

ROOT-SOIL RELATIONSHIPS

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I think most people would agree that root studies have been relatively neglected in the past. The internal anatomy of roots has been studied often, but the study of their distribution and function in soil has suffered from the simple fact that they are concealed. Excavating roots is a tedious matter, and even successful excavation destroys the experimental material. Nevertheless, studies on roots seem to be increasing rapidly, and they received a large impetus from the 15th Easter School at Nottingham University in 1968 which dealt with root growth. Further, the development of the Agricultural Research Councils Letcombe Laboratory has led to some exciting work.

I cannot summarise all recent work in one paper but for convenience we can classify such studies under these headings:

1. Root detection and measurement.
2. Root system morphology and distribution.
3. Root system function in nutrient uptake.
4. Root system function in water uptake.
5. Roots and soil biology.

I want to discuss some recent work in groups 2, 3 and 5.

Root Distribution. The basic question is how much root a plant needs to supply itself with sufficient water and nutrients. It has been suggested, mainly from root pruning experiments, that crop plants have much more root than they now need, because they evolved in competitive situations where this large amount was needed. When cultivated, the plants might manage with less. I think that such generalisations may be dangerous — the amount of root which a plant needs depends upon the soil and climate, as well as the degree of competition and growth.

It is well known that the root/shoot ratio is small in conditions where nutrients and water are in good supply, and vice versa. Adding nutrients, particularly nitrogen, will increase the root proportionately less than the shoot, and if sufficient is applied, the total root mass may actually be decreased. Individual parts of the root system also respond to local soil conditions and either nutrient concentrations or soil compaction or, even the presence of other roots. Thus roots react to a small localised application of P or N by branching and proliferating in that area, though the growth rate of the primary root apex may be greatly diminished. Thus, root systems in poor or dry soils tend to be

sparse, thin and widespreading, whereas root systems in fertile and well-watered soils are dense, compact and heavily branched. If too much fertiliser is added, salinity problems are encountered which may reduce growth of roots, and of tops, drastically. Some of the results of Thiessen and Carolus (3) are quoted in Table 1, to indicate how large the effects may be.

Table 1. Main root elongation in 2 days for tomatoes, growing with various additions of 10-52-17 fertiliser in 6 inch pots with sandy loam soil.

Fertiliser rate g	Osmotic pressure of soil extract, bars	Root elongation cm
0	0.11	0.39
2	0.17	0.85
4	0.18	0.65
8	0.24	0.21

The stimulating effects of small doses of fertiliser, and the detrimental effects of too much soluble salts, are evident. In general, damage can be correlated with the osmotic pressure of the solution, and 1-2 bars seems to be a danger limit, but this depends greatly upon the nature of the salts, and the plant species. It has been known for a long time in general terms that plants react in these ways, but if you ask what the mechanisms are which cause it, or exactly how large the effects are, I cannot give any precise reply.

Root system efficiency. It is laboring the obvious to say that a plant only takes up nutrients because it is growing. It is the speed, or *rate*, of nutrient uptake we should be interested in, not total amounts. If we know the growth rate of the plant, the percentage of a nutrient in it, and the quantity of root, we can calculate the uptake rate per unit length or weight of root. Quite a lot of information on mean uptake rates is becoming available now (2), and it is quite surprising that this average rate, for young, healthy plants is not too dissimilar among different species. Roughly, it seems that 1 gram of plant root needs to supply the plant with about 1.5 mg/day N, 0.2 mg/day P and 3 mg/day K to keep it growing at full speed. The whole question of plant nutrition is whether it can maintain this rate. If the root is to absorb at this rate, it must get the nutrients from the soil around it, and we ask now whether the soil can supply nutrients at the required rate. Obviously, the soil close to the root becomes depleted, and the supply of nutrients to the root depends upon the process of diffusion of ions in this depleted zone.

A lot of effort has been expended on studying the movement of nutrients in this thin layer of soil close up to the root, since this determines the rate at which ions arrive at the root surface. We have had to simplify, because the real state of soil near the root is exceedingly complicated, heterogeneous and variable. Our aim has been to identify those soil properties which determine the rate at which ions arrive at the root surface. Gradually, we build up a mental picture of what is taking place in the soil exploited by a root system, and if we can put this into mathematical form, we call it a 'mathematical model'. One relatively simple one is as follows (1):

$$M_t/M = 1 - \exp \left[\frac{-2\pi a a Lt}{b \left(1 - \frac{a a}{2 b D} + \frac{a a}{Db} \ln \frac{x}{a} \right)} \right]$$

Here M_t is the amount of a nutrient taken out of a unit soil volume by roots up to time t ; M is the total amount present in that volume; a is a coefficient which indicates the root absorbing power, a is the root radius, L the length of root in unit volume of soil, b is the buffer power for the nutrient, which measures the reserve supply, D the diffusion coefficient for the nutrient in that soil, and x the average half-way distance between two roots. I cannot pretend to discuss it in the time available, but it will show those soil and root factors which we consider to be important to the nutrition of plants. We have made tests of this equation with plants growing in simple, uniform conditions, and found that it predicts the uptake of potassium and nitrogen well.

You may enquire what good this is in practice. At present it is of no direct use, but I think that because of this work we can see our way forward more clearly. Our test shows that we now understand the soil system fairly well. With this knowledge, we can (cautiously) predict the effects of changes in root systems. In particular, we can aim to determine how large a root system ought to be for a defined environment and plant system. Perhaps we can design root systems for maximum efficiency. Plant breeders now consider the effect of shape and structure of a plant on light interception; we may expect them to consider the efficiency of the root system in the same way in the future.

I think this sort of work could well have interest in situations where root systems are artificially reduced below normal levels. This occurs with root disease, with transplants and with newly rooted cuttings. In this case the selection of fertiliser rate and type to ensure the most rapid root growth often is critical. There is a limit to the uptake rate of a given piece of root, and too much fertiliser causes salt problems. Such situations should repay a

careful and quantitative study of how much effective root is left on the plant, whether this restricts nutrient and water uptake, and how it can most rapidly be increased.

Root and Soil Biology. I now want to pass on to some questions of soil biology which we are interested in. I must leave out discussion of disease organisms, and I do not intend to say much about bacteria on roots. They certainly exist there, in large numbers, but exactly what they do to or for the plant is still a subject of extreme disagreement.

There is much less doubt about the soil fungi which form mycorrhizal symbiosis with plants. All of us will know the ectotrophic mycorrhizas on trees such as beech and pine, but it is now becoming evident that a different group, the endotrophic arbuscular-vesicular mycorrhizas may have enormously greater importance.

These mycorrhizas are formed by fungi of the genus *Endogone*; and they are found on the great majority of cultivated and wild plants. Table 2 lists some common species which have been investigated. They are virtually ubiquitous, being found in every type of soil and climate. We have found the spores in practically every soil sample we have tested, and it is my guess that they are in all your nurseries, unless the soil has been sterilised.

Table 2. Some species which have been found to be infected with vesicular-arbuscular mycorrhizas.

Maize	Rice	Tomato	Strawberry
Barley	Clover	Apple	Coffee
Strawberry	Tobacco		Rubber
Onion			Cotton
Liquidambar			Maple

The fungal hyphae ramify inside the plant root cortex after initial infection by a spore germ tube. The host plant supplies carbohydrate, and the hyphae increase both inside and outside the root. The external mycelium moves down the root, re-infecting it at intervals. Eventually, there is a network of hyphae outside the root, extending at least 1 cm. out into the soil.

Inside the root the hyphae form a network too, and small highly-branched structures called arbuscules extend into the cell interior. We have pretty good evidence that the interchange between host and fungus takes place in those arbuscules. It is certainly an exchange; the fungus get carbon compounds, but in return the plant gets nutrients. We know for certain that the fungus supplies phosphorus, and it may supply trace elements also.

These are precisely the elements which move slowly in the soil, and which may, therefore, not reach the root easily in sufficient quantity.

The phosphate supplying effect can be dramatic. We have had 100% response to simple infection with this fungus, on phosphate-poor soils. Obviously we do not expect responses with well-developed root systems in fertile soils, and the infection is in fact much less when the plant is well supplied with phosphorus. If the plant does not need more phosphorus, it is possible that the fungus acts as a parasite, and may decrease the plants' rate of growth.

Research on this subject is still in its initial stages. We really know nothing yet of the effects of these mycorrhizas in practice — simply that they are virtually always present in most wild and cultivated plants. It occurs to me that there may be interesting possibilities in getting rapid growth of transplants with poor root systems, by ensuring that the roots are already mycorrhizal. This point is well known in silviculture, with the ectotrophic mycorrhizae. The endotrophic mycorrhizas may prove equally important — on more species — if we look for them.

LITERATURE CITED

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2. Brewster, J. L. and Tinker, P. B. H. 1972. Nutrient flow rates into roots. *Soils and Ferts.* 35:355-359.
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DISCUSSION

Referring to the shape and size of containers and their effect on root development Prof. Tinker said that growing roots close together does not pose a problem as roots rarely compete for space and, therefore, from a physical limitation aspect, container-growing was not deleterious. However, what does cause trouble is the restriction in volume, which may induce problems of salinity and maintenance of the adequate water status, hence the volume must be big enough to provide a sufficient buffer in relation to the rate of uptake.

Bill Flemer was concerned about the mechanical restrictions imposed by the container and the 'pot bound' effect; the speaker

did not deem it deleterious at this stage provided reasonable precautions were taken on planting. In relation to this latter factor he also indicated the importance of the presence of mycorrhiza for quick establishment and the quick development of a good root system.

The confirmation of the necessity for mycorrhizal presence was implied by one speaker who cited the problems associated with methyl bromide sterilisation of citrus orchards in California and good subsequent establishment of citrus was only achieved when the soil had been re-inoculated with chopped citrus roots.