

difficulty in the present investigation was the persistence of high-level noise in the acoustic environment of the pens. Quantitative studies (7) of teleost audition suggest that their intensity thresholds differ little from those of man, though their optimal frequencies — like those reported here — are in a lower part of the spectrum. With an assumed noise level of about 60 db, the shark was faced with a problem in discrimination rather than the simple detection of low-intensity sounds in a sea of silence. That it was able to discriminate in the 400- to 600-cy/sec band, when the signal-to-noise ratio indicated by our equipment was less than unity, suggests that, if these experiments had been done in a silent environment, the shark's thresholds, at each frequency in its range, would conceivably have been as much as 60 db lower. This would modify the shark's audiogram to be more nearly approximate to those of teleosts and, hence, to that of man.

While the question of sensitivity is of basic importance, so also are two other functional dimensions of hearing. We have already mentioned our observations of these subjects' ability to localize accurately the source of sound in the water. The third consideration is the extent to which this shark's provisional frequency range is useful in the perception of its natural sonic environment. If we compare this range to the spectra of sounds in the sea which may be significant to such a predatory animal (Fig. 1b), we find that components of these sounds, in every case we know of (8), fall within the suggested range of *Carcharhinus leucas*. In Fig. 1c, we have compared it to those reported for other fishes (7). Any apparent discrepancies between our results and those of Lowenstein and Roberts may be attributable to the normal differences which might be expected between results from whole, living animals and isolated preparations and, of course, from two different though related species (9).

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### Perspective on Function of Free Space in Ion Uptake by Roots

**Abstract.** An observed effect of longitudinal flow rate through corn roots on phosphate transport is shown to be inconsistent with diffusion theory. R. C. Smith's results confirm rather the existence of a diffusion barrier between the xylem and the free space external to the central cylinder of the root.

Whether apparent free space in roots (the partial volume of the roots into which components of a solution appear to diffuse freely) extends to the xylem elements or is interrupted by a differentially permeable cell barrier (the endodermis) has been much disputed. As Russell and Barber (1) point out, the endodermis is regarded as a free-space barrier mainly on the basis of its structure, but there is no direct proof of such function. Since recent findings (2) would appear to assign free space to cell walls and intercellular space only (and not to the cytoplasm), the suberized Casparian strips of the endodermal cell walls could be an effective barrier to free diffusion and therefore could delimit the radial extent of free space into the root.

The increased solute absorption associated under some conditions with increased transpiration has been a major argument in favor of transport of solute by way of free space directly into the vascular tissues of the plant axis (3). Some 20 percent of the total water absorbed is believed to enter through free space together with the solutes it contains. An alternative explanation for the transpiration effect has been advanced (4). Solutes may accumulate in free space as water is differentially absorbed by cells bordering a free-space system that reaches uninterruptedly only as far as the endodermis. Absorption of solute from such higher concentrations in free space may, according to this theory, account for the transpiration effect.

Smith (5) has presented evidence for

an effect of water movement through the vascular tissue on solute uptake which he believes occurred by simple diffusion through free space into the xylem. Young corn-root segments about 3 cm long were so mounted that nutrient solution lacking phosphate could be forced into one end of the root while nutrient solution containing isotopically labeled phosphate (1 mmole/lit.) bathed the outer surface of the root. The efflux was collected at the other end of the root, and its phosphate content was determined. Curves A and B (Fig. 1) show the relationships of phosphate concentration and total phosphate collected in the efflux to the rate of flow through the root. Contrary to Smith's conclusion, analysis of these data shows that the phosphate could not have moved directly into the stream flowing through the root by simple diffusion through free space. The equation for diffusion into a hollow cylinder is (6):

$$Q = \frac{2\pi D(C_o - C_i)}{\ln \frac{r_o}{r_i}} \quad (1)$$

where  $Q$  equals quantity diffused per second per centimeter of length,  $D$  is the diffusion coefficient in  $\text{cm}^2 \text{sec}^{-1}$ , and  $C_o$  and  $C_i$  the concentrations outside the cylinder and inside it at some radius  $r_i$  respectively;  $r_o$  is the radius of the root, and  $r_i$  is the average radial distance of a system of sinks, the conducting elements of the xylem. For a given system such as a corn root,  $Q$  becomes simply proportional to  $C_o - C_i$  and the remaining components can be lumped into a single constant  $k$ . Thus:

$$Q = k(C_o - C_i) \quad (2)$$

It is immediately apparent that the amount of phosphate recovered from the root was not proportional to the quantity  $C_o - C_i$ , because the concentration  $C_i$  decreased hyperbolically with increasing rate of flow through the root, but the phosphate collected increased linearly. This relationship does not conform to Eq. 2, which would require the amount collected to be a hyperbolic function of rate of flow just as the concentration of phosphate was. (The rate of flow has no direct bearing on  $Q$ . It affects it indirectly through its effect on  $C_i$  only.) Second, with 1  $\mu\text{mole/ml}$  in the external solution and only 0.02 to 0.08  $\mu\text{mole/ml}$  in the solution flowing out of the root, the value of  $C_o - C_i$  would hardly be affected. No such large increase in the amount of phosphate collected could result from the very small changes in gradient. These qualitative conclusions may be assessed quantitatively as follows.

If the values are taken at the lowest flow rate, a  $C_i$  which rose to 0.076

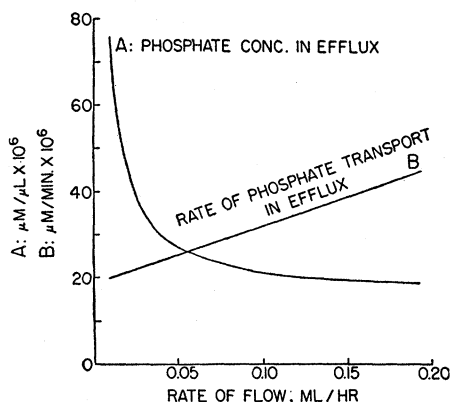


Fig. 1. Effect of longitudinal flow rate through the root on phosphate concentration found in efflux (A) and rate of phosphate transport by effluent stream (B). Graphs for apical corn root (*Zea mays* L.) segments from Smith (5).

$\mu\text{mole/ml}$  yielded  $20 \times 10^{-6} \mu\text{mole}$  of phosphate per minute per root segment. The average  $C_1$ , rising from 0 to 0.076 as the solution flowed through the root was, therefore,  $0.038 \mu\text{mole/ml}$ . Solving for  $k$  (Eq. 2) we obtain  $k = 0.116 \times 10^{-6}$ . With this value of  $k$  and the  $C_1$  values read from curve A (Fig. 1) for different flow rates, the  $Q$  values were computed for each flow rate. These are given in Table 1 (on a per segment per minute basis) and demonstrate the very slight expected effect of the observed changes in  $C_1$  on the diffusional transport of phosphate and also the hyperbolic character of  $Q$  as a function of flow rate. Diffusion into the flowing root stream, therefore, could not have been controlling the amount of phosphate recovered. One must conclude that phosphate was released into the flowing stream by a process that was proportional to some exponential function of the concentration in the flowing stream. Whether leakage or a more specifically controlled secretion of accumulated phosphate into the flowing stream was involved, this process and

Table 1. Theoretical effect of variations in  $C_1$  on the amount of phosphate transported by diffusion across the root into the xylem.

Flow through root (ml/hr)	Phosphate theoretically transported ( $\mu\text{mole/min}$ per root segment)	$\Delta \mu\text{mole/min}$ ml/hr
0.009	20.0	
.025	20.4	25
.050	20.5	4
.100	20.6	2
.194	20.6	0—

not diffusion through free space was the rate-limiting one for transport into the xylem.

Now, what of the absolute magnitude of the diffusion process relative to the observed rate of solute transport? According to Eq. 1 and using a value for  $D$  of  $10^{-5} \text{ cm}^2 \text{ sec}^{-1}$ , letting  $r_o/r_1 = 5$  (actually the radius of the central cylinder is approximately one-third that of the root, so that the factor of  $1/5$  provides a safe margin), and letting  $C_o - C_1 = 1 \mu\text{mole/ml}$  (actually ranging in this case from 0.96 to 0.99), we find that a cylinder 3 cm long should take up  $7020 \times 10^{-6} \mu\text{mole}$  of phosphate per minute. However, diffusion occurs through only about 7 percent of the cross-sectional area of corn roots [the effective radial pathways for an apparent free space for corn roots of 15 percent (4)], and the diffusional path is tortuous (being about 1.5 times the distance along a radius), so that we must multiply the value for an ideal cylinder by the fraction  $0.07/1.5$  to determine diffusion into the root segment. We would, therefore, expect an uptake of about  $350 \times 10^{-6} \mu\text{mole/min}$  per root segment compared to observed uptakes of 20 to 40, or an order of magnitude greater than was actually observed. It has been shown that equilibration of free space in bean roots is in good agreement with the diffusion equation when a normal diffusion coefficient of about  $10^{-5} \text{ cm}^2 \text{ sec}^{-1}$  is employed (4). The discrepancy in this case is large enough to suggest that the diffusion through free space is not the rate-limiting process in phosphate transport through the root.

Increased transpiration ordinarily causes an increased flow of water through the cortex. Smith's experiment is of particular interest because the technique employed allowed variation in the rate of flow through the xylem with little or no water-flow through the cortex. Instead, the movement of water through the xylem of the root was achieved independently of any movement of water or solution across the cortex. Regardless of the rate of water-flow through the root, diffusion alone, with essentially no mass flow, was responsible for the phosphate transport across the cortex to the central cylinder. This diffusion of course occurred, but diffusion was apparently stopped at some barrier, which then interposed its own concentration-sensitive mechanism for the release of phosphate into the stream of water moving through the vascular tissues. If Smith's results are not conclusive proof (a very rare commodity in any case) of the existence of a barrier to free diffusion in the root, they are at least very strong evidence for such a barrier.

Note added in proof: In a personal

communication to one of us (L.B.), Smith affirmed belief in a barrier to free diffusion in the root, correcting an erroneous impression to the contrary given by his paper (5). The present analysis of Smith's data remains useful in refuting those who may still believe in a continuous free-space system leading into the conducting tissues of the plant.

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#### Soil Mineralogy as Factor in Spread of Fusarium Wilt of Banana

**Abstract.** A correlation is established between the spread of *Fusarium* wilt of banana and soil mineralogy. Montmorillonoid-type clay minerals occur in all soils in which disease spread is slow, but, with the exception of two soils, this group of minerals is absent in soils in which it is rapid.

*Fusarium* wilt of banana, commonly called Panama disease, is caused by the soil-borne, root-infecting fungus, *Fusarium oxysporum* f. *cubense* (E.F.S.) Snyder and Hans. The disease was first noted in Central America about 1900 and continues to be one of the main problems in the commercial production of wilt-susceptible banana varieties. The observation that the spread of the disease is not uniform in all soils resulted in the concept that soils differ in their "resistance" or "susceptibility" to the fungus (1). Early investigators classified banana soils as susceptible, semiresistant, or resistant (1), but current usage has modified these terms to short, intermediate, and long life, respectively. The effective banana-producing life of soils is determined by the rate of spread of the disease throughout a plantation and, from an economic point of view, is based on the length of time required for more than 50 percent of the plants there to show disease. Wilt-susceptible bananas can generally be produced on short-