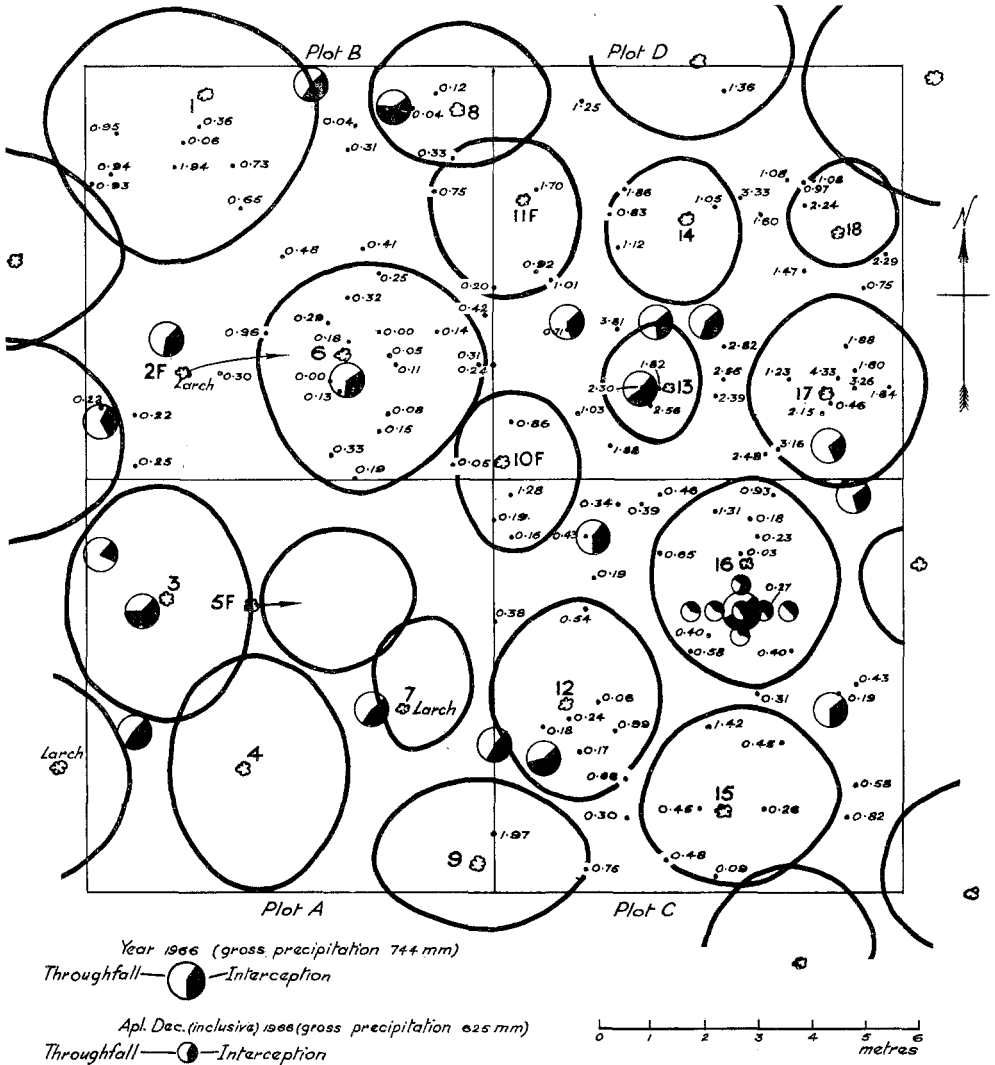


Fig. 1. Douglas fir, Bagley Wood. Crown projection map. Tree numbers bold type. F = felled October 1965. Catch of throughfall relative to gross precipitation (see key). ● = Stratified random sampling points with length of living roots in top 15 cm of mineral soil in km/m^2 (italics).

feature exemplified in Figure 2 for the samples with the greater lengths of root to be found at a distance of a metre from the tree trunk, or about halfway between the trunk and the edge of the

crown (plots B and C) although samples containing small amounts of root could occur at any distance from the trunk. In plot D, the zone yielding some samples having large quantities of roots was located nearer the stem, and horizons below 15 cm presented a similar picture.

It is also instructive to look at the root lengths in samples relative to the crown projection diagram (Fig. 1). In plot B the smaller lengths of root are mostly confined to the eastern half. Although the general values for plot D are much greater, the western edge of the plot adjoining plot B has relatively shorter root lengths. The larger lengths of root in plot D are mainly confined to the south-eastern half of the plot. Any pattern in this plot does not appear to carry into plot C with its almost random disposition of root lengths in samples.

In plot D, where sampling was conducted to greater depths, there was an evident correspondence between the patterns in successive horizons.

While admittedly this description of pattern is very subjective, it noticeable that it gives little or no support to any hypothesis which seeks to relate root distribution to the positions of the trees and their crowns – any contours which are drawn on the basis of sampling position and the amount of roots, appear unrelated to the crown projection map.

Some comments should be made on the relations between the diameter classes of roots, particularly since some workers (*e.g.* Orlov¹⁰) have treated such a classification as reflecting function. In plot C there was on average about three times the length of roots of more than 0.5 mm diameter than there was of roots thinner than 0.5 mm. In the other two plots there were similar lengths of root larger and smaller than 0.5 mm (see Fig. 2). The proportion of roots less than 0.5 mm increased with depth somewhat (plot D). The lengths of roots thicker than 1 mm rarely exceeded 10 per cent of the total in the sample, and often there were no roots of the larger classes. Only in plot C was there a tendency for the proportion of roots less than 0.5 mm in diameter to increase towards the trunk. Perhaps the reverse was true at depth in plot D.

Only in plot D were the dry weights of dead roots in the samples assessed. It was observed that the dead roots were almost entirely of the smaller diameter classes *i.e.* less than 1 mm. The weights would

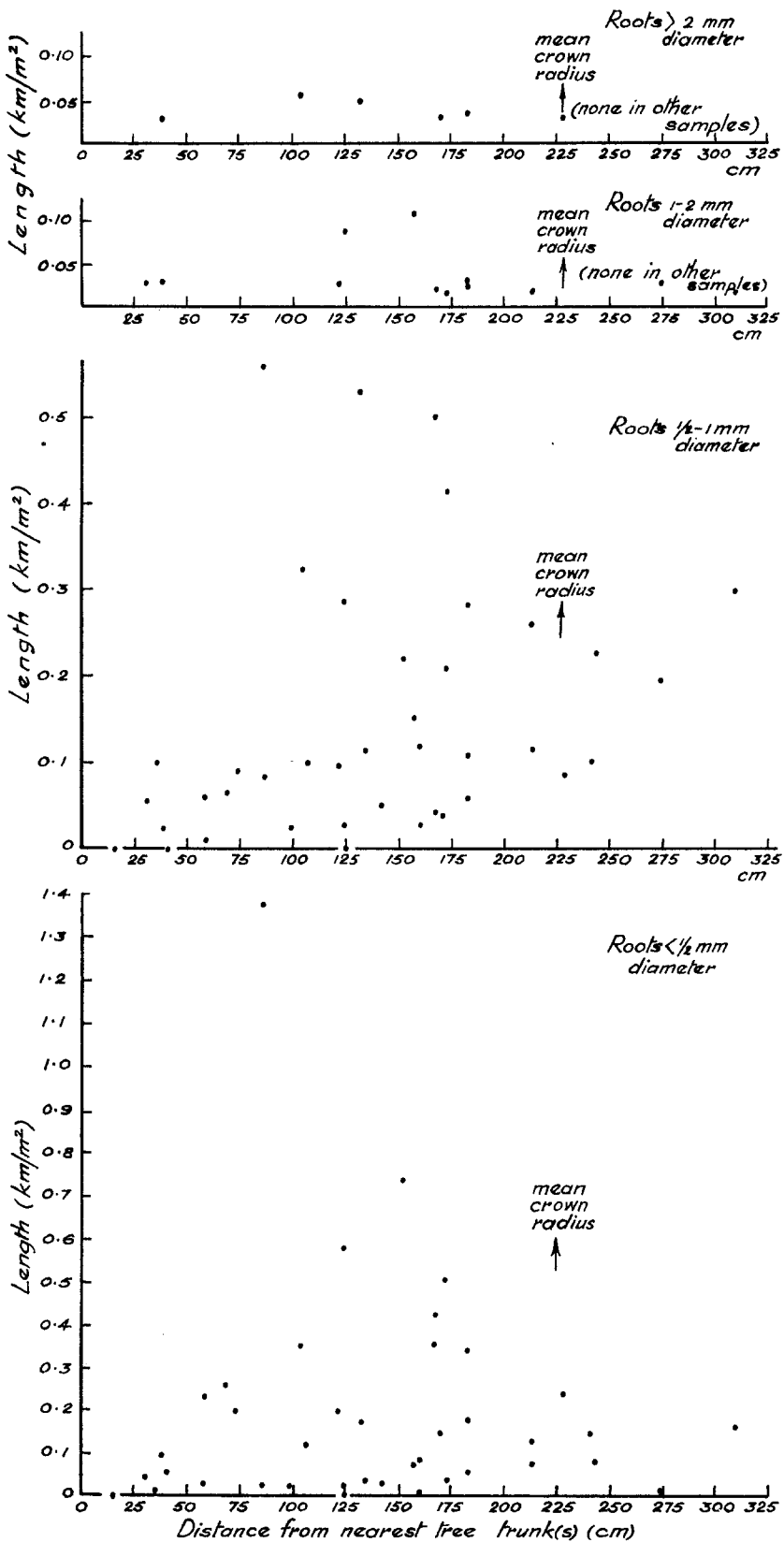


Fig. 2. Douglas fir, plot B. Root length (four diameter classes) relative to distance from tree trunk.

therefore more nearly correspond to lengths than in unclassified live root material. It is probable that dead root material would weigh less when dried than a similar length of live root of the same diameter. On average there was about half the dry weight of dead roots in a sample as live, but the proportion was very variable and, in perhaps 20 per cent of the samples, dead root weight equalled or exceeded live (see Fig. 3). It has been assumed that dead roots belonging to trees felled in the previous thinnings had rotted by the time the samples were taken, though this cannot be proved. The ratio seemed to bear little or no relation with position between the trees or depth (except that perhaps the 15–46 cm horizon tended to have a higher ratio of dead roots than the 77–107 cm horizon). The weight of dead root material per unit soil volume in the 0–15 cm sample was on average approximately one and a half times that in the deeper samples. Mean dead root weights in the deepest samples

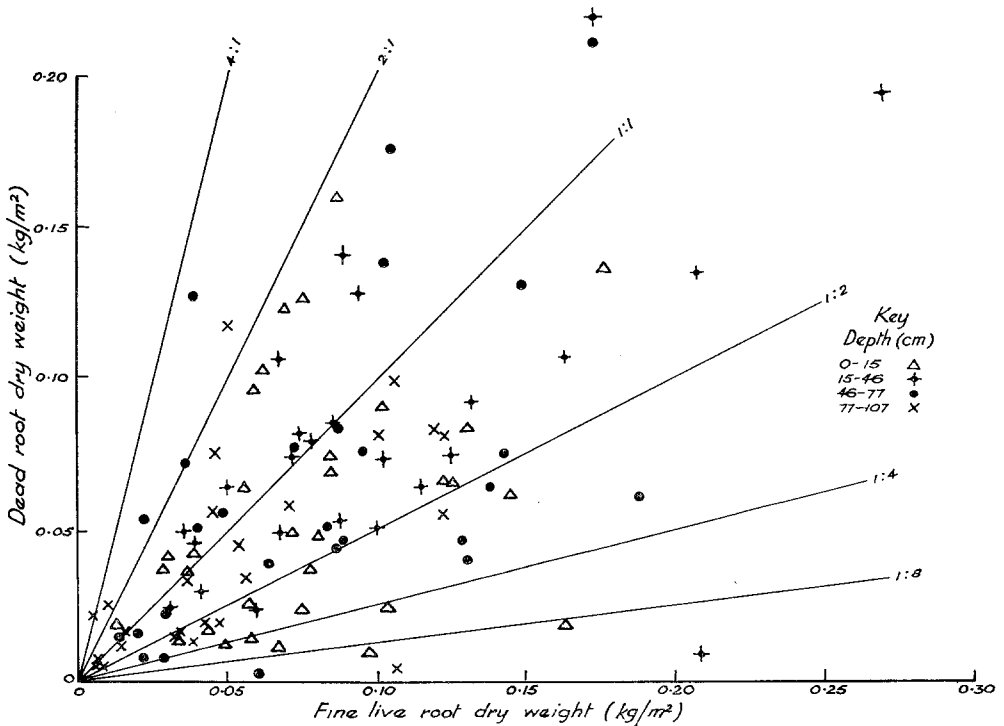


Fig. 3. Douglas fir, plot D, dry weights (kg/m²) of dead roots relative to living fine (< 1 mm diam.) roots.

were about 85 per cent of those taken from 46 to 77 cm which in turn were about 75 per cent of those from 15 to 46 cm, but within any individual vertical profile this pattern was frequently not followed. The mean weight of dead roots per sample fell off with distance from the tree trunks so that the mean weight of dead root at 50 cm (0.14 g per sample) from the trunk was about twice that at 2 m (0.07 g per sample). Samples with small amounts of dead root occurred at all distances from the trunk, but samples with larger weights of dead roots were only found nearer the stems. Thus the distribution of dead roots apparently followed that of live roots despite the variable ratio of live to dead weights in the samples.

DISCUSSION

The data reported in this paper leave some things to be desired and point to improvements which could be made in the methods. The depth discrimination is inadequate for many purposes; the 15- or 30-cm intervals ought to be reduced to 2 cm, but it is difficult to see how this might be accomplished without considerably increasing the number of samples. The loss of fine root material during the washing process is rather high and, since it includes many of the root tips, some valuable information is also lost. The discrimination between dead and living material is somewhat arbitrary and tedious. Radioactive tracers injected into the trees some while before sampling suggests itself as the most appropriate approach (see Ueno *et al.*¹⁴). Photographs and autoradiographs of the roots after washing could then be subjected to Newman's⁹ technique of length determination.

However, accepting the data with their limitations, we will consider their characteristic variability. If we suppose that there is a relatively constant component of this variability, we would expect correlation of the pattern with other factors such as the distribution of soil moisture accession and soil nutrients. We have noted that there is an inverse correlation between root length and distance from the nearest tree trunks, though not sufficient to account for any more than a fraction of the variability. Five rain-gauges (127 mm diameter) were placed completely at random in each of the four plots to assess throughfall. The smallest catch was less than half the largest (see Fig. 1). With the high and rather ragged crowns in this

plantation, the rather variable throughfall may be large at any distance from the stem, but small throughfall points are confined to the region of the inner crown so that it is not easy to see any relation to the pattern of rooting in Figure 2. There was no correlation between throughfall and root lengths in the top 15 cm of soil in samples nearest the gauge sites. It could be that there is an intricate pattern of throughfall which is not very closely related to the tree spacing. However, a more intensive grid of rain-gauges under a single tree crown (Fig. 1, tree 16) confirmed that there was on average the expected increase in throughfall from near the trunk outwards. It is possible that the superficial rooting adjacent to the trunks is more closely related to the accession of rainfall as has been suggested previously¹¹. Using fluorescent dye¹² on Douglas fir of a similar size, it was noted that the stem flow is deposited at discrete parts of the perimeter of the base of the tree trunk (this can be confirmed visually in storms) and runs to the underside of major roots. The distribution of roots in samples round the trunks suggests that they are concentrated according to the inclination of the tree trunk, the presence of hollow channels between ridges corresponding to the major roots, and the slope of the ground which carries the surface run-off component of stem flow. At least in trees 14, 18 and possibly 12 the position of trickles of water observed in storms corresponded to samples with the greatest root lengths. A very weak negative correlation between stem flow and tree size in this stand is recognisable in Table 5. The trees on which larger stem flow was measured (trees 1, 15 and 18) corresponded with the tree of the pair sampled on each occasion having the higher concentration of roots. Conversely, trees 14 and 8 had less stem flow and tree 12 was relatively dry and the smaller concentration of roots was found in samples round their boles.

The humus depths at the points of sampling, or the ease of penetration of the sampler showed virtually no correlation with the amounts of root present.

In two of the plots there was an apparent spatial clustering of samples with similar quantities of roots. This might be taken as an indication of a pattern in the physical or chemical attributes of the soil, possibly related to the previous oak crop. Its apparent horizontal dimensions compared to its vertical make it unlikely to be a reflection of the geological parent material (Plateau Gravel). How-

TABLE 5

Stem flow (litres) on trees during smaller daily precipitations (< 12 mm) from 28 Feb. to 11 Oct. 1966. Trunk girths (m at 1.3 m above ground). Mean root lengths (km/m³), 0-15 cm soil horizon, sampled against trunk

	Plot													
	A				B			C			D			
Tree number (see Fig. 1)	3	4	7 (larch)	9	1	8	6	12	15	16	14	17	18	11
Stem flow	30.6	95.3	0.9	157.4	66.0	42.1	26.7	13.6	62.9	30.0	37.3	60.1	53.0	—
Girth on 5.5.64	0.92	0.84	0.66	0.83	0.53	0.75	0.75	0.81	0.70	0.70	0.62	0.88	0.55	0.66
Mean root length	—	—	—	—	0.67	0.09	—	0.16	0.40	—	0.68	—	1.19	1.29
Number of samples	—	—	—	—	3	5	—	9	10	—	10	—	9	9
Maximum length per sample	—	—	—	—	0.93	0.35	—	0.50	1.10	—	1.05	—	2.53	1.94

ever, the third plot appears to have a more intricate pattern of rooting which cannot be explained in these terms.

From considerations like these, it seems likely that most of the variability in rooting is inexplicable in terms of the micro-pattern due to the distribution of the trees or other variations in the environment.

High concentrations of live roots may be relatively transient. Having largely exhausted the available water in a locality, the density of living roots is likely to revert in a few weeks to a low concentration, leaving a high proportion of dead roots and a few persistent live roots of larger diameter. The former would decay at a rate dependent on temperature, soil moisture potential and, probably, depth. After recharge of this soil with water, the persistent roots may put out new fine roots and complete the cycle. Thus the variability of rooting may be explained as an intrinsic and dynamic characteristic of at least some root systems. The statistic of variability about the mean in Table 3 would thus be an index of this discontinuous root activity in Douglas fir. It may be relevant that Wilcox¹⁸ found that abortion of short roots of *Pinus resinosa* was associated with their relatively small apical meristems, but in this anatomical study no indication could be given of the time scale of these events. Apart from the seasonal development of short roots which he ascribed to endogenous causes, Ladefoged⁷ noted that

considerable development of short roots could occur in any month of summer and autumn when the parent long root tip was damaged, met an obstruction, showed mycorrhizal development or was subject to desiccation.

Such cyclic activity might be linked with a spatial pattern. Rogers and Booth ¹³ speak of the size of pattern they observed in 'absorbing' roots of apple on underground glass windows as composed of 'small' areas, presumably of the order of 1,000 cm² in vertical cross section. They described a cycle of exploration and death in August that took about 50 days. Weller ¹⁷ also observed considerable variability of the concentration of 'absorbing' apple roots within periods of a few weeks, ascribing this to internal physiological causes on the slender basis of a correlation with the fruiting of individual apple trees. Under a weekly watering regime of tomato plants in a greenhouse, Hack ⁴ reported a cycle of root growth, death and regrowth taking about 100 days on a 30 × 30 cm vertical glass observation panel. Adjacent tensiometers indicated that water uptake was subject to a similar cycle. He suggested a wave of root regrowth spreading out from the base of the stem taking a measurable time to affect tensiometers placed at 30 cm from the base. Kolesnikov ⁵ has reported death and shedding of roots sequentially outwards to the crown periphery in top and soft fruits, the cycle taking several years.

If a pattern of similar dimensions occurs in Douglas fir, then the intensity of sampling points used in the present work is larger than the pattern and would be expected to produce extremely variable results. Even the sampling in depth might be expected to show large differences, except perhaps sometimes in adjacent horizons. Watson ¹⁶ has presented figures for numbers of roots on a 116-cm² grid of rectangles on a vertical pit face in Douglas fir on deeply drained Calcareous Grit in Bagley Wood. However, the faces examined did not exceed 80 cm long and 76 cm deep which is not sufficient to demonstrate whether or not there was a repetitive pattern of variability.

The presence of variable proportions of dead roots in the samples may be taken as evidence in favour of the above hypothesis. A high proportion would indicate relatively recent death where previously there had been a high concentration of living fine roots. A low proportion resulting from decay of fine roots which had died might

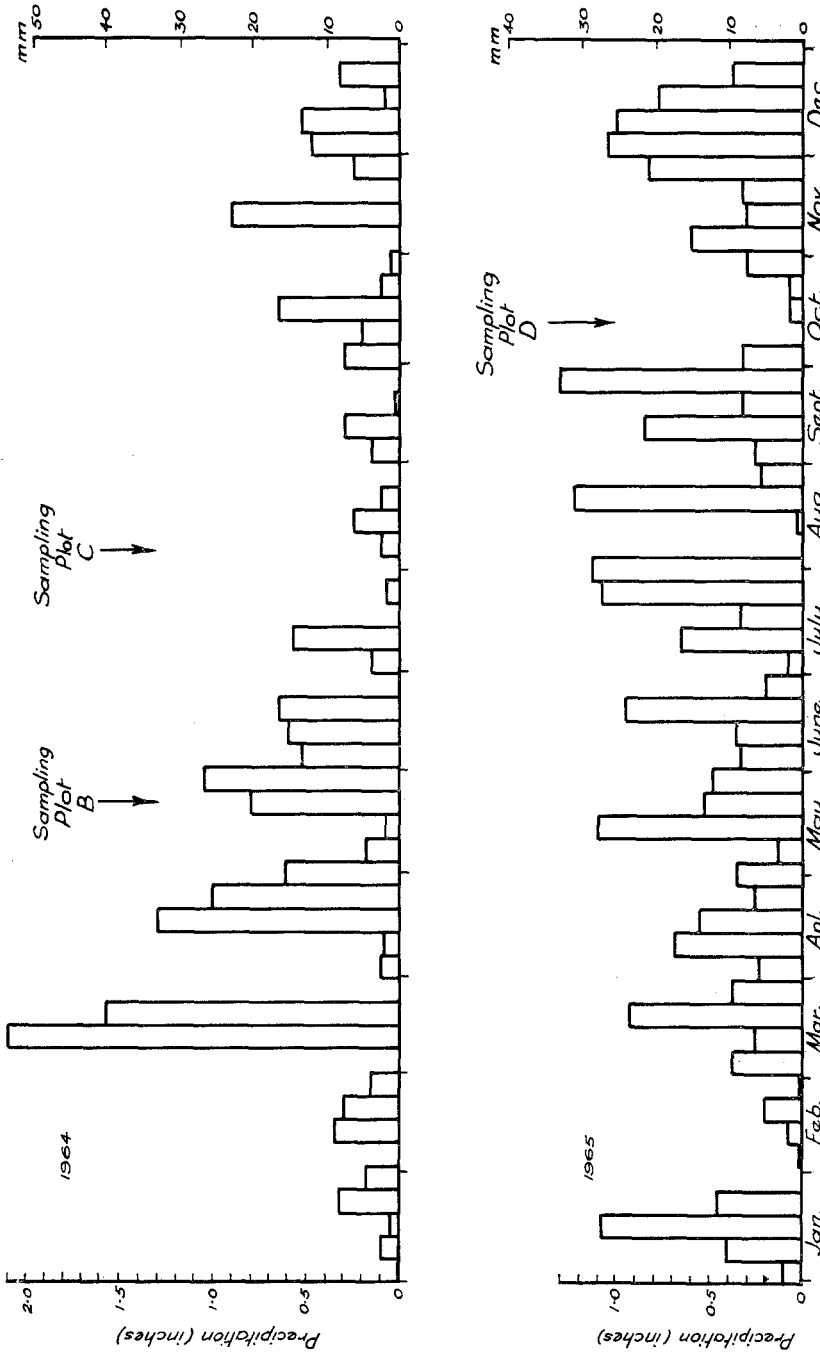


Fig. 4. Weekly precipitation, 1964 and 1965, Kennington Nursery (Bagley Wood, near Oxford) and dates of Douglas fir root sampling.

be enhanced by renewed root growth in the locality. Figure 3 may be interpreted in line with this explanation.

It would be difficult to use the sampling technique for Douglas fir roots to examine the validity of this hypothesis as a function of time because of the effect of sampling on the rooting within the immediate vicinity. Despite its deficiencies, it may be necessary to utilise the root observation chamber to see if the cyclical exploration of soil by roots is as widespread as it appears.

In presenting the results of this study differences were noted between plot C and the other two that were sampled. Summarising these, pattern was virtually non-existent nor continuous with the adjoining plot, and the proportion of live roots which were fine was reduced. If we are correct in attributing transience to the roots less than 0.5 mm diameter, then the observations on the plot are consistent with fairly widespread death of these roots before the sampling date. The gross rainfall (Fig. 4) suggests that these findings may well result from the drying of the soil during six rather dry weeks preceding the sampling of plot C in contrast to the moist conditions supervening earlier in the season when plot B was sampled and the wet summer the following year prior to sampling D. Kolesnikov⁵ suggests that propitious environmental conditions can prolong the life of short roots. Plot C may therefore illustrate general death of fine roots, while under moister soil conditions in the other two plots only locally was there sufficient depletion to 'cause' the death of fine roots.

The evidence thus points to fine roots being produced in response to an external stimulus received by the growing tip of the parent long root (Ladefoged⁷). These fine roots are predisposed to transience (Wilcox¹⁸) and succumb due to local soil moisture depletion rather than to internal causes as postulated by Weller¹⁷. Considerable interest attaches to discovering whether the fine roots dying in a cell arise from a single parent root, or indeed a single tree.

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