BIOLOGIA PLANTARUM (PRAHA)

12 (1) : 47–57, 1970

Structure and Conductivity of the Corn Root System

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Received March 2, 1969

Abstract. When comparing conductivity in 5 mm long segments from the basis of the primary seminal root with that in segments from adventitious roots of the first to fifth node it was revealed that the conductivity is not a general function of the transection area. The conductivity determined experimentally is minimal in the primary seminal root and gradually increases in the adventitious roots. However, when calculating per area unit, roots of the first coleoptile node appear the most efficient, with roots of the second and third node the values gradually decrease, and conductivity in roots of the fourth and fifth node approximately equals that of the primary seminal roots.

The conductivity is not a function of the conducting area. The conducting capacity of tissues which do not function directly as conductors is substantially lower; however, they cannot be neglected in evaluating the conductivity because of their high percentual occurence. The total conductivity in the individual root types is influenced by the ratio of the participation of water-conducting and non-conducting tissues.

The root system of corn is comprised of two types of roots: the primary or seminal roots which originate as early as in the embryo, and the secondary roots originating in whorls on the bases of the individual stem internodes. The highest whorls can take the character of aerial roots. In earlier papers (MARTIN and HERSHEY 1934/35) the seminal roots of corn were also denominated as temporary, and the secondary, adventitious roots as permanent ones. The hypothesis was advanced — which should have been true for *Gramineae* in general — that the seminal roots function only at the beginning of ontogenesis, then wither and their function is taken up by the adventitious roots. However, these data were not confirmed by the results of recent observations and experiments (BALJURA 1959, KAUSCH 1967, VOLYNKIN 1961). According to BROUWER (1965) this may be largely dependent upon external conditions.

When the aerial part of the corn plant becomes larger, an increased number of thicker roots on higher nodes is formed. In this way the absorptive and conducting capacity of the root system increases and its inability to form secondary thickening is thus compensated. As stated by WEATHERWAX (1930/31), "the dimensions of each internode may be regarded as a quan-

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titative expression of a set of physiological conditions present at the time of its formation."

Regularities in structural changes of corn roots in dependence on the site of their origin caught the attention of several authors (MARTIN and HERSHEY 1934/35, HEIMSCH *et al.* 1950, OVČINNIKOV and NIKOLAJEVSKIJ 1961). On the basis of the results obtained they also considered conducting abilities of the individual root types. The aim of the present paper is to verify experimentally the relationship between the inner structure and the conducting capacity in this naturally created model.

Material and Methods

Material

We used an inbred line of corn A 15 (VIR 17) which had been cultivated in the experimental field singly with 80 × 80 cm spacing. Approximately identical individuals were chosen for the experiment. Segments of 5 mm in length were cut from the basal lignified part of the primary seminal root and from adventitious roots of the first to fifth node of the plants chosen. The extent of lignification was checked microscopically by means of the fluoroglucine reaction. In each group ten segments were analysed. The first analyses were performed at the time of flowering.

Anatomical Analysis

In the first part of the work the structure of the efflux area was analysed. From the site of fluid outlet (morphologically the apical end of the segment, Fig. 1a) transections were hand-made which were observed in diluted glycerine. When evaluating them microscopically the following characters were investigated: root diameter, central-cylinder diameter, number of protoxylem poles, and number of large metaxylem vessels.

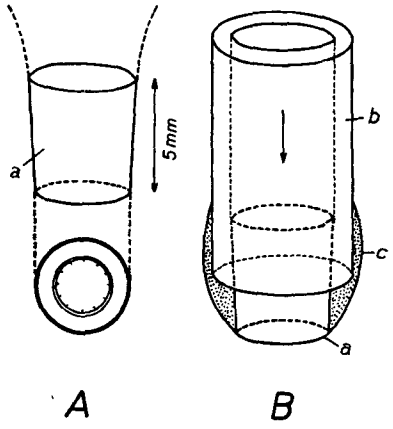

Fig. 1. A — root segment (a) with the schematic transection representing the efflux area. B — method of fastening the root segment (a) in a rubber tube (b) and its sealing with a wax (c).

Three samples from the individual groups were evaluated planimetrically: from the transections permanent slides were made. They were stained diffusibly with a 2 per cent tannin solution and a 10 per cent water solution of ferric chloride, dehydrated through the alcohol-carbolxylol-xylol series and mounted in Canada balsam. By projecting slides through the microscope directly onto photopaper (LUX 1965) contact negatives were obtained. The 350 × linear magnification chosen enabled us to evaluate planimetri-

cally even the small early metaxylem vessels. At the magnification given sections from thicker roots of higher nodes had to be exposed in parts so that sections through the entire central cylinder were obtained as a composition photograph. By means of a planimeter lumina of the individual vessels of the large and narrow metaxylem was then measured (Fig. 2) (these values will be used in later work), their sum representing the value for the total water-conducting area. The area of the entire transections of the individual roots, as well as the area corresponding to the central cylinder were evaluated, in accordance with the capacity of the planimeter, using a lower, 42× magnification. All values obtained in measurements were appropriately converted to actual values.

Conductivity Measurement

Quantitative data for evaluating the conducting capacity of the individual root types were obtained by estimating the ability to conduct water in experiments arranged according to Farmer and Berger in a simplified modification of Huber and Schmidt (Huber 1956). In all measurements the following conditions were employed: length of the root segment measured — 5 mm (lateral roots were carefully removed from the segment); pressure — 20 cm mercury column; duration of the measurement — 15 minutes (a 5 minute preparation time preceded the actual measurement); temperature of water — 25°; the amount of water flow was determined gravimetrically. Reduction of pressure from the commonly used 30 cm Hg to 20 cm Hg was necessary for practical reasons: during measurement at the pressure of 30 cm Hg thin-root segments were extruded from the rubber tubes in which they were fastened. Because of the thin roots relatively short segments had to be used.

The segments to be measured were fastened at first to small lengths of rubber tubes with the inner diameter a little smaller than the diameter of the root measured. The segment was put with its basal end at the bottom of the tube. Further mechanical fastening and sealing was carried out by sealing with a wax consisting of a mixture of honey-bee wax — petroleum jelly-tackiwax in the ratio 48:48:4 (O'Leary 1965). The mixture was applied to the whole lateral segment surface and to part of the tube after inserting the segment. This eliminated the prospective radial water outflow through the bases of lateral roots amputated or through breaches in the epidermis (Fig. 1b). Prior to the application of the sealing mixture the segment surface was wiped with a filter paper and smeared with cotton wool dipped in 96 per cent alcohol.

Conductivity measurements were not repeated. Riedl (1933) and then Bovis (1962) revealed that the quantitative value of the experimental conductivity decreases with the duration of the measurement. Gračanin (1962) drew attention to the fact that, especially in *Gramineae*, after severing the root a relatively fast chemotropical invasion of microorganisms into the vessels occurs. Briggs (1967) conjectures that the experimentally determined upper values of the conductivity can be considered as overvalued.

In the results the absolute conductivity values measured are given as well as the values converted for specific conductivity. The absolute conductivity value represents the amount of water flowing through the root

segment per time unit under the experimental conditions mentioned above (cm^3 $hour^{-1}$). In our experiments the specific conductivity value represents the amount of water flowing per time unit through the area unit (cm^3 cm^2 $hour^{-1}$).

Results

Total Area of the Root Transection/Conductivity

Values obtained by measuring the diameter in the individual root groups are summarized in Table 1. In the first column the mean absolute values for the entire efflux area are given, in the second the total area is expressed in per cent, the primary seminal root being used as the basis for evaluation (= 100 per cent). The smallest diameter was found in roots from the first coleoptile node. Beginning from the third node the total area of the transection increases approximately twice (geometric series with the coefficient of geometric progression $k = 2$).

TABLE 1

TOTAL TRANSECTION AREA of the individual groups of adventitious roots in the ratio to the primary seminal root of the corn plant as related to conductivity

Root type	Area of the root transection		Conductivity		Specific conductivity per surface of the root transection	
	mm^2	%	$cm^3\ h^{-1}$	%	$cm^3\ cm^2\ h^{-1}$*	%
Primary seminal	1·1106	100·00	25·72	100·00	2602	100·00
1st node	0·8097	72·91	65·77	255·56	8481	325·93
2nd node	1·4700	132·36	87·49	340·16	6172	237·20
3rd node	4·9026	441·44	181·01	703·92	3871	148·77
4th node	10·5765	952·32	288·30	1120·91	2783	106·97
5th node	20·0843	1808·41	557·15	2164·40	2757	105·97

* Segment length 5 mm, pressure 20 cm Hg, temperature of water 25°.

Values obtained in conductivity measurements are given in four subsequent table columns. Values for the absolute conductivity gradually increase, in roots of the fifth node the absolute conductivity equals 21-fold in comparison with the primary seminal root. However, when comparing values expressing transection areas with those of the absolute conductivity, it is apparent that the absolute conductivity is not a general function of the transection area. When converting the values for the absolute conductivity to that for the specific conductivity, the maximal specific conductivity appears in roots of the first node (326 per cent), the second place is represented by the roots of the second node (237 per cent), and the third by the roots of the third node (149 per cent). The specific conductivity of the left-over groups is almost identical when expressed per area unit.

Occurence of Conducting Tissues/Conductivity

When expressing conductivity per area unit, differences found between the individual root groups are evidently conditioned by the difference in their inner structure. The participation of water-conducting tissues is significant for the conductivity; with the segments analysed the metaxylem elements are actually in question. They are represented on one hand by

TABLE 2

PARTICIPATION OF CONDUCTING ELEMENTS in the total transection area of the individual groups of adventitious roots in the ratio to the primary seminal root of the corn plant

Root type	Area of the transection through the central cylinder		Proportion of the area of the transection through the central cylinder in the total area of the root transection	Number of protoxylem poles	Number of vessels of the large metaxylem
	mm²	%	%		
Primary seminal	0·265 ± 0·0023	100·00	21·83	14·5 ± 0·84	6·00 ± 0·74
1st node	0·256 ± 0·0032	85·96	27·75	21·4 ± 2·39	10·10 ± 1·41
2nd node	0·428 ± 0·0034	161·02	28·66	25·1 ± 2·16	12·00 ± 1·36
3rd node	1·570 ± 0·0583	589·95	33·99	40·7 ± 4·90	18·40 ± 2·20
4th node	3·833 ± 0·0360	1440·06	37·41	59·2 ± 6·84	32·80 ± 5·24
5th node	8·337 ± 0·0910	3132·95	42·29	88·2 ± 9·69	54·30 ± 7·44

a large central metaxylem containing vessels large in diameter, on the other by the early maturing narrow metaxylem located on the periphery of the vascular cylinder which is centripetally joined to the protoxylem points.

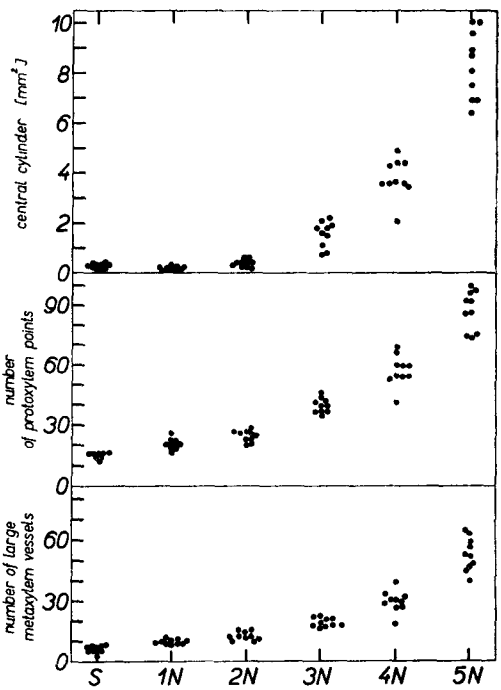

Fig. 3. Schematic demonstration of absolute values obtained on analysing ten segments from each root group. S — primary seminal roots, 1 N to 5 N — roots of the first to fifth node.

In Table 2 the mean absolute area of the central cylinder is given along with its percentual expression, the primary seminal root being used as the basis of the evaluation (100 per cent), next its proportion in the total transection area, and the participation of vascular elements. A good homogenity of the individual root groups is demonstrated in Fig. 3 where the area of the vascular cylinder is given in absolute values, as well as the number of protoxylem points and that of the vessels of the large metaxylem obtained on analysing ten segments of each root group. The results given provide only rough information about the size of the vascular system. The area of the central cylinder increases with the individual root groups, which are formed successively in the course of ontogenesis, with the exception of the roots originating from the first node. Gradually the number of protoxylem poles increases as well as the number of the large metaxylem elements. Whereas the central cylinder of the primary seminal root has only 14 protoxylem poles, in thick roots of the fifth node their number increases in average to 88; 1·6 to 2·4 xylem poles occur per one large metaxylem vessel.

TABLE 3

PARTICIPATION OF THE CONDUCTING AND NON-CONDUCTING AREA in the total transection area of various corn-root types as compared with the absolute conductivity values

Root types	Area of the root transection in mm^2	Total conducting area in mm^2	Total non-conducting area in mm^2	Conductivity in $cm^3 h^{-1}$
Primary seminal	1·1330	0·0405	1·0925	38·4
	1·1897	0·0332	1·1564	25·2
	0·9631	0·0319	0·9312	24·0
1st node	0·6516	0·0404	0·6112	73·0
	0·9064	0·0408	0·8656	69·0
	0·7308	0·0429	0·6879	63·0
2nd node	1·9262	0·0742	1·8520	78·0
	1·7279	0·0531	1·6748	71·7
	1·4843	0·0463	1·4380	57·0
3rd node	5·0138	1·1851	4·8953	195·0
	4·0280	0·9570	3·9323	204·0
	3·8524	1·0953	3·7429	189·0
4th node	8.4979	1.8970	8.3082	360.0
	8·9511	1·2984	8·8213	201·0
	10·0559	1·6481	9·8911	288·0
5th node	17·6757	3·2622	17·4495	363·0
	17·6757	3·2620	17·4495	555·0
	21·5281	2·7901	21·2491	756·0

An exact evaluation of the participation of the conducting area in the total cross-cut area was obtained by evaluating the metaxylem area planimetrically. Only three samples of each root group were processed. Results of the individual analyses are given in Table 3, relative ratios and ratio to the area of the central cylinder are summarized in Fig. 4. The total area in

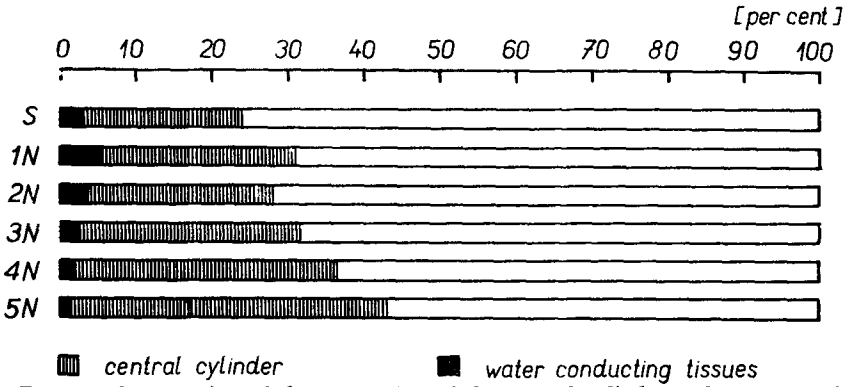

Fig. 4. Percentual expression of the proportion of the central cylinder and of the conducting area to the total transection area (100%). S — primary seminal root, 1 N to 5 N — roots of the first to fifth node.

roots of the first node is smaller in comparison with the primary seminal root, the conducting area slightly increases. Values expressing absolute conductivity are considerably higher. With the roots of the second node both the conducting and non-conducting area increases; however, the same ratio is maintained as with the primary seminal root. Beginning from the roots of the third node the proportion of non-conducting tissues increases markedly, approximately twice that of the second node. It follows from the values representing the absolute conductivity, that the conductivity of non-conducting tissues must be substantially lower than that of the conducting ones. Table 4 shows approximate values expressing the increase in the participation of conducting and non-conducting tissues and that of the absolute conductivity of the individual groups of adventitious roots in comparison with the primary seminal root.

TABLE 4

INCREASE IN THE PARTICIPATION OF CONDUCTING AND NON-CONDUCTING TISSUES and that in the absolute conductivity of the individual groups of adventitious roots in comparison with the primary seminal root of the corn plant

Root type	Conducting tissue	Non-conducting tissue	Specific conductivity
Primary seminal	1	1	1
1st node	$< 1{\cdot}2\times$	$> 0{\cdot}3\times$	$< 2{\cdot}5\times$
2nd node	$< 1{\cdot}7\times$	$< 1.5\times$	$< 3{\cdot}4\times$
3rd node	$< 3{\cdot}0\times$	$< 4{\cdot}0\times$	$< 7{\cdot}0\times$
4th node	$< 4{\cdot}0\times$	$< 7{\cdot}0-8{\cdot}0\times$	$< 11.0\times$
5th node	$< 7{\cdot}0\times$	$< 15{\cdot}0-16{\cdot}0\times$	$< 21{\cdot}0-23{\cdot}0\times$

In roots of the first node higher values of absolute conductivity were obtained. This could be explained also by the fact that in the cortex of these roots large air-spaces were found which could have influenced the conductivity values. However, the proportion of the conducting and non-conducting tissues was altogether in good conformity with the differences in conductivity found in the individual root types.

Discussion

Most papers on the investigation of conductivity in plants concern organs of secondary thickening species of dicotyledons. In the main they deal with conductivity measurements in the complex of conducting, supporting and storage tissues of which the secondary xylem is formed. However, in the secondary xylem the participation of conducting tissues is substantially higher in comparison with our experimental material: thus *e.g.* according to the analyses of SCHELLENBERG (1927) conducting tissues comprise 26 to 30 per cent of the total area of the root transections in the pear-tree. From the point of view of structural analysis the corn roots employed here represent, with their low percentage of vascular tissue concentrated on the periphery of the central cylinder, a very suitable material.

Another different moment is the fact that we did not consider the root segment as a body, and so we did not accept for the same all relationships usually connected with such a conception (HUBER 1956, RIEDL 1937, BOVIS 1962, RAWLINS 1963, GESSNER 1965, BRIGGS 1967). In this first part of our work the conductivity was related to the structure of the efflux area, concretly to its size and to the ratio of conducting and nonconducting tissues.

Values expressing the absolute conductivity in six root groups analysed (*i.e.* in the primary seminal roots and in those of the first to fifth node) give evidence for the increasing conducting capacity of the successively formed whorls. The primary seminal roots exhibited the minimal absolute conductivity, and the maximum was revealed in adventitious roots of the fifth node. However, when relating the values obtained to the area of the corresponding transections, it is apparent that the conductivity is not a general function of the total root area. Of roots analysed the thinnest are those of the first coleoptile node. Identical results, as far as the thickness of the individual types is concerned, were obtained by OVČINNIKOV and NIKOLAJEVSKIJ (1961) on analysing the variety Odeska 10 (area of the transection through the primary seminal root: Odeska 1·85 mm^2, VIR 42 1·13 mm^2; transection area of the root from the first node: Odeska 0·95 mm^2, VIR 42 0·97 mm^2). However, when calculating per area unit, roots of the first coleoptile node were found to be the most efficient. Values for the second and third node gradually decrease, roots of the fourth and fifth node exhibit, per area unit, approximately the same conductivity as do the primary seminal ones. Opinions of authors about the conducting capacity of the individual types of corn roots are not uniform. MARTIN and HERSHEY (1934/35) regard the roots of the first node to be small and limited in their conducting as well as absorptive capacity. According to Kojedžikov and

Božidarevič (Ovčinnikov and Nikolajevskij 1961), the root whorls of three lower nodes, regardless of the relatively small area of their central cylinder, have on the contrary an especially important function in water supply of the plant. The results of Ovčinnikov and Nikolajevskij are in agreement with these data. On the basis of the values obtained for the conductivity per area unit we must agree with the latter authors.

On the basis of the finding that conductivity is not a general function of the total area in root types analysed, one must assume that there exist qualitative or quantitative structural differences between the individual types. The critical occurrence of the conducting tissue in corn plants was confirmed by Postlethwait and Nelson (1957) who analysed the causes of wilting in a chronically wilted mutant. The wilting was conditioned by the insufficiently differentiated metaxylem, and thus no adequate water supply was provided to the plants afflicted.

By determining the size of the central cylinder rough information about the participation of the conducting tissue in the root was obtained; however, the data on the number of elements of the large metaxylem and that of protoxylem poles, which are identical with the number of vessels of the early maturing metaxylem, appear more concrete. Martin and Hershey (1934/35) found and Heimsch *et al.* (1950) confirmed the high level of significance when evaluating the relationship of the total cross-cut area of the corn root and the area of the vascular cylinder to the number of metaxylem elements. The planary evaluation revealed that with the line analysed, roots of the first coleoptile node have the highest percentual proportion of conducting tissue. Ovčinnikov and Nikolajevskij (1961) obtained the same course of the relative percentual participation of the conducting tissue with the maximum occurrence in the first node and with a gradual decrease in roots of lower whorls for the variety Odeska 10 and for the hybrid VIR 42 as well. For comparison we present both our results and theirs:

Percentual proportion of conducting tissue area in the transverse root section

	A 15	Odeska 10	VIR 42
Primary seminal root	3·22	5·70	5·04
1st node	5·42	7·58	7·50
2nd node	3·38	6·17	4·35
3rd node	2·57	6·86	4·02
4th node	1·76	4·69	3·69
5th node	1·33	3·71	2·72
		Material analysed by Ovčinnikov and Nikolajevskij (1961).	

The fact, that on analysing different material essentially identical results were obtained, allows one to assume that the scheme of conducting tissue occurrence found in the individual root groups holds for corn roots in general. The maximal relative participation of the conducting tissue in roots of the first node is in accordance with its maximal conductivity per area unit.

The absolute increase in the water-conducting area in the individual root groups corresponds principally to the increasing total conductivity found. However, results of measurements show that the conductivity is not a function of the conducting area. It follows from our findings that non-conducting tissues, or further factors in addition, took a certain part in the conductivity.

The comparison of the values for conductivity, obtained on analysing the individual root groups, with a different ratio in the participation of conducting and non-conducting tissues gives evidence of the real participation of the non-conducting tissues in conduction. Tissues not directly functioning as conductors have a substantially lower conductivity, however, they cannot be neglected because of their high percentual occurrence.

Among other factors which could interfere with the evaluation of the ratio between the participation of the conducting and non-conducting tissues, the occurrence of air-spaces must be considered. They are discussed in a detailed paper by SIFTON (1945); their origin in the cortex of corn plants was analysed by MCPHERSON (1939). Their occurrence, to which special attention was paid during our anatomical evaluation of the material, appears to be the probable cause of an inadequate increase in the conductivity of the root segments from the first node.

Acknowledgement

The authors wish to thank Mrs M. Takáčová, Miss J. Glasová and Mr. L. Kiššík for their thorough technical assistance.

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MÁRIA LUXOVÁ, V. KOZINKA, Botanický ústav Slovenskej akadémie vied, Bratislava: **Štruktúra a konduktivita koreňového systému kukurice.** — Biol. Plant. **12** : 47—57, 1970.

Na základe porovnania konduktivity 5 mm segmentov z bázy primárneho seminálneho koreňa a adventívnych koreňov prvého až piateho uzla sa zistilo, že vodivosť nie je obecnou funkciou plochy prierezu. Experimentálne stanovená vodivosť je u primárneho seminálneho koreňa najmenšia a u adventívnych koreňov sa postupne zvyšuje. Pri prepočte na jednotku plochy sú však najvýkonnejšie korene prvého koleoptílneho uzla, pre korene druhého a tretieho uzla sa hodnoty postupne znižujú, korene štvrtého a piateho uzla majú vodivosť na jednotku plochy približne rovnakú ako primárne seminálne korene.

Vodivosť nie je ani púhou funkciou vodivej plochy. Pletivá, neslúžiace priamo vodivej funkcii, majú síce vodivú kapacitu podstatne nižšiu, pre ich vysoké percentuálne zastúpenie nie sú však pri hodnotení vodivosti zanedbateľné. Celkovú vodivosť u jednotlivých typov koreňov ovplyvňuje pomer zastúpenia vodivých a nevodivých pletív.

The plates will be found at the end of the issue.

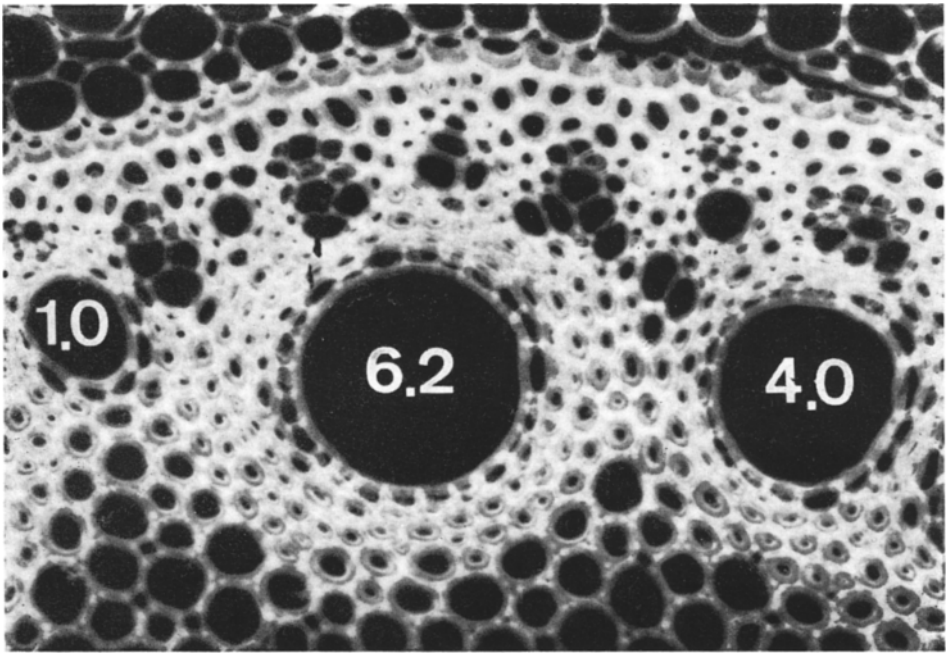

Fig. 2. Microphotograph representing a detail of the transection through the root of the second node at 350× magnification. Numbers in vessels express the vessel area in cm^2 determined planimetrically.