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POTENTIAL SUBSOIL UTILIZATION BY ROOTS

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INTRODUCTION

In agriculture it is usually considered an advantage for a crop plant to have deep roots. Indeed, in many cases the supply of water under drought conditions may be safeguarded by the uptake of moisture from the subsoil. But the question also arises whether the roots in the deeper layers contribute to the mineral nutrition of the crop to any worthwhile extent. In most soil types rooting in the deeper layers is rather sparse and the fertility in these regions is usually less than that of the topsoil. The uptake of nutrients from subsoil has been demonstrated by a number of experiments including those in which tracers have been employed.

The present experiments investigated the potential feeder capacities of roots in the deeper soil layers. This problem becomes important in dry periods when parts of the root system located in the upper soil layers may become inactive. The possibility of any interactions on the performance of deep roots by roots feeding in the topsoil was not taken into account. For this purpose a special technique, related to that used by Millar[11], had been devised (De Roo and Wiersum[15]), so that the part of the root system concerned with the uptake of nutrients was made to develop below predetermined levels.

This technique also made it possible to obtain some information on the problem whether the aeration necessary for root activity in nutrient uptake was higher or at the same level as that allowing growth. It is possible that roots could still grow under conditions of very poor aeration, which would prevent or restrict the uptake of ions.

EXPERIMENTAL PROCEDURES

It has been shown that roots can be trained down to predetermined depths in plastic tubes to allow soil contact of the emerging root system at variable depths (De Roo and Wiersum [15]). For the major part of the experiment the soil moisture conditions were comparable to those occurring in dry periods.

There was generally an increase in moisture content towards the bottom of the vessels, where a stagnant water table occurred. The aeration gradient was inverse to the water content and reached so low a level that growth of roots into the water table was impossible (Figs. 2, 3, and 7). The oxygen diffusion rate data given in Table 3 and Fig. 5 show that this effect was achieved.

The calculated root performance values for wheat, broad bean and Brassica are influenced by the fact that, as the roots are situated at a lower level, there is a relative increase in the mass of young absorbing roots. Each increase in depth implies more older roots being enclosed in the plastic tubes. For this reason the 1965 experiment with potatoes was designed to eliminate this effect This was achieved by planting long-stemmed plants, enclosed in the plastic tubes, at the desired levels. In all cases a complete root system was in contact with the soil and more frequent aeration measurements were made.

The soil profiles in the vessels were homogeneous from top to bottom and fertilizer was applied where necessary in a 20-cm layer at varying depths, corresponding with that of root entrance into the soil.

A schematical drawing of the first experiment is depicted in Fig. 1. The main vessels consisted of either asbestos pipes, 100 cm high and of 12 cm internal diameter or of plastic pipes of the same height and about 14 cm internal diameter. The plastic pipes had been cut lengthwise in halves beforehand and could be laid open at the end of the experiment, facilitating observation of the root system. Twenty-five pipes were filled with soil at the desired density. Twenty of these vessels contained plants grown in plastic tubes, 2½ cm diameter, of 20, 40, 60, and 80 cm length. In five of the vessels plants were planted out without plastic tubes and with the full length of soil at their disposal.

The vessels were placed in a shallow basin and randomized in a latin square. The basin was filled with mud to which fresh organic matter was added. Above the mud was a layer of about 2 cm water which ensured that the water rising into the vessels was anaerobic. The stagnant water table at about 5 cm from the bottom of the vessels provided a barrier to root growth and no roots could escape into the basin.

The different crops used in the experiment were germinated on moist sand and the young seedlings were transplanted into the plastic tubes or a 5-cm flowerpot. These were filled with a loose substrate consisting of 1 part garden soil, 1 part vermiculite and 1 part peat mull. This substrate only contributed slightly to the nutrition of the plants and allowed a very fast root growth downward. Watering was done by immersing the lower ends of the tubes in water. Preliminary growth was continued until roots were visible at the bottom end of all 40-cm plastic tubes. By this time some of the 60-cm tubes were

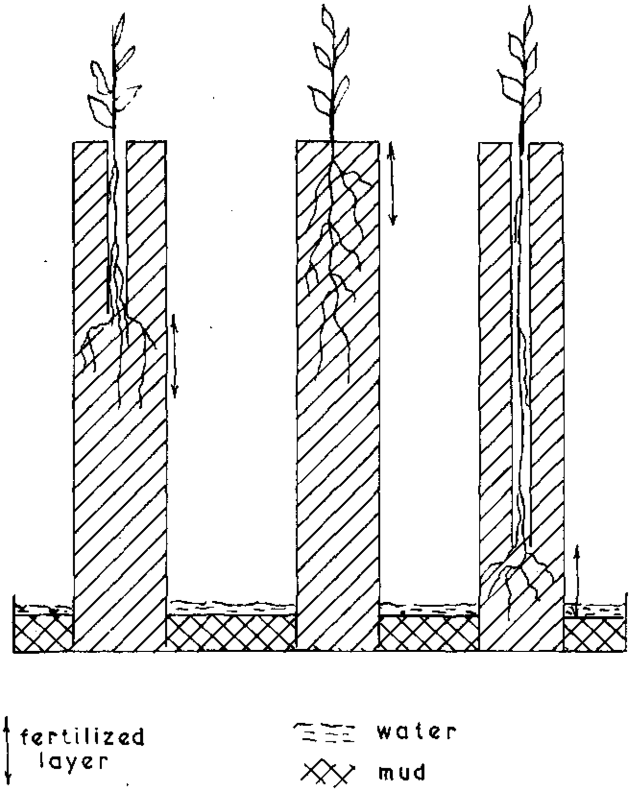

Fig. 1. Schematical drawing of the experimental setup.

traversed by a few roots. At this stage the plants were transferred to their vessels. The plastic tubes with plants were let down to their full length and the surrounding soil filled in. The plants at the moment of starting the experiment were of reasonable uniformity and, exept for those in the 80-cm tubes, were immediately able to enter the soil with new root growth.

After placement of the plants in the vessels water was added where necessary for the first few days to assist establishment. Thereafter no more water was given. The plants had to rely mainly on water rising by capillarity from the bottom water table. As the experiment was placed in the open air under wire netting the plants also received some rainfall.

None of the crops was grown to ripeness, but since they were usually harvested at a stage where fruits were already present, they had mostly attained optimum size.

During the experiment growth measurements were regularly made. At the end of the experiment the above-ground parts were cut off and fresh and dry weight was determined. The root mass was extracted from the asbestos pipes by washing, and also the roots in the plastic tubes were extracted. Fresh and dry weight determinations were made. The plastic pipes were laid open to study root distribution.

At harvest the aeration conditions in a set of vessels was measured electrically with a micro-electrode (Lemon and Erickson[9]) where the platinum tip of the probe (Wiersum[19]) was replaced by a solid golden conus of about 6 mm length.

Uptake of N, P, and K was determined by chemical analysis.

RESULTS

Experiment with spring wheat (Peko)

The pipes were filled with a loam soil of a density of about 1.29 (Table 1). Fertilization of a 20-cm layer was achieved by addition of a mixture of ion-exchange resins saturated with NO_3, H_2PO_4, K, Mg, and NH_4 (± 600 ml on 20 l of soil). This was done to prevent displacement of the added nutrients, either by leaching or capillary rise.

TABLE 1

Sample	pH (KCl)	Humus %	$CaCO_3$ %	Particles $< 16\ \mu$ %
Loam soil	6.85	1.7	7.2	13.8
Sandy peat soil	5.80	5.2	0.05	1.9
Sandy soil	5.40	4.3	0.06	4.0
Soil mixture in plastic tubes	6.93	2.8	0.68	7.4

It took the seedlings 22 days to let their roots grow down to the bottom of the 60-cm plastic tubes. After this period of initial growth the experiment was planted on May 30 and lasted until August 20.

The plants in the 60-cm long tubes showed the best development, with the plants in the 40-cm tubes second best (Table 2). The lowest yield occurred in the 80-cm tubes. The favourable growth in the 60-cm tubes is most probably due to the fact that after planting the new roots protruding from the tube immediately enter soil with a very favourable moisture content. The plants without tubes have to start in a much drier soil and also to use more dry matter in the formation of an extensive root system.

Net production was calculated by subtracting the plant weight obtained in the control plastic tubes of equivalent lenght from that of the yield obtained in the tubes in the soil-filled pipes. Free roots are those that have entered the soil in the main vessel.

It is clearly evident that the net sprout/free root ratio progressively increases as the roots have been forced down to a deeper level. We must conclude that at these lower levels a relatively small amount of roots can still feed a plant.

That a small mass of mainly young roots at a depth below 80 cm still functions well is clearly demonstrated by the amount of nutrient absorbed per unit root weight. It is about ten times as high as that calculated for a root system occupying the whole soil column. This very high figure may also be influenced by the relative uncertainty of the net amount of N-, P- and K-uptake, which has been calculated by subtraction, and the values obtained will be enlarged since a complete root system will include inactive and suberized roots.

The observed facts, however, clearly demonstrate that these roots, which are situated in the deeper soil levels and partly near the stagnant water table are able to absorb nutrients as vigorously as roots in the other layers of soil.

Experiment with broad bean ('duiveboon')

Here the pipes were filled with a sandy peat soil ('veenkoloniale grond') (Table 1). The soil was filled in with a density of 1.23.

The experiment was planted on May 29, after a period of four weeks, during which time the seedlings were able to get established in the plastic tubes and in which time roots grew down to at least 40 cm. Six weeks later, during flowering, the plants were topped to obtain more even ripening. The experiment lasted until August 12.

The best start was again obtained with the 40- and 60-cm plastic tubes, although ultimately the plants in full soil and in the 20-cm tubes gave the highest yields. In Fig. 2 both the growth of the tops and the development of the root system is depicted. It can be seen that the roots suddenly stop in their downward growth, especially in the 60- and 80-cm tubes, and are close to the stagnant water table. It is evident that the roots leaving the plastig tubes stay below the bottom end, and that only an occasional root grows slightly upwards. The data obtained are compiled in Table 2.

TABLE 2

Yield, nutrient uptake, and root performance

Crop	Treatment	Average net production and net uptake of sprout				Average amount of free roots, dry weight	Ratio net sprout/ free roots	mg uptake per gram of free roots (dry weight basis)		
	Roots below	Dry weight g	N-uptake mg	P-uptake mg	K-uptake mg	g		N	P	K
Spring wheat 'Peko'	0 cm	16.2	227	44	278	3.7	4.4	61	11.9	75
	20 cm	8.3	122	26	155	0.8	10.0	152	32.5	194
	40 cm	17.9	264	45	316	1.3	13.8	203	34.6	238
	60 cm	21.0	307	54	350	1.4	15.0	219	38.6	250
	80 cm	4.4	66	10	89	0.1	44.0	660	100	890
Broadbean 'Duiveboon'	0 cm	24.3	632	75	581	3.4	7.1	186	22	171
	20 cm	23.1	603	62	508	1.4	16.5	431	44	363
	40 cm	15.3	410	50	321	0.7	21.8	586	71	459
	60 cm	15.3	398	44	317	0.7	21.8	569	63	453
	80 cm	2.0	53	6	40	0.2	10.0	265	30	200
Brassica type 'Snijmoes'	0 cm	9.6	210	30	260	2.7	3.6	78	11	96
	20 cm	17.2	233	59	322	2.4	7.2	97	25	134
	40 cm	15.0	219	39	290	2.1	7.1	104	19	138
	60 cm	9.6	137	18	98	1.5	6.4	91	12	65
	80 cm	1.2	34	8	36	0.3	4.0	113	27	120

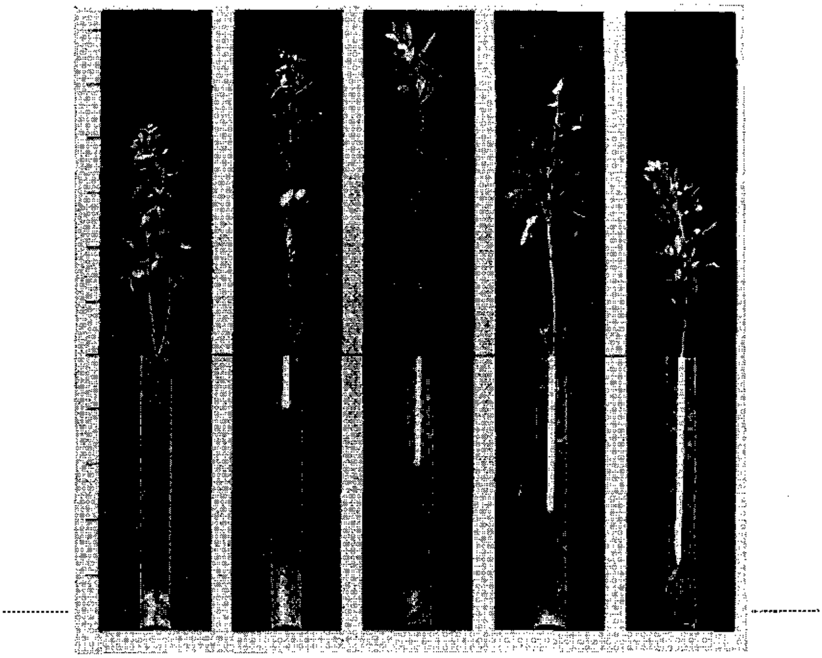

Fig. 2. A series of five plants of the experiment with broad bean. All roots stop downward growth above the stagnant watertable (------). No. upward growth of roots.

TABLE 3

Average values of relative oxygen diffusion rates at different depths

Depth in cm	50	70	80	90
Wheat . . .	33	33	32	28
Broad bean .	20	20	16	8
Brassica. . .	23	30	21	17
Average	25	28	23	18

The results confirm those obtained in the experiment with wheat. The lowest net sprout/free root ratio is found with plants with the normal root system. The deeper the mass of feeder roots is situated in the soil the larger this ratio becomes, with a decline for the plants with their free roots below 80 cm depth. Even at this depth and under aeration conditions near to the critical point (Table 3) the roots still behave well.

Experiment with Brassica napus *var.* tabularia (*'Snijmoes'*)

For this experiment a sandy soil was used to fill the pipes (see Table 1). The soil was filled in with a density of 1.35 and no extra fertilizer was applied.

The seedlings were grown for about four weeks and then placed in the pipes along with their tubes on May 24. The experiment lasted till July 8, when the plants were harvested. Plants in the 20-cm tubes were the best in this case, followed by those on the 40-cm tubes. The yields (Table 2) again suggest that the topsoil layers may have been dry for part of the time.

The behaviour of the roots of these plants, however, was quite different from that of the two other crops. Many roots grew upwards, towards the surface, after leaving the plastic tubes. The rooting was not restricted to below the preset level.

Also the roots of this species did not penetrate as near to the groundwater level as did the other plants, although the aeration was better than for the beans. This fact along with the upward growth suggests a strong preference for well aerated layers. It can also be seen (Fig. 3) that the roots leaving the 80-cm tube grew in a zone adjacent to that where aeration prohibited further root growth. Oxygen supply must certainly have been rather restricted at this depth for this species, which seems to have a high requirement.

As a result of this aberrant root behaviour the results obtained in this experiment show a slightly different trend. Deeper rooting enhances the performance of the roots, but the differences have been levelled off. There is no clear cut optimum as the highest sprout/root ratio was observed at 20 cm depth and optimal N- and P-uptake was at 80 cm depth.

Therefore with Brassica also it appears that potential root performance in soil layers at greater depths was not markedly impaired. As long as the roots were able to grow they were also absorbing ions. The amount of nutrient uptake per unit root weight was variable, but at least the deeper situated roots performed well.

Experiment with potatoes

Although the evidence obtained in the previously described experiments clearly points to the fact that the deep situated root systems are able to perform normal uptake of nutrients, some anomalies

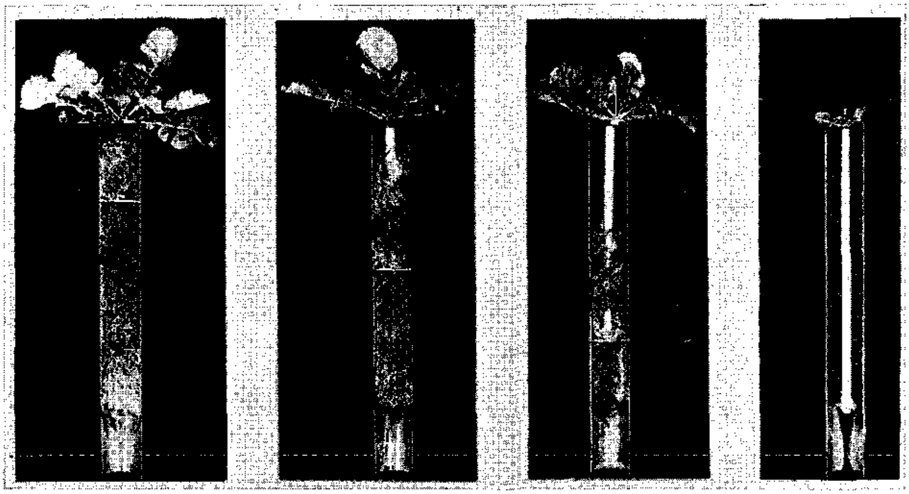

Fig. 3. Part of the Brassica plants at the end of the experiment. Upward growth of the roots is clearly evident and also the greater distance to the stagnant watertable (------).

still remained. This led us to devise a new experiment in which the total root system was allowed to develop at different depths with long stemmed plants, enclosed in plastic tubes, entering in the soil at predetermined depths.

The root systems always consisted of old suberized roots and of young active rootlets. Also more numerous aeration measurements were performed.

Experimental procedure. The experiment was performed with the potato cultivar Prefekt.

Using a cork borer, single eyes were removed from pregerminated seed potatoes with about 1 ml flesh attached. These small pieces were given a pretreatment with gibberellic acid to force them to grow long, slender and unbranched stems. They were then planted in moist peat mull. After the stems had attained about 30 cm length the young plants were placed in small flowerpots (diameter 6 cm) filled with the same soil as was used in the experiments. Small leaves along the stem were cut off and a plastic tube (diameter 2.5 cm) of 60 cm length was put around the stem. Under these conditions the plants were further cultivated until the tips of the stems of most plants had reached the top of the tubes.

At this stage the plants with their enclosed stems and rooted clod of soil were planted in the vessels. These consisted of plastic pipes, diameter 12.5 cm, filled with a sandy mixture and either 80, 60, or 40 cm long. After planting

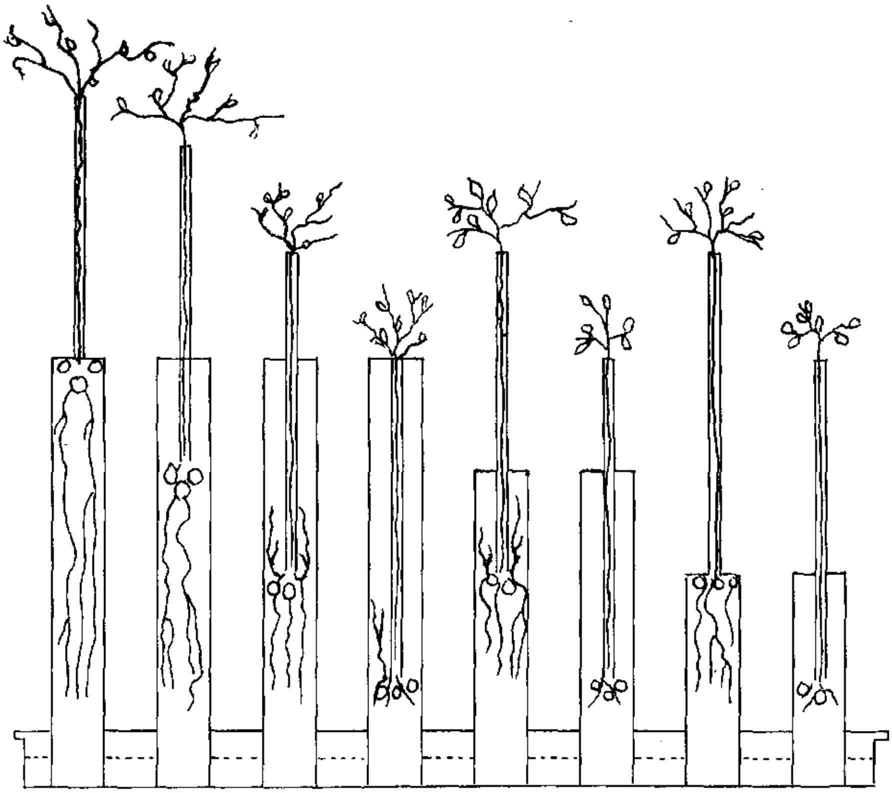

Fig. 4. Schematical drawing of the treatments in the potato experiment. ------ level of anaerobic water in the closed trough.

some silicone rubber was poured into the narrow plastic tubes around the stem to form an air seal at the bottom of the tube.

The whole batch of 32 pipes was placed in a large trough filled with about 5 cm of water. The trough was covered with a lid, containing holes for the pipes. By letting a stream of nitrogen gas flow underneath the lid the 'ground water' was kept as anaerobic as possible.

A diagram of the experiment is given in Fig. 4. The planting depth was 0, 20, 40, and 60 cm in the 80 cm vessels, 20 and 40 cm in the 60 cm vessels and 0 and 20 cm in the 40 cm pipes. Every treatment was replicated four times.

The experiment was in the open air. As the plants grew out of their tubes and took on a normal healthy growth the plants were fixed to a wire netting to prevent damage by wind. After a growth period of about 10 weeks the plants were harvested, the pipes were laid open to study the root system and ultimately the tubers and roots were washed free of soil.

A few young plants were not planted in the experiment but used as a control for analysis of the nutrient content at the start of the experiment. After analysis of sprout + tubers the net uptake during the experiment was calculated by subtracting the control value from the final quantities.

After harvest the plants were split into roots and sprout + tubers. Fresh and dry weight was determined and the N,- P-, K- and Ca-content of sprout and tubers was analysed.

TABLE 4

Data on yield, nutrient uptake and root performance of potato

Treatment	Rooting depth / Height of vessel	Dry weight g	N-uptake mg	P-uptake mg	K-uptake mg	Ca-uptake mg	Average amount of roots dry weight g	Ratio sprout/roots
A	0/80	29.6 ± 10.0	515	52	834	265	1.33	22.1
B	20/80	21.0 ± 7.0	409	38	696	204	0.80	26.2
C	40/80	30.8 ± 12.1	348	38	592	223	0.59	52.2
D	60/80	23.0 ± 5.6	438	37	632	240	0.79	29.1
E	20/60	25.0 ± 5.2	406	40	594	221	0.67	37.3
F	40/60	5.7 ± 1.7	79	7	122	52	0.33	17.3
G	0/40	25.0 ± 3.2	326	43	558	175	0.65	38.5
H	20/40	4.5 ± 1.2	44	7	112	29	0.46	9.8

Results. The main data are given in Table 4. It is evident that in nearly all cases reasonable growth has occurred. Only treatments F and H have resulted in poor growth of the plants, also accompanied by a smaller top/root ratio and root mass.

The top/root ratio values suggest that the plants with their total root mass in the soil layers with an intermediate to high moisture content have the best root performance. This confirms the previous results, although the general rise in activity as the roots are situated at deeper levels is absent here. This is partly the result of the fact that always the weight of the total root system could be taken into account and may partly be influenced by the upward growth of some of the root systems. Treatment A (Table 5) again demonstrates that the roots in the top soil layers may partly have been less active on account of low moisture content.

Root performance (net uptake per mg of dry roots) and oxygen diffusion rate values at the depth of root entrance into the soil are given in Table 5. Here it can be seen that root performance stays at a high level even if the relative O.D.R.-values decrease to 30. Thus

TABLE 5

Rate of uptake in relation to relative O.D.R.-readings

Treatment		O.D.R.	Root performance, mg/g roots				Upward growth
			N	P	K	Ca	
A	0/80	60*	387	39	627	119	–
B	20/80	57 ± 3.1	512	47	870	255	–
G	0/40	47 ± 1.0	502	66	858	269	–
C	40/80	47 ± 4.1	590	64	1001	378	+
E	20/60	45 ± 7.6	606	60	887	330	+
D	60/80	30 ± 2.3	554	47	800	304	+
H	20/40	25 ± 2.7	96	15	244	63	–
F	40/60	24 ± 1.0	239	21	370	157	–

* Extrapolated value.

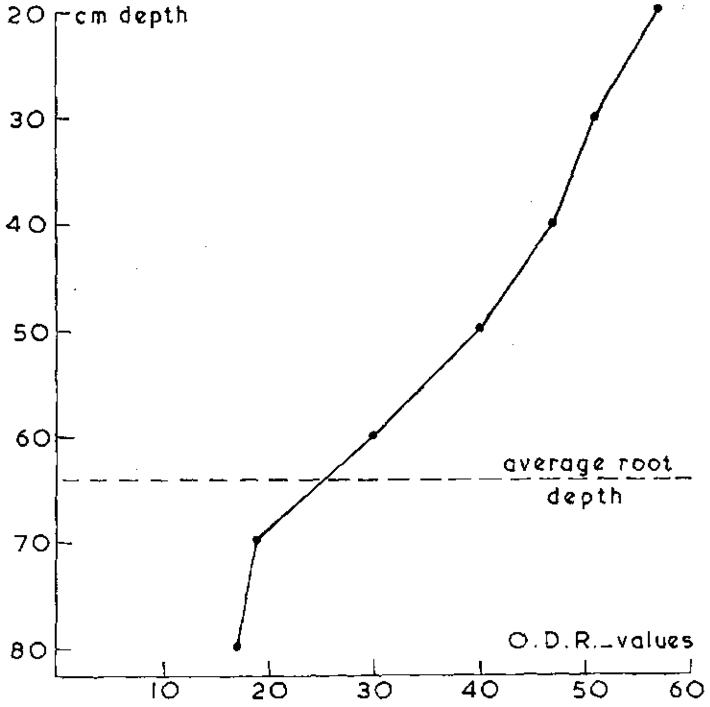

Fig. 5. Graph of the oxygen diffusion rate measurements at different depths and rooting depth attained in the 80 cm vessels.

even roots below 60 cm depth in the 80-cm vessels perform well. Only if the oxygen supply is still lower a sudden decrease in root growth and activity is clearly evident. In these treatments (F and H) the oxygen supply of the root mass was so low, that if the roots had not been planted at that level they would not have penetrated into these layers. That this is the case can be derived from the graph in Fig. 5, in which the O.D.R. readings at different depths are plotted and in which the ultimate root depth attained is shown. This shows us that roots are inhibited from further growth downward at a value of 26.

In the Treatments F and H the roots already developed during the period of early growth have managed to keep alive and have hardly made new growth. It is no wonder that under such conditions below the normal limiting value root performance is impaired, as is also shown by the fact that the roots have not managed to grow upwards.

This upward growth of part of the root system, when released at greater depth, is indicative of a search for better aerated layers (Wiersum [20]). This rather uncommon behaviour underlines the fact that aeration values between 30 and 45 are relatively low for potatoes.

DISCUSSION

In considering the quantity of nutrients the subsoil can contribute to the crop a number of factors have to be taken into account. The most important are root density, the nutrient status of the subsoil, and its moisture content. The differences in these variables may account for the large variation in the published data.

With only a very few exceptions all information in the literature has been obtained on undisturbed complete root systems. The extent to which the subsoil roots have contributed to the nutrition of the plants may have been influenced by the ability of superficial roots to absorb nutrients. If only part of a root system has nutrients available a certain compensation in the form of increased uptake may occur. But this phenomenon enhances the importance of subsoil roots if stress conditions occur in the superficial layers. In case favourable conditions along with high chemical fertility exist in the topsoil the contribution of the subsoil roots might be relatively reduced.

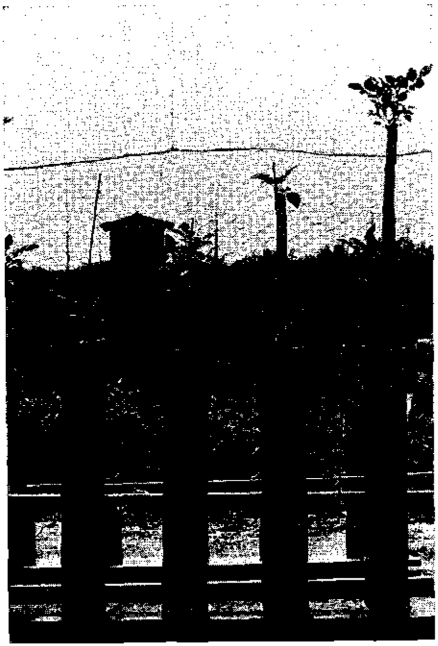

Fig. 6. Part of the experiment with potatoes. The rubber stops are removed when taking O.D.R.-readings.

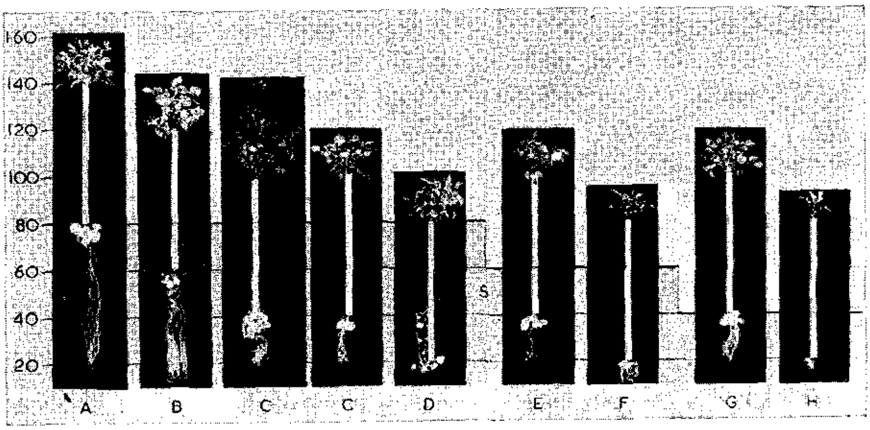

Fig. 7. Results obtained with potatoes. In some cases upward growth of roots and stolons. S = depth of soil columns.

Millar[11] showed that the development of roots in the topsoil could be prevented by the use of glass cylinders of 20 cm length and that a reasonable uptake of nutrients could be obtained from a zone below 40 cm depth.

A review of the research on the uptake of nutrients from the subsoil including evidence that phosphate could be absorbed from depths to below 75 cm is given by Schütze[16]. Goedewaagen[7] also gives some examples.

In more recent work the availability of radioactive tracers has made it possible to calculate the contribution of separate soil layers. Both Murdock and Engelbert[12] and Shain and Kashmanova[17] conclude that P can be absorbed in substantial amounts from the subsoil, even from depths of about 100 cm.

Information on nutrient absorption from the subsoil may also be found in papers by Calvert[2], Ellis *et al.*[3] and Beauchamp[1].

The results obtained in experiments on subsoil tillage (De Roo[14]), liming of subsoil (Sluysmans *et al.*[18]) and information correlating growth and depth of rooting (Henin and Gras[8]) or thickness of favourable subsoil layers (Ford[6]) all suggest extensive activity of roots in deeper layers of the soil.

Far more interesting are the results of experiments where both uptake from and the amount of roots in the deeper layers of the soil have been established. Fox and Lipps[4] (1960) came to the conclusion that where the topsoil became dry 3 per cent of the roots of alfalfa at 200 to 400 cm depth absorbed 62 per cent of the mineral uptake. Also Van Lieshout[10] showed that for corn and oats the contribution in nutrition from the soil at 60 to 80 cm depth exceeded that of the percentage of roots, *viz* 1.7 per cent roots contributed 9.2 per cent of the uptake of phosphate. Nakayama and Van Bavel[13] also noted that P absorption of 7 per cent of the total could be accomplished by a 2 per cent root-mass at 60 cm depth. Fox and Lipps[8] (1964) demonstrated that 60 per cent of the total root activity of alfalfa took place at depths below 7 feet as a result of the more favourable moisture conditions.

The results obtained in the present experiments confirm the observations mentioned above. The results, especially those obtained with broad bean, Brassica and potato demonstrate that roots growing on the fringe of layers where lack of oxygen prevents further growth downward, still retain their capacity for uptake of nutrients.

Thus the conclusion can be made that the limiting oxygen requirement for growth and absorption of minerals are the same. This means that any live root in the subsoil has the potential ability to absorb nutrients.

The fact that uptake per unit weight of roots usually rises along with the depth at which they occur can be considered as the result of two factors. First, as the absorbing roots are forced downwards by means of the plastic tubes an increasing part of the main, thicker roots is not taken into account.

The amount of free roots shows a rising proportion of feeder roots as they are at a deeper level. The root systems having the whole depth of soil at their disposal also tend to grow downwards to the more moist layers and so partly consist of older, thicker and more suberised roots.

Secondly, the moisture gradient in the soil column must be considered. Except for rainfall, the main supply of water must have occurred by capillary rise. The upper layers were rather dry during part of the experiment. This must have reduced the activity of the roots in these layers. In the experiment with Brassica and potato where the feeder roots grew upwards again, this effect can be seen. Here the efficiency of the free roots shows less variation and not such a clear trend.

The general conclusion is that the roots in the subsoil certainly are of potential value in feeding the plant provided that plant nutrients are available. Their relative performance may even rise to high values depending on the circumstances in the topsoil. Their contribution to plant nutrition will further depend on the fertility of the subsoil layers, the moisture content of these layers and the amount of roots that have been able to develop in these regions.

SUMMARY

By training root systems through narrow plastic tubes down to below predetermined levels the potential capabilities for uptake from deeper soil layers was investigated.

In the experiment, carried out in asbestos pipes of 1 meter height, a soil column with an increase in moisture content downwards coupled with an inverse aeration gradient was established.

Uptake per unit of roots in contact with soil was higher in the deeper layers. The increase in activity must partly be attributed to the method of calcula-

tion, but is in line with other observations in the literature. Roots growing in soil layers, where aeration is limited, still perform well, demonstrating that growth and uptake have about the same oxygen requirements.

Any root in the subsoil can thus be considered as a potential absorbing unit for nutrient uptake.

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