ROOT-SYSTEM DEVELOPMENT

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INTRODUCTION

Under normal field conditions the root system supplies the crop plant with both the necessary water and the mineral nutrients. For an adequate performance the root system must be able to establish a certain area of contact with the soil. The larger the absorptive area the higher the potential intake. The absorptive area is highly correlated with density of ramification. But, in the soil the extractable stock of water and nutrients rise with a volume increase. Therefore, the amount of soil encompassed by the root system is a contributing factor. Thus, the development of the root system in spread and depth is an important factor and regulates the possibilities of soil utilization. Therefore, a knowledge of root development at a certain site is important to evaluate its crop-carrying capacity and to devise adequate cultural practices.

In the study of root systems several different techniques have been employed. Firstly, this paper reviews these methods - both traditional and those using tracer techniques - and compares their respective merits. Secondly, there is an attempt to summarize the main information that has been obtained in studying relationships between rooting and soil-moisture content and soil density. Finally, some remarks are made on the performance of roots in the subsoil.

METHODS OF INVESTIGATING ROOT SYSTEMS

Let us first consider what kind of information is desired.

First, it is necessary to know the total volume of soil occupied by the root system. This volume of soil should at least give an idea of the amount of available water and should be indicative of the amount of extractable nutrients. The desired information will necessitate obtaining data on both root spread and rooting depth. The investigation must also give data on the development over a period of time.

To be able to estimate the possibilities of soil-mass utilization one must also know the root densities in various parts. In extreme cases it might be necessary to estimate the total root surface. Although the morphology of the root system is fully characterized once this information has been obtained, the knowledge about its performance in still lacking. So, the activity in different parts of the root system must also be measured.

The methods for obtaining the desired data can be divided into the more traditional types and those utilizing tracers.

In studying the morphology of the root system the following main methods have been devised.

(1) Careful excavation of the whole or part of the root system

This method has mainly been used on woody-root plants [5, 37].

(2) The trench method

A trench is dug, usually passing close to the centre of the plant. Following this, two techniques are possible. By carefully removing a layer of soil at one side of the trench a vertical layer of roots will be exposed [42, 48]. Another method is to free the cut root ends by removing some soil and then mapping them in their position. Different symbols can be used according to thickness [11, 36].

(3) The pinboard method

In this case a trench is dug passing close to the centre of the plant after which the pinboard is pushed into the soil with its pins at the side toward the plant. The soil behind the monolith pierced by the pins is cut. The whole pierced monolith is taken to the laboratory to be washed. The pins serve to keep the root system near its original position during washing. Thus, part of the root system is made quite visible and data on form, distribution and density are obtained [11, 42].

(4) Soil-core sampling and extracting the enclosed root mass by washing procedures

The cores can be taken from subsequent layers when working downwards, but in some cases, such as in stony soils, it may be advantageous to take single samples horizontally from the side of a trench [22, 42, 49].

Good quantitative data can be obtained by this method if sufficient replicates are taken from different layers of the soil profile. The laborious washing of the soil cores can be eliminated and replaced by approximately estimating the root content by breaking the cores in two and examining the roots protruding from both surfaces [42, 49].

(5) The root observatory

This method allows continuous observation of all root behaviour in a very thin layer of soil adjoining the glass panes [37, 38].

(6) Application of tracers to the soil at predetermined locations

By the tracer method a substance, which is only slightly liable to dispersal, is introduced into the soil in a regular pattern of spots at different distances and depths. Once the tracer substance can be recorded in those parts of the plant above ground it can be concluded that the roots have extended to or beyond this spot [6, 13, 17, 19, 24, 26, 40].

It is a method especially adaptable for field work and has the advantage of only minimally disturbing the soil. In principle any absorbable substance foreign to the normal soil constituents could be used. Ease of detection is, of course, an important characteristic. The applied substance should, however, only be liable to slight dispersion, as otherwise its exact location is in doubt. This dispersion can occur as a result of diffusion and by transport along with the movements of the soil solution. This dispersion can be best eliminated by choosing substances that are apt to enter into an adsorbed or fixed state, without becoming unavailable. In this respect all cations may be considered. Elements such as rubidium and strontium [6] could be used. As far as the anions are concerned phosphate is a definite exception because this ion is, to a great extent, bound and therefore only demonstrates a slight mobility [4]. In this case the radioactive isotope is an excellent tag. Strontium-89 can also be used for easy detection.

Phosphorus-32 is now mainly used because this phosphate is absorbed in reasonable amounts, which makes early detection possible. Another advantage is its half-life value, which results in a relatively short contamination. Its hard β-rays permit the use of simple apparatus for detection, while precautions against radiation are fairly easy. It is also easily available and not expensive. Strontium-89 has the advantage of a much longer half-life; and ^{42}K has also been used [29].

(7) Application of tracers to the plant

In this new technique a radioactive element liable to rapid redistribution in the plant is administered to the stem. After a certain lapse of time - 6 hours to a few days - core samples of soil plus roots are taken. The amount of radioactivity measured in a representative part of the sample gives a measure of the amount of live roots in a certain spot. Thus, all root washing is eliminated [4, 34, 35]. Phosphorus-32 has been used for this purpose, but ^{86}Rb could also be used. The use of ^{42}K could also be considered as it would give no residual contamination on account of its very short half-life. Carbon-14 and sulphur-35 would also be suitable substances as they are well redistributed, but their soft rays make them less easily detectable.

This elegant procedure has the advantage that it only measures the amount of live roots present at a certain moment. A comparison of the seven methods leads us to the following conclusions.

(a) Time necessary to obtain the data

The trench method, although involving much digging will yield immediate results.

The pinboard method and core-sampling methods are rather laborious and time-consuming because of washing procedures and the removal of organic debris.

The excavation method also involves careful time-consuming soil removal.

In applying tracers to the soil a relatively fast procedure in injecting the numerous aliquots is possible. But the time which elapses before measurable amounts are detected in the sprout may be long.

Data can be obtained much faster by applying the tracers to the plant.

(b) Disturbance of the soil

In this respect the soil application of tracers has the advantage of giving minimal disturbance. Core sampling, which is also necessary when applying tracers to plants, only results in a series of narrow holes. All other methods, however, are accompanied by a lot of deep digging and large holes.

(c) Amount of information obtained

As far as information on the depth and extent of rooting is concerned and also as regards data on the extension rate of the root system, all methods are useful.

When more detailed information on the variation in rooting density in various soil layers is required, the trench, pinboard, core-sampling and plant-applied tracer methods are to be preferred. Although the relative amount of soil-applied tracer absorbed from different injection patterns will be correlated with rooting densities at different zones, interactions with other variables such as soil-moisture content and differences in E-values will interfere. The best quantitative data can be obtained by the core-sampling methods, followed either by washing or a determination of the root-contained radioactivity.

The fact that the application of tracers to the plant makes it possible to distinguish between live and dead roots need not always be an advantage. In several problems (production of organic matter by the root system, questions of soil utilization) all roots produced in the course of time must be considered.

As rooting behaviour is often highly dependent on characteristics of the soil profile, those methods that can at the same time yield auxiliary information have a distinct advantage. The trench, pinboard and core-sampling methods all fulfil this requirement to varying degrees.

In conclusion it may be said that most of the traditional methods will give more detailed information than the soil-applied tracer techniques as far as knowledge of the morphology of the root system is involved.

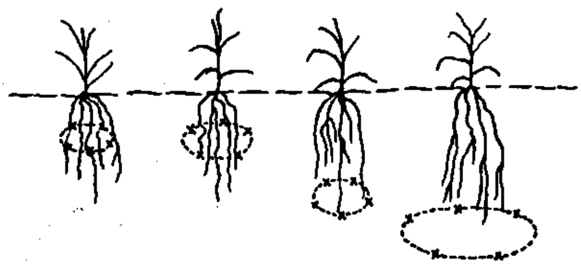
Usually, however, information concerning the performance of the root system is also necessary. Of course, a knowledge of the gross morphology will allow a number of assumptions to be made on its performance. But more specific information will have to be derived experimentally.

Some information, such as whether or not subsoil layers contribute to the nutrition of a plant, may be obtained by means of appropriate field experiments [21]. Also, some estimates can be derived from a knowledge of root physiology and data on soil fertility and water content of the soil layer in question.

It is in this field that the tracer technique is unequalled. By this means the performance of any desired part of the root system can be directly determined. For this the tracer used should be an isotope of a normal nutritional element, or an element that can replace an ordinary one without discrimination, if unnecessary labour is to be avoided. In this manner both performance, and relative performance in relation to other parts of the root system, can be measured. Local root performance is calculated by the amount of isotope dilution determined in the plant.

The technique employed has already been described in its general aspects by Hall et al. [13].

With a soil probe, containing an interior channel and an outlet near the tip, a small amount of tracer-containing solution is injected into the soil. The injection spots are chosen in a series of patterns at different distances from the plant stem and at different depth levels in the soil. At each distance and depth level several spots are arranged in a concentric circle or in a row (Fig. 1).



x injection spot

FIG. 1. An example of a series of injection sites at which a tracer is placed to study root growth or performance.

Different types of injectors have been used and a description of these can be found in the literature [13, 14, 25, 26]. In some cases the tracers were administered as solid substance and placed at the bottom of a narrow well [18, 19, 27].

After careful, slow injection to prevent the solution seeping upwards along the probe, the probe is extracted. The channel left in the soil should then be carefully refilled with soil. This is necessary to prevent the roots possibly taking advantage of this pathway without mechanical impedance and growing downwards fast and beyond normal development. To eliminate this difficulty some investigators have used an oblique entrance into the soil, and some have even first dug a trench at some distance away and then inserted the probe horizontally.

Mostly ^{32}P has been used as a tracer [1, 13, 15, 17, 19, 25, 26]. Recently research has reported the use of stable strontium [6], and also ^{35}S [30].

For some purposes it is advisable not to noticeably alter the amount of available nutrients at the location of injection. A change of nutrient content of the spot might result in enhanced local rooting density [52], a fact that would obscure information on relative performance. In these cases high specific activities, with as little of the inert substance as possible, should be used. This is not necessary when the uptake of added fertilizer is to be investigated.

As long as the study is only directed towards a determination of the gross extent of the root system no further complications are encountered. Then the presence or absence of the tracer in the shoot is a sufficient indicator (Fig. 2).

But much more information can be obtained if the total amount of tracer in the shoot and its specific activity are determined. The specific activity in the plant or part of it is related to the specific activity of the application spots in the soil by the same factor as uptake from these spots is related to uptake by the total root system [15, 17, 18].

$$\frac{\text{specific activity absorbed tracer}}{\text{specific activity application zone}} = \frac{\text{uptake by roots in application zone}}{\text{uptake by the total root system}}$$

To be able to do this, however, there must be information on the specific activity in the application spots. This specific activity will usually be

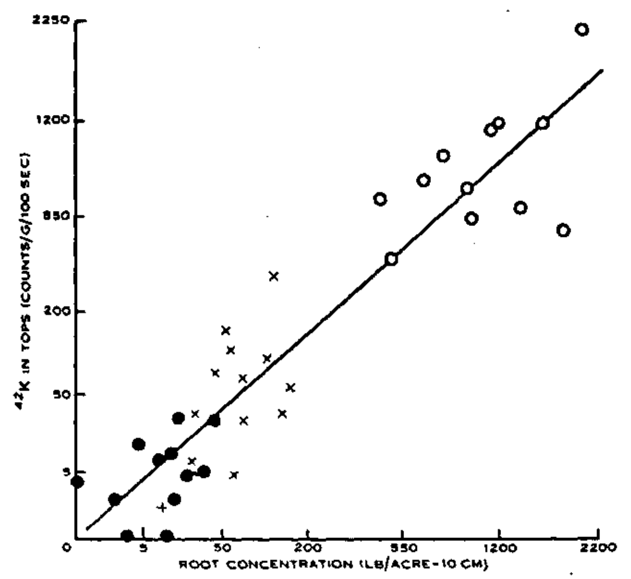


FIG. 2. Evidence that the amount of tracer detected in the plant is related to the amount of roots at the different injection depths.

much lower than that of the injected solution as a result of dilution and exchange with the native nutrient. Determination of the E-value for different layers in the soil profile will then give the necessary value, since isotopic dilution with all available nutrients is then measured. Should a tagged fertilizer be added a correction must be applied by determining A-values for the different soil layers [7, 17, 28, 55].

Under certain conditions determination of the specific activity in the shoot can be omitted, but a correction for differences in the labile pool of the element in different soil layers remains necessary [15].

If the amount of roots in the application spots is known, as well as the total amount of roots, the relative performance of a unit mass of roots in different layers in the soil profile can be evaluated. The relative performance of roots is calculated as:

$$\frac{\text{\% contribution of the tracer containing spots in total uptake}}{\text{\% root mass in the tracer containing soil volume}}$$

A value smaller than 1 means a restricted performance in uptake and a value exceeding 1 means an enhanced performance in relation to the over-all performance of the total root system [17, 28].

It is thus possible to obtain information on the performance of the different parts of the root system if a tracer technique is supplemented by a determination of the root-density distribution.

Effects of soil moisture and soil density on development of the root system

Although the optimal performance of the root system in supplying the plant with water and nutrients is not necessarily correlated with its maximum development a restriction of root growth can frequently decrease plant performance. Numerous soil characteristics may affect root development: aeration, soil moisture, pH, physical impedance, lack or excess of certain elements etc.

Some remarks will now be made on the effects of soil moisture and soil density.

Water is one of the primary growth requisites for the root. Therefore, it is evident that the ease of extraction must have an effect on growth rate. A number of investigators have published data on observed relationships between soil-moisture tension and root elongation [9, 10, 32, 39]. In Table I some data published by Bierhuizen and Ploegman are given [3].

TABLE I. EFFECT OF pF IN CLAY ON ROOT-GROWTH RATE (at pF 2.0 100% and at pF 3.0 still 50% available water [3])

Crop	Growth rate in cm/d pF 2.0	Growth rate in cm/d pF 3.0	Decrease in rate (%)
Lettuce	3.40	1.50	56
Spinach	2.10	1.25	40
Radish	2.75	0.55	80
Broad bean	1.75	0.20	89

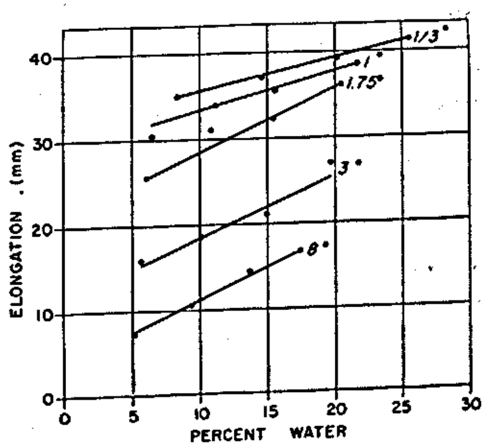


FIG.3. Elongation of corn roots as affected by the ease of water extraction. The same moisture content results in a higher growth rate at lower tension (1-3).

It is evident that the elongation rate decreases as the water tension rises and that, per unit of increase in tension, the effects are higher in the low tension range. A graph published by Peters [31] may serve as an example (Fig. 3).

The large differences noticeable between the different substrates used in the experiments must be partly related to the differences in water content at the same tension. See Fig. 3.

Some other interactions, however, must also be considered. One of the most important is the inverse relationship between water content and aeration. A rising water content in the soil will result in a decrease of the volume of air-filled pores, which, in most cases, should retard gaseous exchange. Besides this, however, a decreasing pF in the soil will cause an increased thickening of the water-films surrounding the root. As this water-film forms the main diffusion barrier in the oxygen supply to the root any thickness increase retards the rate of supply [9, 43, 56]. Enhanced availability of water with its favourable effects may be thus partly counteracted by a restricted oxygen supply or a retarded efflux of carbondioxide.

The relationship usually observed between soil-moisture content and root-growth rate might, in some cases, be partly caused by an increase in soil rigidity, as measured by penetrometer values or shearing strength, as the pF rises [47]. In the field this effect should be more pronounced in loam and clay soils than in sand.

Even though the root-growth rate may be greatly different for separate species, quite often the same ultimate depth of rooting is attained. Since, in many cases, the top soil layers may loose all their available water, the plant has the possibility of compensating for this by sending more roots downwards into moist soil layers [44].

Besides the effect of soil-moisture content on the growth rate in length an effect on root branching has also been noticed [16, 44].

The depth of the ground-water table can be a dominating factor in soil utilization possibilities. Generally the soil below the capillary fringe of the ground-water table will contain so little oxygen that the root growth of the majority of plants is prevented. Therefore, nearly always a high water table in the soil restricts the rooting depth. It is only during winter conditions that roots can survive flooding for some time, as a result of their restricted respiration at low temperatures.

The voids in the soil consist of a large range of spaces between the solid particles. The larger cracks, channels (mostly biopores), and very large capillary spaces will not impede root growth. As the diameter of the channels approaches root diameter the tortuosity of the pathway will be effective. In a completely rigid structure roots will be unable to grow unless the pore diameter is more or less the same as the root diameter, or exceeds it [51].

But, if the growth of the root system were restricted to the abovementioned spaces and pores, the permeation of the soil would be extremely sparse. A dense root system can only originate if the greater part of the roots have been able to push their way through the soil mass. The physical impedance encountered by the minute root tips is thus a decisive factor in the establishment of a well-developed root system.

The mechanical resistance that roots encounter in the soil is strongly related to its density and its texture. Depending on the type of soil, root growth is prohibited somewhere within the range from 1.3 - 1.8 mg/ml volume weight [41, 45, 50]. There is also evidence that some species can overcome a slightly higher resistance than others [20].

But, even before soil density becomes restricting, root growth is already affected [2, 23]. For a fine sandy loam soil a gradual decrease in root elongation was observed as the volume weight increased from 1.2 - 1.9, and for a clay soil the same was found for a density range from 0.94 - 1.33 [45].

In more recent research attempts have been made to obtain a better specification of the forces involved. Root-growth data have been compared to those on impedance as measured by a needle penetrometer or by measuring shearing strength (Fig.4) [23, 46].

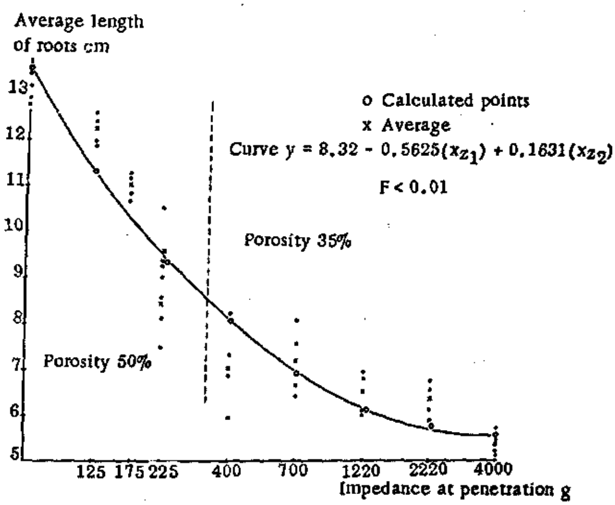


FIG.4. Root growth in relation to penetrometer resistance

The old data, given by Pfeffer [33], showing that the roots can exercise a pushing power of over 10 kg/cm^2, have been confirmed. More recent research mentions critical soil-strength values of 20 - 30b [47].

Observations both in the field and in laboratory research have shown that the soil's mechanical resistance can be strongly influenced by water content. On drying, clay soils become completely impenetrable to roots and they may even restrict a secondary thickening of larger roots already grown through [47]. But, even at much lower pF values, soil cohesion increases as water content diminishes [46, 47]. An example of such a relationship is given in Fig. 5, from a work by Maertens [23].

Soil density, however, is also inversely related to pore space and aeration. A restricted oxygen supply can be the limiting factor, especially in the lower pF-ranges. But, even if the oxygen supply is not low enough to prohibit root growth, the force the root can develop is related to its aeration. In experiments better and faster root penetration has been observed under an increased rate of oxygen supply [8, 45].

By means of the Pt micro-electrode a rate of oxygen supply below 18 to 23 $\times 10^{-8}$ g cm^{-2} min^{-1} has been shown to be the lower limit at which the roots of a number of species will grow [43]. Other investigators also give limiting values of 20 to 30 $\times 10^{-8}$ g cm^{-2} min^{-1} for oxygen flux [53, 56].

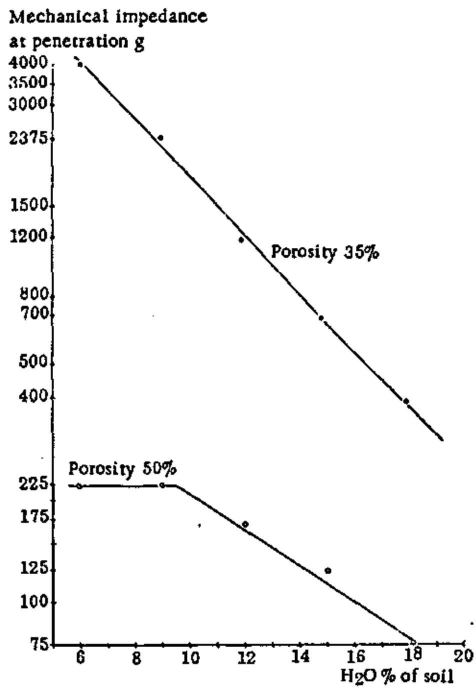


FIG. 5. The decrease of soil strength (mechanical impedance) at two densities with increasing moisture content

SUBSOIL UTILIZATION

In general the top soil will be the layer that contributes most to providing the plant with mineral elements. It is usually more fertile than the subsoil and also contains the largest part of the total root mass [11, 12, 29, 49]. But, it must be asked what is the importance of the roots in the subsoil, except for supplying the plant with an amount of auxiliary water.

A highly mobile nutrient such as nitrate may be easily transported down to deeper layers by means of percolating water. However, extensive research at our institute has shown that, below a fully developed crop, no nitrate can be recovered from the main part of the soil permeated by the roots. This absorption must have been performed by the subsoil roots.

Also, several investigations by tracers has demonstrated that roots in the deeper soil layers are certainly able to absorb any available nutrient [6, 18, 25, 29].

It might be asked if roots at greater depths near a water table, where aeration is gradually approaching a limiting value, are still able to absorb nutrients. Model experiments have definitely revealed that live roots in the subsoil, near their limits of growth possibilities, are still functional in absorption [54]. If there are nutrients available in these subsoil layers (60-100 cm deep) the performance per unit root mass may even exceed that of topsoil roots [17, 28, 54]. This fact must be related to the higher moisture content at these depths – especially under normal field conditions – which facilitates mineral absorption (Table II).

TABLE II. COMPARISON OF RELATIVE AMOUNTS OF ROOTS AND RELATIVE UPTAKE FROM SUBSOIL HORIZONS [17, 28]

Depth of soil layer	Total absorption (%)			Total root-mass (%)	
50-75 cm	21	11	(^{32}P)	7	4
50-60 cm	42	46	(^{32}P)	29	29

SUMMARY

After enumerating the diverse methods for investigating root systems in the field a comparison is made of their respective merits. If the information required concerns only the morphology of the root system the traditional systems would in most cases be preferred.

The tracer techniques, however, are indispensable when data on the performance of the different parts of the root system are required and are to be compared. For this purpose some radioactive isotopes can be used to advantage. The relative activity of different parts of the root system can be compared if the tracer techniques are accompanied by root-mass distribution data.

The average factors of the influence of soil-moisture content and soil density on root-growth are briefly discussed. In general, the rate of root elongation is enhanced at low pF and low density. But the many interactions and relationships with aeration are illustrated.

Finally, some remarks are made concerning the utilization of the subsoil. It is pointed out that the sparse root system in the deeper soil layers still has its full potential for the uptake of nutrients. If sufficient nutrients are available in the subsoil the generally higher moisture content may lead to a relatively high rate of uptake per unit root mass.

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DISCUSSION

M. FRIED: The more I hear about water use, nutrient utilization, the more I wonder if in fact plants grown under irrigated systems really need extensive root systems. If the plant does not need the root system, are we not wasting nutrients and photo-synthetic potential to grow useless plant material. I am sure that plant breeders, given the task, could develop varieties with smaller root systems providing this is advisable.

L.K. WIERSUM: I would agree with the notion that plants under irrigation do not need the extensive root systems they could grow. Experience has already definitely shown that the volume of soil occupied by the root systems can be severely restricted if it is possible to maintain a sufficient rate of water and nutrient uptake (supply). In these cases a large shift in shoot/ratio is also observed. As the volume of soil occupied by the root system decreases it can be partly compensated for by greater rooting density resulting in more absorptive surface per unit soil volume.

Experience would have to show what rooting depth is acceptable to obviate periodical stress periods.

To a certain extent the root system would adapt itself to a shallower wetting of the profile. Possibly breeders could assist in selecting appropriate varieties and similar suggestions have already been made elsewhere.

M. FRIED: It seems that the choice of means for studying the roots depends entirely on the question one is asking. If one is interested in nutrient absorption activity, then uptake from labelled nutrients from different places in the root zone would be the method of choice. If one is interested in water absorption, labelled water might be the method of choice. Other questions might result in other methods of choice.

L.K. WIERSUM: I certainly agree.

M. GAIRON: Do you think that the specific activity measured on aerial parts of the plants are directly and linearly related to the specific activity applied in a given layer of the root zone? That is, can you say that the ratio of these specific activities is directly representative of the ratio of roots uptaking the tracer to those which do not get tagged material?

L.K. WIERSUM: The specific activity in the aerial parts in many cases will not be directly and linearly related to the specific activity of the different zones of tracer application, mainly because the differences in soil-moisture content affecting the rate of uptake will interfere. Thus the data obtained are far more informative on root performance than on root-mass distribution. Also root mass per unit soil volume is not related to surface active in uptake because, in some regions, part of the root mass is thicker and more suterized and therefore only a slightly active root surface.

Where perennials are being considered the issue could be further confused if only part of the aerial mass is analysed since the distribution may not be even throughout the plant, but may follow special xylem tracks, thus carrying the tracer from certain roots to certain main branches.

M. GAIRON: The method of estimating root activity by measuring the rate of change of moisture content in different soil layers has been used in Israel. It has been found that 90% of the water extracted from a root zone of 2 m, came from the top 1 to 1.5 m. This estimate has been used to cut down seasonal consumption in certain crops (deep-rooted) by as much as 15%, irrigating only what we may call the effectively active root zone.

L.K. WIERSUM: The evidence you have just given corroborates results obtained elsewhere. In Australian research on onions a suggestion was made to restrict irrigation to about two-thirds of total rooting depth.

If, however, water-extracting data are to be used in assessing ultimate root depth the situation differs. Above a water table and moist subsoil there will be a soil layer permeated by sparse roots not showing water loss as the inflow will be as fast as the extractions.