FLOW OF WATER THROUGH PLANT ROOTS [1])

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SUMMARY

By applying POISEUILLE's law to the vessels of grass roots it is possible to calculate the pressure gradients required to ensure a certain flow of moisture. It appears that, in the case of layers deeper than 10 to 20 cm in a grassland soil, these gradients are greater than those required to ensure capillary flow through the soil. Accordingly, there are so few roots below this depth that the moisture flow through them is negligible compared with the notoriously slow capillary flow.

INTRODUCTION

The transpiring plant withdraws water from the soil. This water has to be transported from the soil to the leaves, where it is transformed into vapour. In so far as transport takes place below (soil surface), water can flow through the roots of the plant as well as through the soil. WIND (1955) showed that, in the case of grass vegetation on a heavy clay soil, transport of water at a level of more than 10 cm below the surface took place almost exclusively via the soil. Accordingly, below that level the grass roots transported only a very small part of the water transpired by the vegetation.

In the experiment concerned, we found roots at more than 10 cm below the surface of the soil; and the question therefore arises as to why they transported hardly any water. The answer to this question must be that, from the point of view of energy required, in this case it was more economical for the plant to raise water through the soil than through its roots. For every movement labour is required. Apparently movement through the soil consumed less energy than movement through the roots.

It is known that soil, especially in unsaturated condition, is an unfavourable medium for flow of water. What can be the reason for the fact that, in the case dealt with, roots were an even more unfavourable medium for the flow of water ?

FLOW THROUGH XYLEM VESSELS

Upward flow of water through the plant root mainly takes place via the metaxylem vessels. These are thin round tubes, in which some perforated cross walls are often found. In grass roots the radius of the vessels is very small; the largest we have found was 0.004 cm. Most vessels are much smaller.

According to POISEUILLE's law, the quantity of water flowing through a cylindrical tube is proportional to the fourth power of the radius of the tube. This means that the quantity of water that can flow through a very thin tube,

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such as a xylem vessel, is very small. The quantity can be calculated with POISEUILLE's formula:

$$\frac{dq}{dt} = \frac{\pi r^4}{8\eta} \frac{dp}{dx}$$

In this formula $\frac{dq}{dt}$ indicates the quantity of water passing per second through a section, perpendicular to the direction of the tube; r is the radius of the xylem vessel; η is the viscosity of the fluid (about 0.011 in the case of water); $\frac{dp}{dx}$ is the pressure gradient in the direction of flow.

Table 1 gives an impression of the quantities of water which can be transported through narrow tubes.

Table 1. Flow of water in grams per day, through tubes 10 cm in length, under a difference in pressure of 1 atmosphere between the ends of the tubes.

Radius of the tube in microns	Transport of water in grams per day
1	0.000031
2	0.00049
5	0.019
10	0.31
20	4.9
50	190
100	3.100

From this table it appears that trees, with xylem vessels of a radius of 100 microns or more, do not encounter real difficulties as regards transport of water. However, the difficulties are greater in thin grass roots, in which vessels seldom have a radius of more than 20 μ.

VESSELS IN GRASS ROOTS

In roots of *Lolium perenne*, only one xylem vessel is usually present. There are often some smaller vessels, but these are generally much smaller than the central one, their radius being seldom greater than one fourth of the radius of the central vessel. From Table 1 it will be clear that these small vessels are of but little significance in water transport. Some other grasses show a different anatomical picture. *Phleum pratense*, for instance, has 5 to 10 vessels per root and *Dactylis glomerata* often more than 10 vessels, all of about equal radius.

We propose the introduction of the term "equivalent vessel radius of the root". This hypothetical "equivalent vessel" is a vessel of such a radius that it can transport the same quantity of water as all the vessels of a certain root together. From POISEUILLE's law it follows that the equivalent radius r can be calculated from the vessel radii r_1, r_2, r_3, etc., in the following manner:

$$r = (r_1{}^4 + r_2{}^4 + r_3{}^4 \ldots\ldots\ldots\ldots + r_n{}^4)^{\frac{1}{4}}$$

There is a certain relationship between the radius of a root and its equivalent vessel radius. In Fig. 1, vessel radii found in roots of the trial field in question are shown.

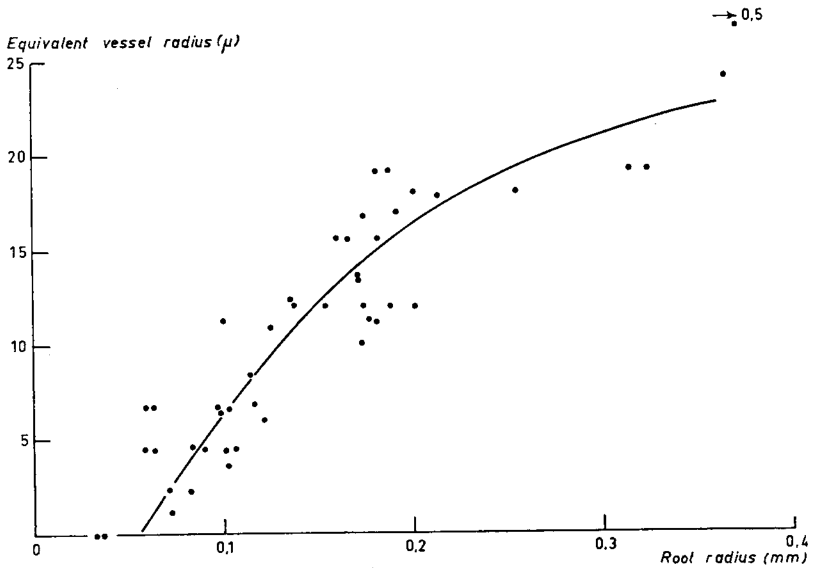

FIG. 1. THE RELATION BETWEEN EQUIVALENT VESSEL RADIUS AND RADIUS OF THE ROOT.

In very thin roots, with a radius of less than 0.05 mm, no vessels are found. In roots of a radius up to about 0.2 mm, the equivalent vessel radius is about 8% of the root radius. In thicker roots this percentage becomes smaller.

CALCULATION OF WATER FLOW THROUGH GRASS ROOTS IN THE FIELD

If we know how many roots are present, and what radius they have, we can calculate how much water can be transported through them and what pressure differences are required.

If in a certain soil 1 gram of living roots is present per litre of soil, we can assume that the total root volume is 1 cm^3, because the density of the roots is about 1.0. If the radius of all roots is 0.2 mm, the total length of all roots in a litre of soil is $\frac{1}{0.0004\ \pi}$, or 795 cm. This means that, if all roots are in a vertical position, 0.795 roots cross a horizontal plane of 1 cm^2.

We can now calculate what pressure gradient has exist if each day 1 mm of water has to flow upwards through these roots. 1 mm per day is $\frac{0.1}{24 \times 3600}$ g/cm^2 sec. According to POISEUILLE's law:

$$\frac{1}{0.795} \times \frac{0.1}{24 \times 3600} = \frac{\pi\ r^4}{0.088}\left(\frac{dp}{dx} - g\right)$$

According to Fig. 1, the equivalent vessel radius of roots with a radius of 0.2 mm is 16.3 μ. The term g is added, because in this case we are dealing with a vertical upward flow. Here $\frac{dp}{dx}$ appears to be 6.800 dynes/cm^3 or 0.0068 atm/cm.

For this calculation we have assumed that the radius of the roots was 0.2 mm. If a larger root radius had been assumed, the number of roots would have been smaller, but those roots would have had greater vessel radii. The former would have resulted in a greater pressure gradient, the latter in a smaller. Fig. 2 shows the influence of the assumed root radius on the pressure gradient required.

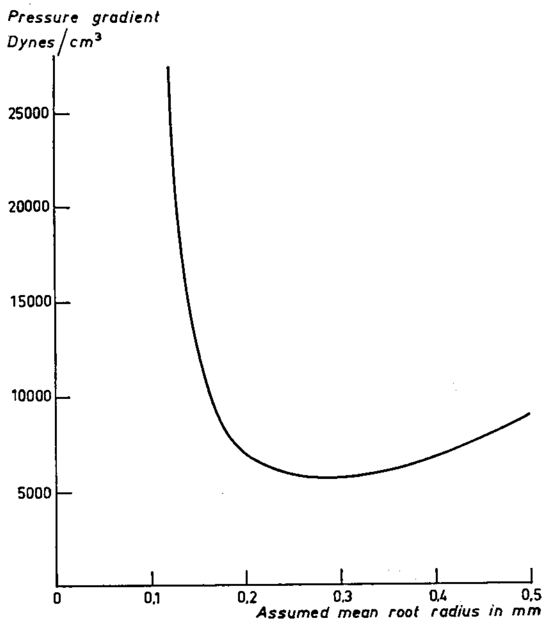

FIG. 2. THE INFLUENCE OF THE ASSUMED ROOT RADIUS ON THE PRESSURE GRADIENT REQUIRED FOR A FLOW OF 1 MM PER DAY, WITH A ROOT DENSITY OF 1 GRAM PER LITRE OF SOIL.

According to this figure movement of moisture through thin roots requires much more energy than is required to cause moisture to flow through roots with a radius of about 0.3 mm. In roots thicker than 0.3 mm the required pressure gradient increases again. This is due to the fact that, when the root radius becomes larger than 0.3 mm, the vessel radius increases in proportion considerably less than the root radius. Between the root radii of 0.2 and 0.4 mm, the curve is rather flattened. A change in root radius between these values has only a small influence on the result of the calculation. Unfortunately, in our trial field the mean radius of the grass roots was probably less than 0.2 mm, but estimation of this value is very difficult. We therefore assume a mean root radius of 0.2 mm. In that case the pressure differences calculated are certainly not too high.

The perforated cross-walls in the vessels offer a certain resistance to the flow of moisture. Owing to this, the actual quantity of water flowing through a root is smaller than the amount calculated. For *Lolium perenne* EMERSON (1954) found that the quantity measured was only half the quantity calculated. BROUWER and VAN ZANTEN (1955) found that the quantity of water sucked by a mechanical force through the vessels of roots of *Vicia faba* varied from half to one tenth of the quantity calculated.

It is therefore necessary to multiply the calculated pressure gradients by a certain factor. We have chosen 2 as this factor. It probably approximates more closely to reality than any other value.

If we assume that all the roots are in a vertical position, and that all of them participate in transport of water, we can calculate the pressure distribution in the roots at a given flow velocity. In our trial field the root distribution [2]) was as follows:

Table 2. Root distribution in the trial field.

Depth in cm	Root density: grams of roots per litre of soil
4– 5	36
5–10	19
10–20	2.2
20–30	1.33
30–40	0.56
40–50	0.27
50–60	0.23
60–70	0.08

The pressure gradients required for a vertical water flow through these roots have been calculated in the manner already mentioned. They are shown in Fig. 3.

Comparison of flow of moisture through grass roots and through the soil

From Fig. 3 it appears that, in the deeper layers of the soil, the flow of moisture through roots requires much energy. In the upper 10 cm the pressure gradient is very small, owing to the large quantity of roots present. In

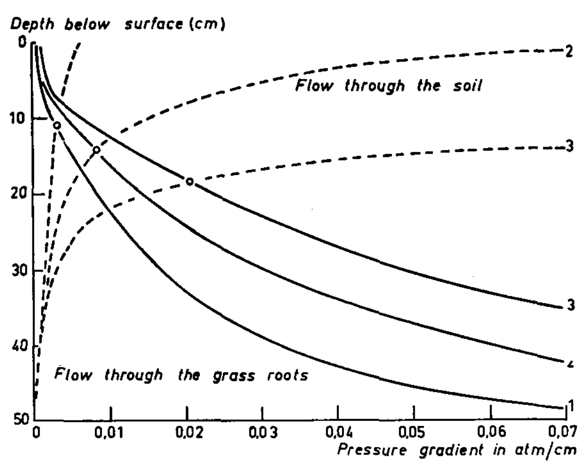

Fig. 3. The pressure gradients required at different depths for a continuous moisture flow of 1, 2 and 3 mm per day, through grass roots (continuous line) and through soil (dotted line).

this figure the dotted lines represent the pressure gradients required for moisture transport through the soil if the water table is at a depth of 50 cm.

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[2]) The root densities have been determined by Dr. J. J. Schuurman.

These are the tangents to the lines in Fig. 7 of the article by Wind (1955). It will be noted that, in the case of flow through roots, the pressure gradient increases in deeper layers; in the case of flow through soil, on the contrary, there is a decrease in deeper layers.

The intersection of the curves for root-flow and soil-flow represents the depths at which the energy required for flow through both media is the same. Below the points of intersection transport of water through the soil is the most economical; above the points, root-flow requires the least energy. It is likely that moisture will enter the roots at about the depth of the point of intersection, because in that case the energy of the whole system remains lowest.

The point of intersection for 1 mm per day lies at 11 cm, for 2 mm at 14 cm, and for 3 mm at 18 cm. It is probable that the depth of entry of water into the roots will be a little shallower, because entry of water requires energy. According to Brouwer (1953) this energy is inversely proportional to the quantity of roots. As there are more roots at shallower depths, the entry energy is the smaller, the shallower the depth at which entry occurs. But as a feed-back the transport energy is the greater, the shallower the depth of entry. So there will be another point of equilibrium at which the total energy is lowest, at a depth somewhat shallower than the depths mentioned before.

From measurements of soil moisture tensions the present author, Wind (1955), concluded that, below a depth of 10 cm, practically all water was transported through the soil. If account is taken of the fact that, in his material, the ground water level was often shallower than the 50 cm assumed here, his statement is surely substantiated by this article.

Old grassland, obviously either has too few roots below a depth of 10 cm, or has roots which are inefficient owing to an inappropriate anatomical structure.

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