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Transfer cells in the vascular parenchyma of roots

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Abstract

Structural adaptations to increased transport activities were investigated in the cells of vascular parenchyma at the site of the lateral root junction, in non-stressed plant roots. Typical transfer cells were differentiated in dicotyledonous *Helianthus tuberosus* and in two different genotypes of *H. annuus*, the cv. IBH166 and a decorative form. In the representatives of monocotyledonous, no structural adaptations occurred in the roots of *Hordeum vulgare* but small and rare cell wall protuberances were found in xylem and phloem of *Zea mays* inbred line VIR17. Some degree of cell wall labyrinth differentiation was seen in xylem and typical transfer cells were found in phloem of the roots of the maize hybrid CE380. The capability of vascular parenchyma to differentiate transfer cells did not depend on species, genotype, or on the growing conditions with *Helianthus*. On the other hand, the development of the structural adaptations in monocotyledonous representatives depended on both the species and the genotype. This capability may be linked with the taxonomic and evolutionary position of plant species.

Introduction

Transfer cells have been recorded in many plant species in generative organs (Johri 1984) or vascular parenchyma of leaves and stems (Pate and Gunning 1969, Wooding 1969, Gamalei and Pakhomova 1983, Lörcher *et al.* 1987). In the root vascular parenchyma, the transfer cells were observed less frequently: In xylem parenchyma of *Phaseolus coccineus* (Kramer *et al.* 1977), *Pisum sativum* (Newcomb and Peterson 1979) and in both xylem and phloem parenchyma of *Hieracium florentinum* (Letvenuk and Peterson 1976). Only 3 of 42 species belonging to the family *Valerianaceae*, showed very poorly developed protuberances in the cells of root vascular parenchyma (Lörcher *et al.* 1987). The occurrence of transfer cells has always been associated with lateral roots, root nodules or root buds. At lateral root

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insertion point, connective vascular system develops (Luxová 1990) which also can bear transfer cells. There they may be involved in loading ions into the xylem or withdrawing assimilates from the sieve tubes (Läuchli *et al.* 1974, Letvenuk and Peterson 1976, Kramer *et al.* 1977). In plant roots, the differentiation of rhizodermal cells into transfer cells can also be induced by iron deficiency or salt stress (Kramer *et al.* 1978, 1980) and in xylem parenchyma by salinity (Yeo *et al.* 1977).

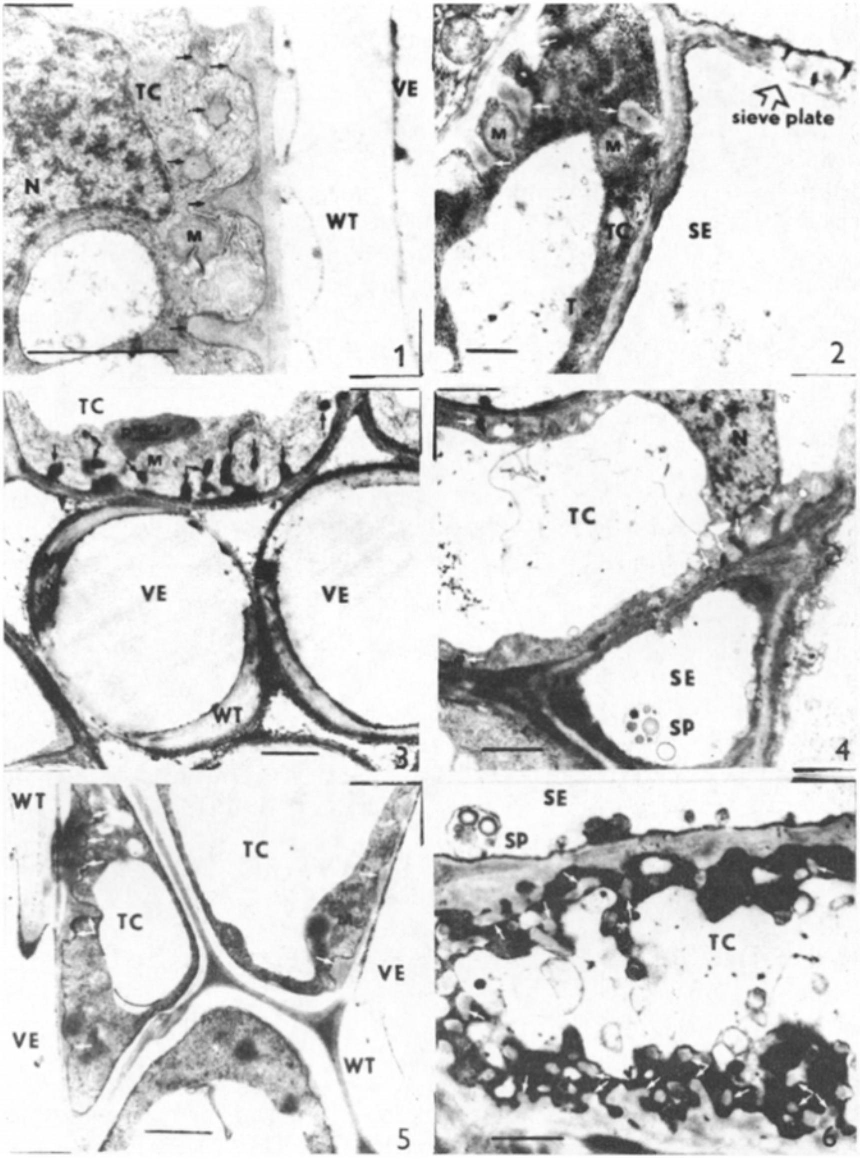
The occurrence of transfer cells in vascular parenchyma of leaves and stems was related to the taxonomic position of a particular species (Pate and Gunning 1969, Gamalei and Pakhomova 1983, 1984, Lörcher *et al.* 1987). Transfer cells have not yet been reported for the roots of non-stressed monocotyledonous taxons. The roots of different monocotyledonous and dicotyledonous species and genotypes under non-stress conditions were investigated for the presence of transfer cells or some less developed structural adaptations to increased transport activities.

Materials and methods

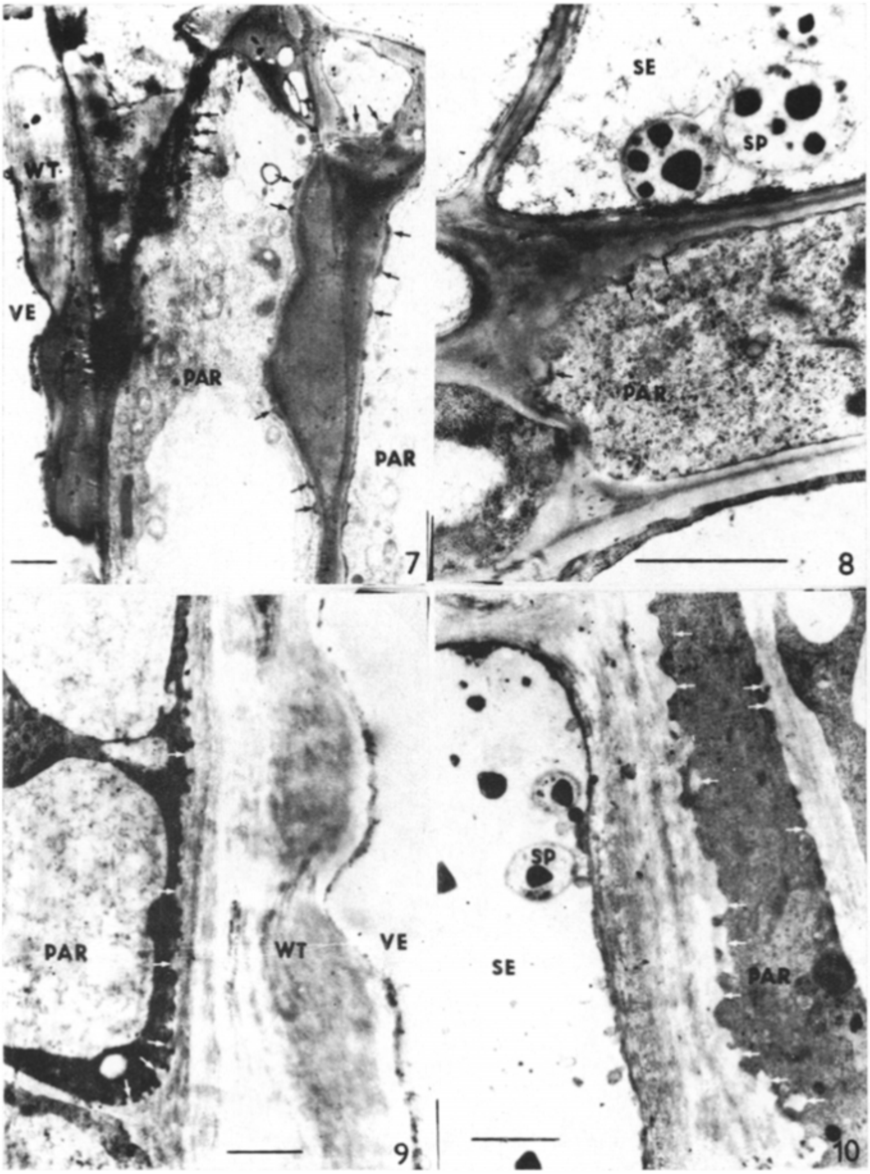
The tubers of *Helianthus tuberosus* were allowed to develop roots in the soil or, wrapped in filter paper moistened with half strength Hoagland nutrient solution, in the greenhouse. The seeds of the other experimental plants: *Helianthus annuus*, cv. IBH 166, a decorative form of *H. annuus* representing two different sunflower genotypes, *Zea mays* (inbred line VIR 17 and a hybrid CE 380), and *Hordeum vulgare* cv. Slovenský dunajský trh, germinated and grew wrapped in sheets of filter paper moistened with the same nutrient solution for 7 to 10 d at 25 °C. Root segments 1 mm long, with or without the basal part of a lateral root were fixed for electron microscopy (EM) with 3 % glutaraldehyde in 0.1 M Na-cacodylate buffer (pH 7.2) and postfixed with 1 % OsO_4 in the same buffer. The samples were dehydrated in an ethanol series and in propylene oxide, and embedded in Epon-Araldite mixture. Semithin sections stained with Toluidine blue were used for orientation within the root segment. Ultrathin sections were stained with uranyl acetate and Pb citrate and investigated with the EM *Tesla BS 500*. Parenchymatous cells accompanying sieve and tracheary elements of both main and lateral roots as well as those of the connective vascular system were investigated.

Results

Well developed transfer cells were observed in the roots of all dicotyledonous *Helianthus* samples (see Material and methods) at the point where the lateral root conducting system joins the stele of a parent root (Figs. 1 - 6). They were present in phloem and xylem parenchyma of the main root, in the connective vascular system as well as at the base of lateral roots. Transfer cells were present in the roots of *H. tuberosus* grown in both soil and nutrient solution. The cell wall labyrinth was well developed and the cytoplasm typically rich in mitochondria and other cell



Figs.1 - 6. Part of xylem (1, 3, 5) and phloem (2, 4 ,6) in the roots of *Helianthus tuberosus* (1, 2), *Helianthus annuus* cv. IBH166 (3, 4) and a decorative form of sunflower (5, 6). Transfer cells (TC) with cell wall protuberances (*arrows*) are adjacent to vessel elements (VE) with secondary wall thickenings (WT) or, to sieve elements (SE) with characteristic sieve plastids (SP). The transfer cells contain nucleus (N) and other organelles like mitochondria (M) or plastids (P). The bars represent 2 μm.



Figs. 7 - 10. Part of xylem (7, 9) and phloem (8, 10) in the roots of *Zea mays* inbred line VIR 17 (7, 8) and hybrid CE 380 (9, 10). Cell wall protuberances in the parenchyma cells (PAR) accompanying vessel elements (VE) with secondary wall thickenings (WT) and to phloem elements (SE) with typical plastids (P). The bars represent 2 μm.

organelles. Transfer cells were not found in the main root sections between the insertions of lateral roots.

The development of transfer cells in the roots of the monocotyledons depended on species and varied also with genotypes. No structural adaptations of vascular parenchyma were found in the roots of *Hordeum vulgare*. Xylem and phloem parenchyma cells in the roots of *Zea mays* inbred line VIR 17 (Figs.7, 8) develop only small and rare cell wall protuberances. Some degree of cell-wall labyrinth development was observed in xylem parenchyma of maize hybrid CE 380 (Fig.9). Cell wall protuberances were even more developed in the parenchymatous cells adjacent to sieve elements (Fig.10). However, the wall labyrinth in maize genotypes was not as well differentiated as in the roots of any of the *Helianthus* taxons.

Discussion

At the sites of the lateral root junction, well developed transfer cells were shown in phloem and xylem parenchyma of the main root, the connective vascular system and at the base of lateral roots in *Helianthus tuberosus*, and in the two genotypes of *H. annuus*. In contrast, the development of transfer cells in the roots of monocotyledonous species seems to depend on both species and genotypes of the same species. While there were no cell wall protuberances in *Hordeum vulgare*, small and rare protuberances were formed in xylem parenchyma of the inbred line VIR 17. More elaborated structural adaptations reminiscent of typical transfer cells were found in xylem and particularly in phloem parenchyma of the maize hybrid CE 380. Such structural adaptations have not yet been recorded in the roots of non-stressed monocotyledonous plants. However, the degree of transfer cell differentiation was always higher in the dicotyledonous *Helianthus* species.

Transfer cells in the xylem and phloem root parenchyma of *Helianthus* species and genotypes were found under non-stress conditions. In the roots of some dicotyledonous species the transfer cells are common in relation to lateral root traces of plants grown in nutrient solution (Letvenuk and Peterson 1976). The suggestion of these authors that transfer cells can also develop in the roots of naturally growing plants, could be confirmed by our observation of transfer cells in *Helianthus tuberosus* grown in soil. The occurrence of transfer cells associated with vascular tissues in leaves suggests some relationship to the taxonomic distribution of plant species developing transfer cells (Pate and Gunning 1969, Gamalei and Pakhomova 1983). In some families, the frequency of such species is higher than in others. The rise of transfer cells is suggested to have occurred somewhat late, and on several isolated occasions, during the evolution of the angiosperms (Pate and Gunning 1969). The family *Asteraceae* to which *Helianthus* belongs is one of those with a high frequency of species bearing transfer cells (Pate and Gunning 1969, Gamalei and Pakhomova 1983). The species of such families are probably more prone to differentiate also transfer cells in their root vascular tissues and, as in *Helianthus*, regardless of plant species or genotype. On the other hand, transfer cells have been recorded in monocotyledonous plants very rarely (*e.g.* in caryopses of maize, Davis *et al.* 1990). Our results on *Hordeum* and *Zea* reveal the lower capacity of their vascular parenchyma to differentiate cell wall labyrinth. However, this capacity does exist to some degree and it depends on both the species and the genotype of the particular species.

References

Davis, R.W., Smith, J.D., Cobb, B.G.: A light and electron microscope investigation of the transfer cell region of maize caryopses. - Can. J. Bot. **68**: 471-479, 1990.

Gamalei, Yu.V., Pakhomova, M.V.: [Minor veins of dicotyledonous leaf. II. Taxonomical distribution of the main types]. - Bot. Zh. **68**: 428-438, 1983. [In Russ.].

Gamalei, Yu.V., Pakhomova, M.V.: [Minor veins of dicotyledonous leaf. III. Structure, functions, evolution]. - Bot. Zh. **69**: 1159-1166, 1984. [In Russ.].

Johri, B.M. (ed.): Embryology of Angiosperms. - Springer Verlag, Berlin - Heidelberg - New York - Tokyo 1984.

Kramer, D., Läuchli, A., Yeo, R., Gullasch, J.: Transfer cells in roots of *Phaseolus coccineus*: Ultrastructure and possible function in exclusion of sodium from the shoot. - Ann. Bot. **41**: 1031-1040, 1977.

Kramer, D., Anderson, P.W., Preston, J.: Transfer cells in the root epidermis of *Atriplex hastata* L. as a response to salinity: A comparative cytological and X-ray microprobe investigation. - Aust. J. Plant Physiol. **5**: 739-747, 1978.

Kramer, D., Römheld, V., Landsberg, E., Marschner, H.: Induction of transfer-cell formation by iron deficiency in the root epidermis of *Helianthus annuus* L. - Planta **147**: 335-339, 1980.

Läuchli, A., Kramer, D., Stelzer, R.: Ultrastructure and ion localization in xylem parenchyma cells of roots. - In: Zimmermann, U., Dainty, J. (ed.): Membrane Transport in Plants. Pp. 363-371. Springer Verlag, Berlin - Heidelberg - New York. 1974.

Letvenuk, L.J., Peterson, R.L.: Occurrence of transfer cells in vascular parenchyma of *Hieracium florentinum* roots. - Can. J. Bot. **54**: 1458-1471,1976.

Lörcher, H., Weberling, F., Hildebrand, M.: Transferzellen im Xylem der *Valerianaceae*. - Plant Syst. Evol. **156**: 69-89,1987.

Luxová, M.: Effect of lateral root formation on the vascular pattern of barley roots. - Bot. Acta **103**: 305-310, 1990.

Newcomb, W., Peterson, R.L.: The occurrence and ontogeny of transfer cells with lateral roots and root nodules in *Leguminoseae*. - Can. J. Bot. **57**: 2583-2602, 1979.

Pate, J.S., Gunning, B.E.S.. Vascular transfer cells in angiosperm leaves. A taxonomic and morphological survey. - Protoplasma **68**: 135-156, 1969.

Wooding, F.B.P.: Absorptive cells in protoxylem: Association between mitochondria and the plasmalemma. - Planta **84**: 235-238, 1969.

Yeo, A.R., Kramer, D., Läuchli, A., Gullasch, J.: Ion distribution in salt-stressed *Zea mays* roots in relation to ultrastructure and retention of sodium. - J. exp. Bot. **28**: 17-29, 1977.

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