

Fig. 2. Details of root-soil contact of wheat as observed on thin sections. (A) Longitudinal section of branching root with 100% root-soil contact. (B) Transverse section of root growing in a void with direct soil contact on two sides, root penetrating the soil matrix. (C) Transverse section of root with partial contact; note cortical aerenchyma. (D) Transverse section of root without direct soil contact, but with root hairs extending towards the soil matrix and a branch root with partial contact.

roots growing in pre-existing macropores a larger part had no direct contact with the soil. In the latter group root hairs may still establish partial contact with the soil, but only on a fraction of the roots without soil contact root hairs were seen. Table 2 summarizes root-soil contact data for the plough layer at the two fields. Average root-soil contact differed significantly between the two fields.

Part of the macropores in which roots were found were stained with meth-

Winter wheat 1990 Lovinkhoeve

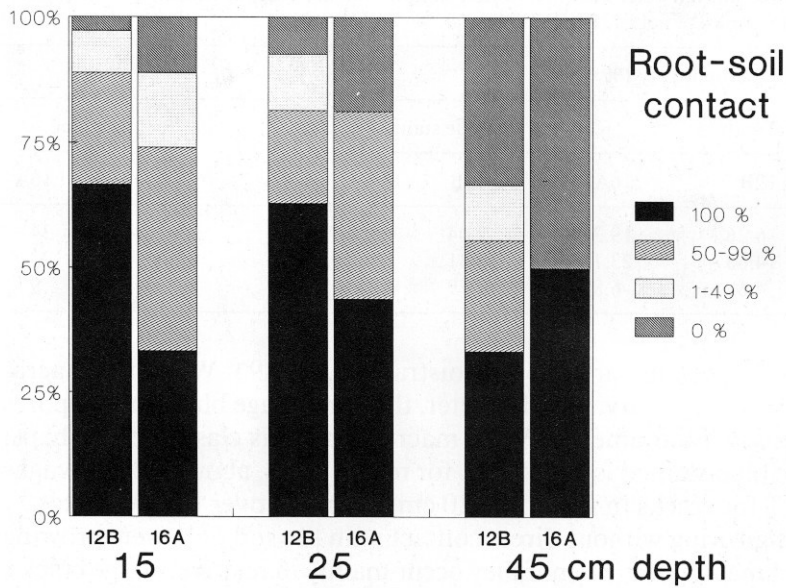


Fig. 3. Frequency distribution of root-soil contact of wheat in horizontal thin-section samples taken at three depths in two fields of the Lovinkhoeve experiment. Number of roots observed in the 640 fields of view (0.94 mm² each) on six thin sections: 36, 27, 27, 16, 9 and 4, respectively.

TABLE 2

Root-soil contact of wheat for horizontal thin sections at 15 and 25 cm depth for two fields, 12B and 16A

Root-soil contact class (%)	Percentage of roots		Average contact	
	12B N=63	16A N=43	12B	16A
0	4.8	14.0	0	0
1-99	30.2	48.8	61.7	58.6
100	65.1	37.2	100	100
Total	100	100	83.7	65.8

ylene blue and are thus considered to be surface-connective. Table 3 shows the macroporosity (diameter > 30 μm) for vertically oriented thin-section samples, taken close to the horizontally oriented ones used for evaluating root-soil contact. The macroporosity on the thin sections is relatively high, especially on field 16A, compared to previous measurements (Kooistra et al., 1989). About 30% of the macropores in the upper 20 cm of the soil is blue

TABLE 3

Macroporosity ($> 30 \mu\text{m}$ diameter) in thin-section samples for three depth zones of vertically oriented thin-section samples of field 12B and 16A

Depth (cm)	Macroporosity (% v/v)					
	Total		Blue stained		Percentage blue	
	12B	16A	12B	16A	12B	16A
01-09	6.26	19.35	2.04	6.61	33	34
11-19	14.63	23.15	6.81	5.06	46	22
21-29	4.65	6.80	0.79	0.63	17	9

stained, similar to results for 1985 (Kooistra et al., 1989). When the macropores are classified by equivalent diameter, the percentage blue-stained pores tends to increase with diameter. When macroporosity is classified by shape, the percentage blue-stained is about 20% for round pores, about 25% for vughs and about 40% for cracks in the upper 20 cm, averaged over the two fields.

Of the roots growing without direct contact with the soil 56% were growing in blue-stained macropores; even if they occur mainly in relatively large cracks, they appear to prefer blue-stained and thus surface-connective cracks. Of the roots with 1-49% and 50-99% contact 20 and 7%, respectively, were growing in blue-stained macropores. Roots with 100% soil contact were not stained.

DISCUSSION

The average root diameter on the thin sections was 10% less than the diameter of roots washed from auger samples. This might be caused by root shrinkage during sample preparation, or by losses of fine rootlets when washing or by a different criterion for separating live and dead roots. Root shrinkage is probably not a major cause as we observed many roots with 100% root-soil contact. When the thin-section method was tested on a maize pot experiment, with soil without root remains, the root intensity observed (N , cm^{-2}) agreed with the root length density (L_{rv} , cm/cm^3) from washed replicate samples, following the theoretical relation $L_{rv} = 2N$ (Van Noordwijk et al., 1992). For the current samples we found $L_{rv} = 0.97N$ on field 12B and $L_{rv} = 1.3N$ on field 16A, averaged over 15 and 25 cm depth. This could be due to the fact that the thin section samples had a higher than average root density (the data fall within the range of root densities on individual auger samples) or to the fact that part of the roots observed on the thin section would be discarded as dead roots in the washed samples. In discussing the data the possibility of the latter explanation should be kept in mind.

Roughly two thirds of the roots formed their own root channels on the thin

sections of field 12B, as derived from the frequency of 100% root-soil contact, and only one third on 16A. The considerably higher macroporosity of the plough-layer samples of field 16A, with its higher soil organic matter content, suggest that more roots could follow pre-existing pores on that field, while roots on field 12B had to penetrate the soil matrix. Roots occupied only a small fraction (1–5%) of the available, blue-stained macropore space, however, even on field 12B. The small size of the thin section samples, taken from one soil pit in each field, makes it impossible to extrapolate from the samples to the field scale. Because cropping history and current management are confounded in the comparison of the two fields (Kooistra et al., 1989), no conclusions on the influence of either of them can be made. The differences found in root-soil contact are primarily related to a difference in macroporosity, not to specific causes of this difference in macroporosity.

The average values for root-soil contact in this study are within the range found earlier for maize (Kooistra et al., 1992). Root hairs which may make up for incomplete root-soil contact were seen only rarely, although some examples show that they survive sample preparation without apparent damage. As noted in a pot experiment (Kooistra et al., 1992), roots growing in existing macropores and cracks have more contact with the soil than would be expected for a random positioning in the macropore space. Roots can apparently find and follow the walls of the macropores and cracks.

Roots without direct contact with the soil were growing mostly in surface-connected (blue-stained) macropores. Roots with 1–49% root-soil contact occurred in macropores with an average fraction of blue staining, while roots with 50–99% root-soil contact occurred mostly in relatively small, non-stained pores. Roots penetrating the soil matrix (100% root-soil contact) probably depend on internal aeration through cortical air spaces. A certain part of each root axis should have air contact to serve as “breathing sections”. The observation that roots with complete air contact grow mostly in surface-connected pores agrees remarkably well with this interpretation.

REFERENCES

- Altemüller, H.J. and Haag, Th., 1983. Mikroskopische Untersuchungen an Maiswurzeln im ungestörten Bodenverband. *Kali-Briefe (Büntehof)*, 16: 349–363.
- Altemüller, H.J. and Vorbach, A., 1987. Veränderungen des Bodengefüges durch Wurzelwachstum von Maispflanzen. *Mitt. Dtsch. Bodenkundl. Gesellsch.*, 55: 93–98.
- De Willigen, P. and Van Noordwijk, M., 1984. Mathematical models on diffusion of oxygen to and within plant roots, with special emphasis on effects of soil root contact. I. Derivation of models, II. Applications. *Plant Soil*, 77: 215–241.
- De Willigen, P. and Van Noordwijk, M., 1987. Roots, plant production and nutrient use efficiency. Doctoral Thesis, Wageningen Agricultural University, 282 pp.
- De Willigen, P. and Van Noordwijk, M., 1989. Model calculations on the relative importance

- of internal longitudinal diffusion for aeration of roots of non-wetland plants. *Plant Soil*, 113: 111–119.
- Faiz, S.M.A. and Weatherley, P.E., 1982. Root contraction in transpiring plants. *New Phytol.* 81: 19–23.
- Herkelrath, W.N., Miller, E.E. and Gardner, W.R., 1977. Water uptake by plants. II. The root contact model. *Soil Sci. Soc. Am. Proc.*, 41: 1039–1043.
- Huck, M.G., Klepper, B. and Taylor, H.M., 1970. Diurnal variations in root diameter. *Plant Physiol.*, 45: 529–30.
- Kooistra, M.J., Lebbink, G. and Brussaard, L., 1989. The Dutch programme on soil ecology of arable systems. 2. Geogenesis, agricultural history, field site characteristics and present farming systems at the Lovinkhoeve experimental farm. *Agric. Ecosyst. Environ.*, 27: 361–387.
- Kooistra, M.J., Schoonderbeek, D., Boone, F.R., Veen, B.W. and Van Noordwijk, M., 1992. Root-soil contact of maize, as measured by a thin-section technique. II. Effects of soil compaction. *Plant Soil*, 139: 119–129.
- Tennant, D., 1975. A test of a modified line intersect method of estimating root length. *J. Ecol.*, 63: 995–1001.
- Van Noordwijk, M., Kooistra, M.J., Boone, F.R., Veen, B.W. and Schoonderbeek, D., 1992. Root-soil contact of maize, as measured by a thin-section technique. I. Validity of the method. *Plant Soil*, 139: 109–118.
- Veen, B.W., Van Noordwijk, M., De Willigen, P., Boone, F.R., Kooistra, M.J., 1992. Root-soil contact of maize, as measured by a thin-section technique. III. Effects on shoot growth, nitrate and water uptake efficiency. *Plant Soil*, 139: 131–138.