

Specific Conductivity of Conducting and Non-Conducting Tissues of *Zea mays* Root

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Received September 7, 1970

Abstract. The structure of the maize root enables one to determine the experimental specific conductivity of conducting and non-conducting tissues for the longitudinal water transfer. Using the method of Farmer and Berger in Huber and Schmidt's modification, successive differences in orders of magnitude were revealed among the experimental specific conductivities of the tissues of pith, cortex, and those of the area with concentrated xylem. The highest values of specific conductivity ($\text{cm}^3 \text{cm}^{-2} \text{h}^{-1}$ at 400 mbar per 5 mm distance, at 20° C) were determined in the area with concentrated xylem (mean value $10\,018 \text{ cm}^3 \text{cm}^{-2} \text{h}^{-1}$); in the cortex area values by one order of magnitude lower were obtained (mean value $1\,206 \text{ cm}^3 \text{cm}^{-2} \text{h}^{-1}$); in the pith area by two orders of magnitude lower (mean value $167 \text{ cm}^3 \text{cm}^{-2} \text{h}^{-1}$). The tissues of the area with concentrated xylem participated in the experimental root conductivity by 72 per cent, cortex tissues by 27 and pith tissues by one per cent. In this paper the individual tissues of maize root are characterized in detail from the anatomical viewpoint and the possible causes of the differences are discussed.

Longitudinal water flow in a plant takes place above all in the root and stem xylem. SLATYER (1967) and KRAMER (1969) suggest that longitudinal water flow can occur in the tissues of the entire cross-section area of the stem or root. The participation of the individual tissues in water conducting is in indirect proportion to the resistance of these tissues to the flow (*ibid.*). The suggestion mentioned is important when interpreting the results of empirical determination of the capacity of root or stem tissues to conduct water in the experiments arranged according to Farmer and Berger (reviews by HUBER 1956, BRIGGS 1967). Using this method the volume of water flowing through the isolated root or stem segment per time unit at constant pressure and temperature is related to the cross-section area. Its numerical value represents the degree of specific conductivity.

By virtue of its structure, the maize root permits us to determine separately the experimental conductivity of tissues in the individual regions. In the present paper it was used as a model for the determination of experimental specific conductivity of conducting and non-conducting tissues for longitudinal water transfer.

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Material and Methods

Experimental Material

An inbred line of maize A 15 (VIR 17) grown in the experimental field singly with 80×80 cm spacing, was employed for the experiments. Conductivity was investigated with segments from the base of adventitious roots of the fifth node. The base of these roots does not branch in the section of 2 to 3 cm and is not convergent, unlike the nodal roots of lower nodes. From

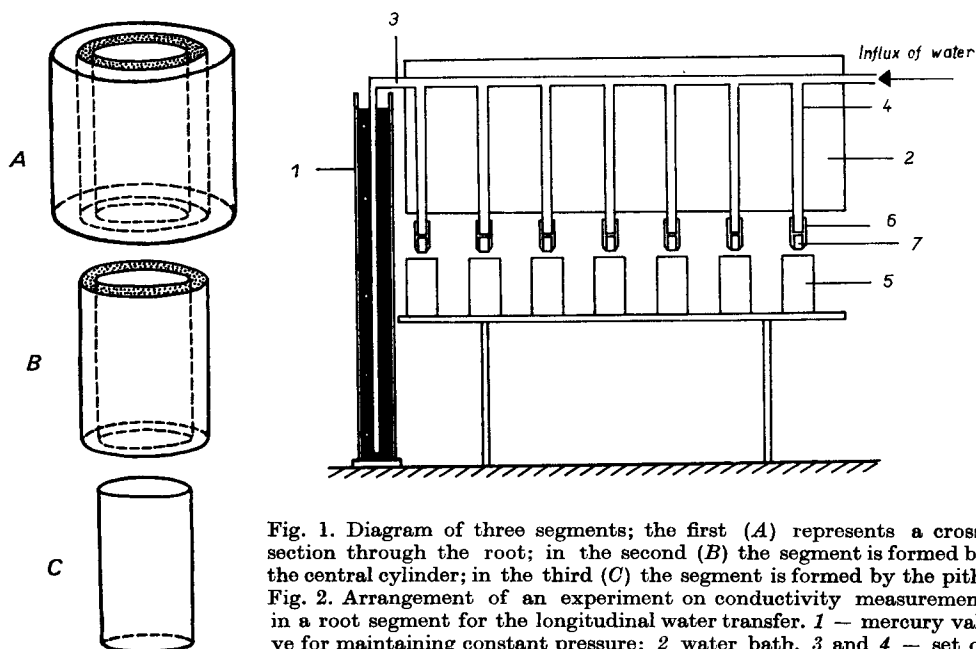


Fig. 1. Diagram of three segments; the first (A) represents a cross-section through the root; in the second (B) the segment is formed by the central cylinder; in the third (C) the segment is formed by the pith. Fig. 2. Arrangement of an experiment on conductivity measurement in a root segment for the longitudinal water transfer. 1 — mercury valve for maintaining constant pressure; 2 water bath, 3 and 4 — set of glass tubes, 5 — vessels with water from the overflow, 6 — rubber tubing, 7 — root segment.

the material mentioned three successive 5 mm long and equally thick sections were obtained which were then arranged in the following way (Fig. 1): the first segment (A) was left in the original state. In the second segment (B) the cortex was carefully removed, so that in fact the segment was formed by the central cylinder. In the third segment (C) the cortex was removed as well as the peripheral part of the central cylinder in which the conducting tissue is concentrated, so that only the pith was left. If the area of the cross-section through the entire root is designated as a , the central cylinder area as b , and the area of pith cross-section as c , the cortex area equals $(a-b)$ and the area of the region with concentrated xylem is equal to $(b-c)$.

The method of employing a single segment for successive conductivity measurements, removing the individual tissue regions one by one would be substantially simpler. However, as referred to in our first paper, several authors showed that the values obtained for conductivity decreased with

the duration of measurement (RIEDL 1937, BOVIS 1962, GRAČANIN 1962 BRIGGS 1967, PETTY 1970).

For the procedure chosen, which employs three successive segments their structural identity had to be confirmed. The suitability of the experimental material was verified by comparing the values of conductivity in triads of segments. In proper experiments only those triads were evaluated which had identical cross-sections through the central cylinder as determined planimetrically, as well as identical numbers of vessels of the large metaxylem in the first and second segment.

In maize cortex, air spaces can occur. Their participation in conductivity was verified by measuring the conductivity of a series of 5 mm long successive segments from one root with a various occurrence of air spaces. The conductivity of every other segment was evaluated.

Anatomical Analysis

For anatomical analysis we employed free-hand sections of the efflux areas of the individual segments and sections of identical segments, which

TABLE 1

BASIC DATA CONCERNING CROSS-SECTION AREAS of an adventitious root of *Zea mays* (5th node), central cylinder, cortex, pith, and region with concentrated xylem. Values of the experimental conductivity of the individual tissue regions for the longitudinal water flow are shown in bold-face type. From these data, the specific conductivity given in Table 2 was calculated.

Sam- ple	Cross-section area [cm ²]				
	Entire root	Central cylinder	Cortex	Pith	Region with concentrated xylem
	<i>a</i>	<i>b</i>	<i>a-b</i>	<i>c</i>	<i>b-c</i>
Experimental conductivity [cm ³ h ⁻¹]					
1	0.249 683.8	0.122 456.5	0.128 227.2	0.064 12.9	0.058 443.6
2	0.193 514.2	0.088 417.5	0.104 96.8	0.044 11.7	0.045 405.7
3	0.151 382.6	0.050 244.7	0.101 137.9	0.020 2.1	0.030 242.6
4	0.182 450.0	0.066 306.3	0.117 143.7	0.030 2.2	0.035 304.1
5	0.163 340.7	0.051 239.1	0.112 101.6	0.024 2.0	0.028 237.2
6	0.204 495.5	0.078 341.4	0.126 153.1	0.035 4.1	0.043 337.3
7	0.211 762.3	0.069 568.3	0.142 194.0	0.031 3.4	0.038 564.9
8	0.209 722.1	0.074 522.2	0.135 199.9	0.030 6.8	0.044 515.4
9	0.230 671.0	0.085 542.9	0.145 128.1	0.040 5.7	0.045 537.2
10	0.266 768.7	0.095 614.7	0.170 154.0	0.047 16.2	0.049 598.5

were fixed using FPA and transferred into paraffin through methyl salicylate. The sections were stained diffusibly with tannin and ferric chloride and mounted in Canada balsam. Cell elements were macerated with Schultze's mixture (potassium chlorate plus nitric acid) at a higher temperature (NĚMEC *et al.* 1962) and stained in the same way as the sections.

Conductivity Measurement

The experimental specific conductivity was determined using the method of Farmer and Berger in Huber and Schmidt's modification (HUBER 1956). Root segments were not fixed directly in glass tubes, but in small lengths of rubber tubing slipped on glass tubes (Fig. 2). Details of the waterproof fastening of the segments were described in our preceding paper (LUXOVÁ and KOZINKA 1970). During measurements, the following conditions were maintained: segment length 5 mm; water pressure 400 mbar (temperature of water 20° C, Fig. 2); measurement duration 5 min with segments *A* and *B*, and 15 min with segment *C* (prolongation of measurement was necessary because of the low conductivity of pith tissues). Actual measurement of the amount of water flow was preceded by a 5 min preparation period. The amount of water flow was determined gravimetrically. The final results were obtained by evaluating ten triads of segments.

Results

The numerical values obtained by measuring areas of the individual root regions in cross-sections through ten root segments are summarized in Table 1. They represent in succession areas of cross-sections through the entire root, the central cylinder, cortex, pith, and region with concentrated conducting tissue. The values of conductivity measured are shown in bold-face type under the individual data. The anatomy of the tissues investigated is demonstrated in Fig. 3.

Fig. 4 represents a graphical comparison of relative participation of areas of the individual tissue types in the total area of the root cross-section with relative participation of conductivity of these tissues in the conductivity of the entire root. While the participation of the cortex, region with concentrated xylem and that of the pith is expressed by the ratio 63 : 20 : 17, the relative participation of the individual tissues in the experimental root conductivity is given by relative values 27 : 72 : 1.

Specific conductivity of the individual tissue types is expressed in Table 2. There exist successive differences in orders of magnitude among the specific conductivities of the pith, cortex, and region with concentrated xylem. The highest specific conductivity was revealed in the region of tissues with vessels (mean value $10\,018\text{ cm}^3\text{ cm}^{-2}\text{ h}^{-1}$). For the cortex region, values approximately ten times lower were obtained (average $1\,206\text{ cm}^3\text{ cm}^{-2}\text{ h}^{-1}$), for the pith region approximately a hundred times lower (average $167\text{ cm}^3\text{ cm}^{-2}\text{ h}^{-1}$).

When describing the arrangement of the individual segments the peripheral part was mentioned simply as cortex (Fig. 5A). The walls of epidermal cells in the root parts analysed are fine and thin, and at the time of analysis only their remainders were left. The function of ephemeral epidermis is taken

up by the peripheral cortex layer, exodermis, formed by cylindrical, unilaterally thickened cells. A few cell layers under exodermis have the character of more compactly arranged filamentous elements of a small diameter with sclerified and lignified walls. The characteristic feature of this part of cortex is an irregular cell arrangement of the cross-section. Parenchyma of the central and inner cortex part is formed by more or less successive concentric layers with radially arranged rows and with an abundant occurrence of intercellulars. The cells have a prismatic or a cylindrical character with thinner walls. Radial cell walls as well as the inner tangential wall of the innermost cortex layer, endodermis, are intensively thickened and lignified.

Fig. 4. Relative participation of the tissues of cortex (C), of the region with concentrated xylem (X), and pith (P) in the total area of root cross-section (left); relative values of experimental conductivity of these tissues with regard to total experimental conductivity of the root (right).

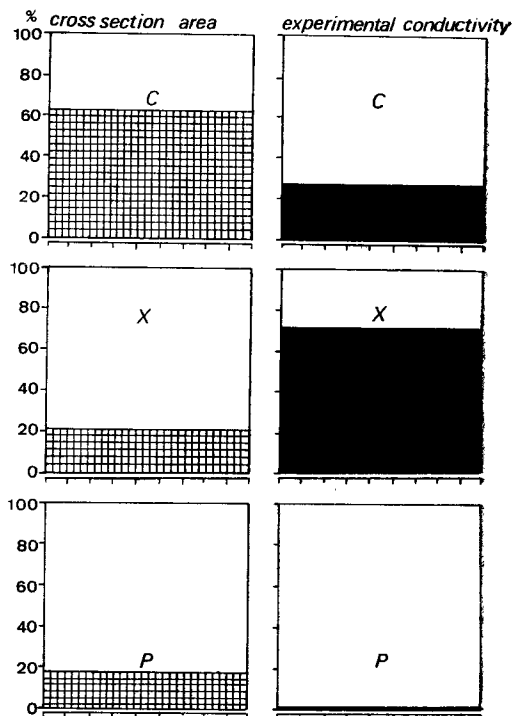


TABLE 2

VALUES OF EXPERIMENTAL SPECIFIC CONDUCTIVITY of various tissue regions of an adventitious nodal root of *Zea mays* (5th node) for longitudinal water flow.

Sam- ple	Experimental specific conductivity [cm ³ cm ⁻² h ⁻¹ at 400 mbar; 20° C; 5 mm distance]				
	Entire root	Central cylinder	Cortex	Pith	Region with concentrated xylem
	<i>a</i>	<i>b</i>	<i>a-b</i>	<i>c</i>	<i>b-c</i>
1	2 543	3 749	1 783	203	7 653
2	2 664	4 692	930	268	8 946
3	2 530	4 447	1 365	103	8 152
4	2 472	4 679	1 223	74	8 494
5	2 085	4 669	906	81	8 567
6	2 424	5 380	1 215	117	7 886
7	3 617	8 212	1 371	109	14 874
8	3 452	7 018	1 483	227	11 600
9	2 916	6 362	885	142	11 869
10	2 894	6 407	908	347	12 135
	$\bar{x} \pm s_{\bar{x}}$ 2 760 ± 149.7	$\bar{x} \pm s_{\bar{x}}$ 5 462 ± 455.3	$\bar{x} \pm s_{\bar{x}}$ 1 206 ± 95.5	$\bar{x} \pm s_{\bar{x}}$ 167 ± 28.7	$\bar{x} \pm s_{\bar{x}}$ 10 018 ± 768.5

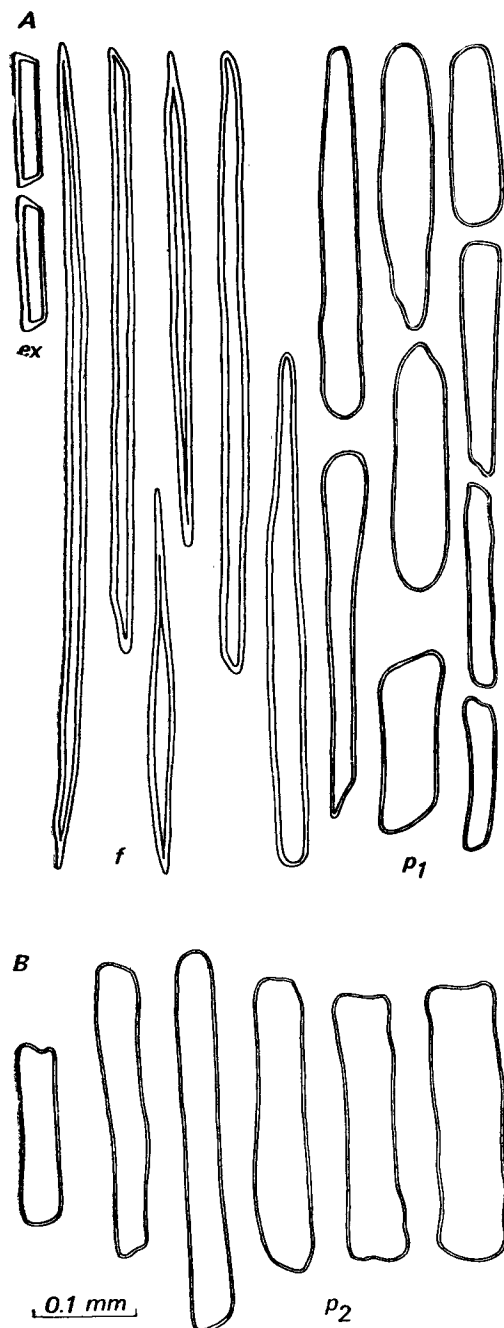


Fig. 5. Isolated elements of the cortex (A) and pith (B); ex — cells of exodermis; f — filamentous elements; p₁ — parenchyma of the inner cortex part; p₂ — pith parenchyma.

The pith (Fig. 5B) is formed by fine thin-walled parenchymatic cells of cylindrical shape and various sizes. For both cortex and pith the occurrence of smaller intercellulars is common in the site of the tissue where three and more cells are connected. In addition to the system mentioned large lysigenous lagoons functioning as air spaces can occur in the cortex. Their ability to con-

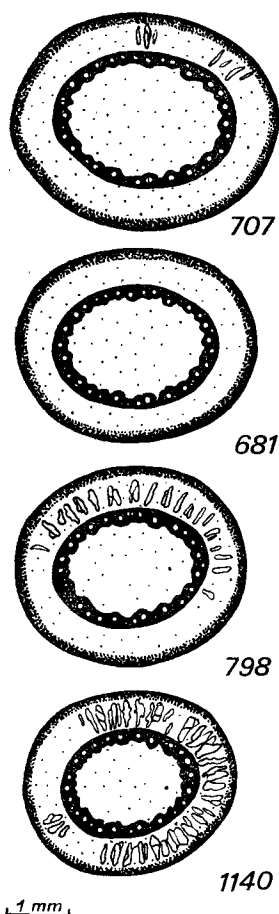


Fig. 6. — Cross-sections through a series of root segments analysed with various occurrence of air spaces in the cortex. The figures given represent the values of experimental conductivity [$\text{cm}^3 \text{h}^{-1}$].

duct water was confirmed by analysing a series of segments with different occurrence of these large spaces (Fig. 6). They were shown to be able to affect substantially the experimental results obtained. Their frequency is directly connected with the conductivity measured. Therefore, it is necessary to check the segments microscopically prior to conductivity determination; the segments with air spaces in the cortex should be discarded from the experiment.

Discussion

High values for the experimental specific conductivity determined in our experiments correspond to several authors' opinions on the high conductivity of roots (HUBER and HÖFFLER 1930, RIEDL 1937, EMERSON 1954, BRIGGS 1967, KRAMER 1969). When comparing the relative specific conductivity of various species and organs of plants, HUBER (1956) considers the specific conductivity of roots as highest. The experimental conductivity which would be identical or almost equal to the theoretical has been obtained so far only with root xylem or with lianas (BERGER 1931, RIEDL 1937, BOVIS 1962, GESSNER 1965). It usually represents 34 to 80 per cent of theoretical conductivity.

Roots display a distinct relationship between the quality of conducting tissues and their conducting capacity. The area of water-conducting tissues in the cross-section is not large, however, conditions for rapid flow exist there (RIEDL 1937). The data mentioned were obtained with roots of deciduous woody plants where xylem can be considered as a bunch of capillaries. The compact character of the secondary xylem permits one to investigate conductivity of the conducting elements proper, *i.e.* vessels and tracheids. With roots without secondary growth, to which also maize roots belong, the cell arrangement is much freer, so that such a possibility does not exist. The experimental conductivity of maize roots is affected by the ratio of the participation of water-conducting and non-conducting tissues (LUXOVÁ and KOZINKA 1970).

Water transfer in xylem is comparable to flow in a capillary system in which the resistance to the flow is the lowest of all possible paths of water flow between the root and transpiring tissues (RAWLINS 1963, DIMOND 1965). At the same time, the resistance of xylem to flow is most constant in comparison with all the other resistances of plant tissues (WAGGONER and DIMOND 1954, SCHOLANDER *et al.* 1965). In xylem, water and solutions are transported by a stream induced by hydrostatic pressure or a gradient in pressure potential which exists in roots and stem (KRAMER 1969).

When emphasizing the longitudinal water transfer in xylem, flow taking place outside xylem must not be disregarded. Water enters radially through parenchymatic cells into the roots and can move laterally, as well (SLÁVÍKOVÁ 1967, KOZINKA 1970). It is considered likely that during the longitudinal flow small water amounts move in the parenchymatic cells of the cortex and pith (SLATYER 1967, KRAMER 1969). Slatyer presumes the longitudinal flow in parenchymatic cells to occur mainly outside the vascular system. This assumption is in accordance with our results which confirm the predominance of conductivity of the cortex over that of the pith. BIRCH-

HIRSCHFELD (1920) investigated the water flow in the cortex of branches and claims that the amount passing through the cortex is measurable but that it represents as little as 0.1—0.01 per cent of the amount required by a normally transpiring branch. According to SLATYER (1967) the vascular conductivity should exceed that examined outside xylem by three orders of magnitude. In our material the amount of water flowing through the cortex represented on the average 27 per cent of the total water amount passing through the root segment.

BIRCH-HIRSCHFELD (1920) investigated also the water transport in the pith parenchyma with *Sambucus nigra*, *Sylphium Hernemannii*, and further species and in general she obtained very low values. A surprisingly low capillary effect of parenchymatic tissues from the stem pith and leaf mesophyll was reported by several authors, e.g. by HÄUSERMAN (1944), LEWIS (1945), and others. Analogously, in our material only a small portion of the total water amount passing through a root segment arrived at the pith — as little as one per cent.

As far as the path of the extrafascicular water flow is concerned, it is effected, according to the classical view, by moving from vacuole to vacuole in the direction of the water potential gradient. As reported by TYREE (1969), "there is, however, an increasing body of evidence from the study of the movement of fluorescent dyes by STRUGGER (1938/39), from theoretical considerations by LEVITT (1956), and from the study of the kinetics of water uptake by leaves and roots by WEATHERLEY (1963, 1965) that the water of the transpiration stream moves predominantly round the cells — *via* the cell walls". RUSSEL and WOLLEY (1961) state that the cell wall resistance represents as little as 5 per cent of the resistance of cortex cell protoplasts. According to WEATHERLEY (1963) the walls of mesophyll cells are fiftyfold more permeable than their protoplasts. On the basis of conductivity values, as determined from the pressure which was required for inducing water transfer through cellulose walls and protoplasts of root cells, BRIGGS (1967) deduced that the majority of extrafascicular water transport in the root must take place in the cell walls. If the walls of cortex and pith cells can be considered as the paths of the lowest resistance in water transfer, then the cortex region has the advantage over the fine thin-walled pith parenchyma.

A further cause of differences in conductivity of the cortex and pith could consist in the different occurrence of intercellulars. With a normally functioning parenchyma of a root, leaf or stem the intercellulars are filled with air and do not serve as a space for the transport of water and water-dissolved substances (HÜLSBRUCH 1953). However, it is well known that if filled with water they can serve this purpose (BERGER 1931, ROUSCHAL 1941, KRAMER 1956). Using infiltration into wheat roots LUNDEGÅRDH (1950) succeeded in increasing water uptake, for 80 per cent of which cortex intercellulars were responsible. From this point of view the occurrence of large air spaces in the cortex was especially important, affecting substantially the results of our experiments on conductivity. When fixing the pith segments, there was the danger that mechanical injury could occur. However, immediate microscopic examination after completing conductivity measurements revealed their relative intactness.

Acknowledgement

The able technical assistance of Miss J. Glasová, Mrs. M. Takáčová, and Mr. L. Kiššík is gratefully acknowledged.

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V. KOZINKA, MÁRIA LUXOVÁ, Botanický ústav Slovenskej akadémie vied, Bratislava: Špecifická konduktivita vodivých a nevodivých pletív koreňa *Zea mays* L. — Biol. Plant. 13 : 257—266, 1971.

Koreň kukurice umožňuje svojou stavbou stanovenie experimentálnej špecifickej vodivosti vodivých a nevodivých pletív pre pozdĺžny tok vody. Huberom a Schmidtom modifikovanou metódou Farmera a Bergera sa zistilo, že medzi experimentálnou špecifickou vodivosťou pletív stržňa, kôry a oblasti s koncentrovaným xylómom existuje postupný rádivý rozdiel. Najvyššie hodnoty špecifickej vodivosti ($\text{cm}^3 \text{cm}^{-2} \text{h}^{-1}$ pri 400 mbar na vzdialenosť 5 mm pri 20°C) sa stanovili v oblasti s koncentrovaným xylómom (priemerná hodnota $10\,018 \text{ cm}^3 \text{cm}^{-2} \text{h}^{-1}$); pre oblasť kôry sa stanovili hodnoty rádovo jedenkrát nižšie (priemerná hodnota $1\,206 \text{ cm}^3 \text{cm}^{-2} \text{h}^{-1}$); pre oblasť stržňa rádovo dvakrát nižšie (priemerná hodnota $167 \text{ cm}^3 \text{cm}^{-2} \text{h}^{-1}$). Pletivá oblasti s koncentrovaným xylómom participovali na experimentálnej vodivosti koreňa 72, pletivá kôry 27 a pletivá stržňa 1 percentom. V práci sa podrobne charakterizujú jednotlivé pletivá koreňa kukurice z hľadiska anatomickeho. Uvažujú sa zistené a predpokladané príčiny rozdielnej experimentálnej špecifickej vodivosti.

V. KOZINKA, MÁRIA LUXOVÁ
SPECIFIC CONDUCTIVITY IN ROOTS

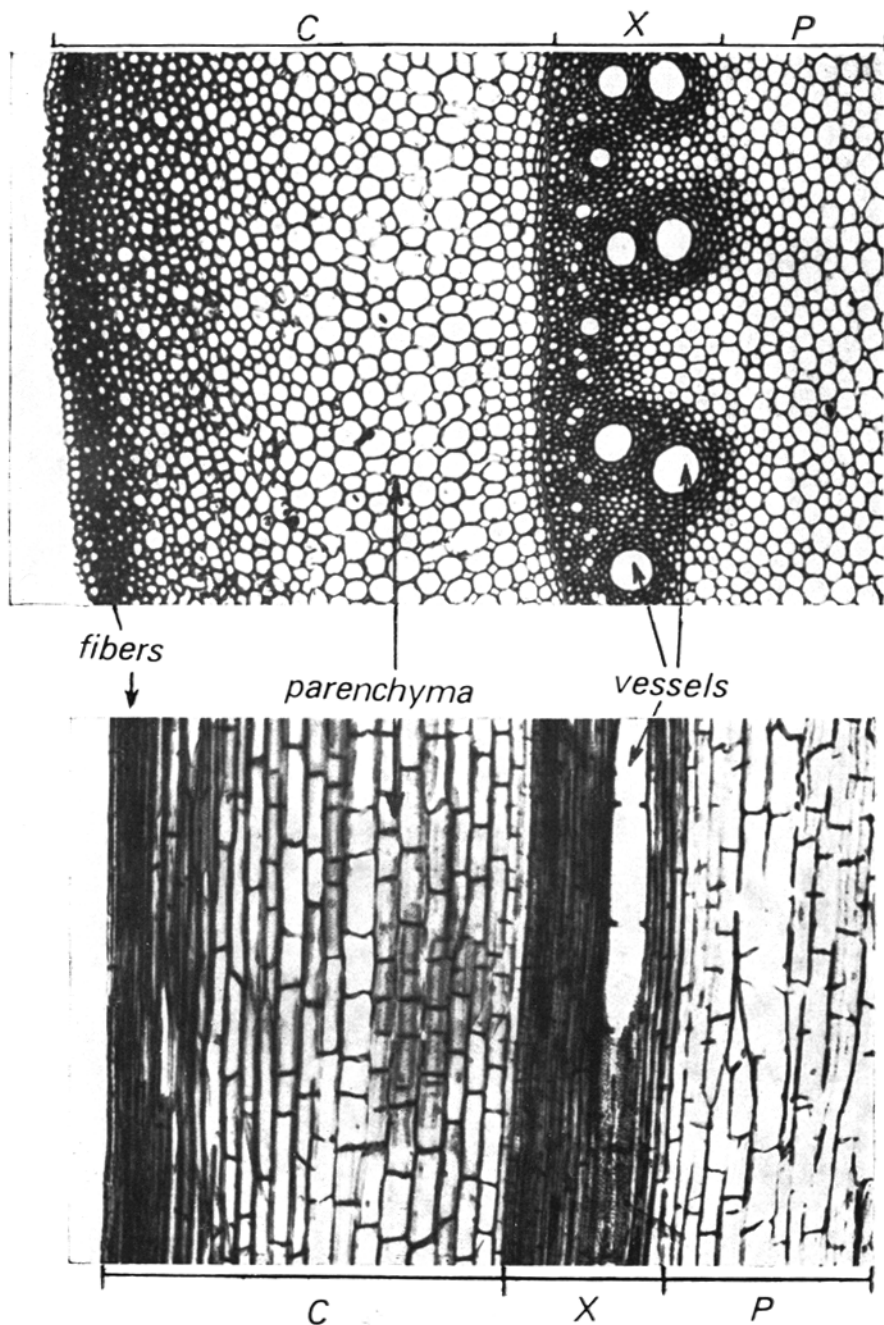


Fig. 3. Sections through an adventitious maize root (5th node). *A* — transection, *B* — longitudinal section with designation of the individual analysed regions, *C* — cortex, *X* — region with concentrated xylem, *P* — pith. Magnification 70 $\times$.