Communications in Soil Science and Plant Analysis

ISSN: 0010-3624 (Print) 1532-2416 (Online) Journal homepage: http://www.tandfonline.com/loi/lcss20

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To cite this article: U. Buczko & R. O. Kuchenbuch (2013) Spatial Distribution Assessment of Maize Roots by 3D Monolith Sampling, Communications in Soil Science and Plant Analysis, 44:14, 2127-2151, DOI: 10.1080/00103624.2013.799682

To link to this article: http://dx.doi.org/10.1080/00103624.2013.799682

Accepted author version posted online: 24 May 2013.
Published online: 24 May 2013.

Communications in Soil Science and Plant Analysis, 44:2127–2151, 2013

ISSN: 0010-3624 print / 1532-2416 online
DOI: 10.1080/00103624.2013.799682

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Spatial Distribution Assessment of Maize Roots by 3D Monolith Sampling

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Spatial distribution of roots is of paramount importance for nutrient acquisition by crop plants. The objective of this study was to assess the spatial distribution of root length density (RLD), root mass density (RMD), and root morphological parameters in maize. Soil monoliths were completely sampled in form of 84 cubic samples of 10-cm edge length. Total root length and mass were dominated by fine roots (<1 mm diameter). Root parameters revealed variability in all three spatial dimensions, notably also parallel to the plant row. Root morphological parameters depended more on the horizontal location with respect to location of plants than on depth. Multiple regression analysis indicated that RLD, proportion of fine roots, and root diameters can be predicted from RMD, soil depth, and distance to plant. These three-dimensional (3D) data could be utilized for evaluation of 3D root growth and nutrient uptake models.

Keywords Maize (*Zea mays* L.), nutrient acquisition, root diameter, root length density, root morphology, spatial variability

Introduction

Knowledge about the spatial distribution of parameters describing the root system of crop plants such as maize is of paramount importance to assess water uptake and mineral nutrient uptake by plants. Uptake efficiency for water and nutrients depends to a large degree on root length density (RLD) distribution. Biomass allocation into the soil is adequately described by root mass density (RMD) distribution (Amato and Ritchie 2002; Amos and Walters 2006). Root systems consist of different root types with different properties as regards morphology (Pagès, Jordan, and Picard 1989; Varney et al. 1991), elongation rates (Cahn, Zobel, and Bouldin 1989), uptake efficiency of water and nutrients, hydraulic conductivity, and position within the architectural framework (McCully 1999; Waisel and Eshel 2002). Therefore, a full characterization of a crop root system must encompass both the spatial distribution of root length (RL) and root mass (RM) and the spatial distribution of different root types. This has been endeavoured by modeling and measurement approaches. Approaches focused on the single plant typically characterize the root system architecture in much detail. This has been done by detailed excavations of root systems

Received 12 September 2011; accepted 31 December 2012.
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(Weaver 1926; Kutschera, Lichtenegger, and Sobotik 2009) and more recently by root system architecture models (e.g., Pages, Jordan, and Picard 1989, Pagès et al. 2000; Dunbabin, Diggle, and Rengel 2002; Wu et al. 2005; Pierret et al. 2007).

Evaluation of detailed three-dimensional (3D) root architectural models using field data of root growth has been scarce until now (Pagès and Pellerin 1996; Pellerin and Pagès 1996; Grabarnik, Pagès, and Bengough 1998), because of the high experimental effort coupled with a lack of well-defined methodologies to determine detailed root distributions in 3D (Pagès and Pellerin 1996). Therefore, Pagès and Pellerin (1996) and Pellerin and Pagès (1996) used two-dimensional (2D) maps of root intersections. Another method to obtain root distributions is spatially distributed monolith sampling. Such monolith samplings have been mostly restricted to two dimensions (Buman, Schumacher, and Riedell 1994; Gajri, Arora, and Kumar 1994; Li et al. 2006). However, it has been demonstrated recently (Kuchenbuch, Gerke, and Buczko 2009) that in row crops such as maize, spatial variability of root parameters is of importance in all three directions, that is, also parallel to the plant row. In such cases, sampling methods that capture spatial variation in all three dimensions are necessary. With other methods to characterize the root system in soil (Böhm 1979), it is mostly not feasible to assess the spatial distribution of roots adequately. For instance, it is well known that auger or core sampling yields large errors, unless very large numbers of cores are analysed (Buczko, Kuchenbuch, and Gerke 2009).

Similarly as in other monocotyledonous plants, the root system of maize is formed from an embryonic seminal system that appear at germination and an adult root system of nodal, crown, or adventitious roots that arise later from successive nodes (on average six) of the shoot (e.g., McCully 1999; Hochholdinger 2009). The mean diameter and number of shoot-borne roots per node increase at higher nodes (Hoppe, McCully, and Wenzel 1986; Pellerin and Pagès 1994; Kutschera, Lichtenegger, and Sobotik 2009). It is generally recognized that lateral roots correspond to fine roots (for maize, defined as roots with diameters < 0.8 mm, McCully 1999) and that they play a key role in the acquisition of water and nutrients (McCully 1999).

Several studies focused on the frequency and occurrence of different root types and diameters without consideration of spatial distribution (Cahn, Zobel, and Bouldin 1989; Varney et al. 1991). On the other hand, detailed excavations of the root system of separate maize plants as conducted by Weaver (1926) and Kutschera, Lichtenegger, and Sobotik (2009) are extremely laborious and require some very special skills. Moreover, the results of these detailed excavations are plant-based maps of the root system (2D), and the link from these maps to 3D spatial distributions of soil-related root parameters for soil water flow models is not straightforward.

Thus, there is a general scarcity of spatial distributions of root parameters within the soil. A previous spatially distributed monolith sampling study (Kuchenbuch, Gerke, and Buczko 2009) has shown that root length (RL) and root mass (RM) exhibit spatial heterogeneity in all three spatial dimensions, and that the commonly applied auger core sampling can incur large errors when characterizing spatial distributions of roots (Buczko, Kuchenbuch, and Gerke 2009), especially when different root diameter classes are investigated.

In general, root diameters of roots separated from the soil by elutriation can be determined by scanning and with image analysis systems (Himmelbauer, Loiskandl, and Kastanek 2004; Qin, Stamp, and Richner 2005). The limiting step, however, in these procedures is not scanning but preparation of a suitable sample, e.g., by washing roots from soil. Therefore, these methods may be too time-consuming for large soil volumes. Moreover, estimation of root length and root diameter distribution is extremely sensitive to the scanning protocol (Bouma, Nielsen, and Koutstaal 2000; Himmelbauer, Loiskandl, and Kastanek 2004). Alternative, more rapid methods based on root mass distribution determined by sieving have been proposed for instance by Blouin, Barot, and Roumet (2007). However, with this method only RD distribution of RM is obtained. In the present study, large soil volumes should be analyzed, both RL and RM were of interest, and the main focus was on differentiating between fine roots (lateral roots) and larger roots (nodal roots). Therefore, it was not necessary to measure the root diameters with excessive accuracy. Instead, roots were categorized with the aid of binocular diameter measurements and according to visual criteria into a few distinctive diameter classes during the washing procedure.

In summary, the objective of this study was to analyze the spatial distribution of RL and RM for different root diameter classes and compare spatial distributions for two different plant row widths. A further aim was to analyze whether RLD and root morphological parameters (proportion of fine roots, root diameter) could be predicted using RM and/or other readily available parameters.

Material and methods

Field Site and Experimental Design

The field site was located near the village of Paulinenaue (52° 41′ N; 12° 42′ E), 50 km northwest of Berlin in the flat lowlands of the landscape "Havelländisches Luch." The soil was a Mollic Gleysol (FAO 2006) with predominantly sandy texture, originating from a degraded shallow fen lying on fluviatile sands. The soil profile was characterized by a sharp contrast between the cultivated humic topsoil and the subsoil at about 30 cm deep. Redoximorphic soil patterns occurred at approximately 30–40 cm deep and below. Organic carbon (C) contents in the cultivated topsoil (0–30 cm deep) amounted to 21–22 g C kg^{-1} soil.

Altogether, samples were taken once in 2003 and twice in 2004 (Kuchenbuch, Gerke, and Buczko 2009). In the present paper, only samples taken at the second date in 2004 were used, because only at this sampling date different root size classes were differentiated.

The two plots of 37.5- and 75-cm row spacing used for this investigation have been conventionally managed by soil tillage in autumn using a moldboard plow and by fertilizer application of 32 kg ha^{-1} phosphorus (P) and 99 kg ha^{-1} potassium (K) in March and 140 kg ha^{-1} nitrogen (N) as urea in the beginning of April. In both plots, maize (cv. Tassilo) was planted on 28 April 2004 with a density of 74,000 plants ha^{-1}. Consequently, the mean within-row distance between plants is 18 cm for the plot with wide row spacing (wrs, 75 cm) and 36 cm for that with narrow row spacing (nrs, 37.5 cm). Samples were taken at tasseling stage on 10 August 2004, 104 days after planting (DAP). The cumulative growing degree day (GDD, assuming a base temperature of 10 °C) for the period between planting and sampling in 2004 is 656 °C × day, and the precipitation is 214 mm for 104 days (Kuchenbuch, Gerke, and Buczko 2009).

Samples for determination of RLD, RMD, root diameter (RD) class, soil bulk density (SBD), and soil water content (SWC) were taken according to a complete 3D soil sampling scheme as described in Kuchenbuch, Gerke, and Buczko (2009) (Figure 1). The soil monolith was 70 cm long (perpendicular to plant rows, x direction), 40 cm wide (parallel to plant rows, y direction), and 30 cm deep (z direction). The soil volume of 0.084 m^3 in total was sampled completely in form of 84 cube-shaped 1-L (i.e., 0.001-m^3) samples (Figure 1) for both row spacings. Sampling was carried out from a trench at the side by horizontally

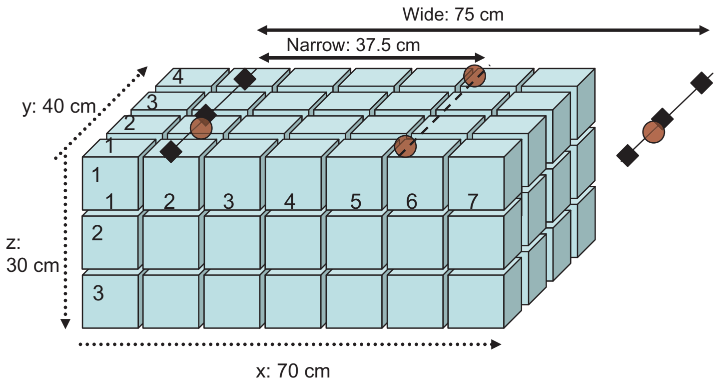

Figure 1. Illustration of the 3D monolith sampling scheme. Rhombic filled symbols denote locations of maize plants for wide row spacing; circular symbols denote the locations of maize plants for narrow row spacing (color figure available online).

pushing 1000-cm^3 metal frames with sharpened edges into the soil profile wall perpendicular to the plant rows and cutting the back parts with a blade. The procedure allows capturing all soil and roots of the monolith in defined volumes such that full spatially distributed information is available. The mass of the field-moist samples was determined directly in the field; afterward, the samples were filled in plastic bags and transported to the laboratory for further processing. On the following day, all samples were removed from the bags and spread on open trays in a greenhouse for air drying.

Soil and Root Analyses

From each of the samples, an aliquot of about 50 g was taken and oven dried at 105 °C for 24 h to obtain soil dry mass for calculating SWC and SBD values. A second subsample of about 80 g was dried at 60 °C for 24 h for chemical analyses (C and N contents).

Each time, the remaining fraction of an air-dried sample was submerged in water for 24 h before starting with the root measurements; the rehydrated roots were then washed out by sieving, using two sieves of 1-mm and 0.4-mm mesh sizes (more details can be found in Kuchenbuch, Gerke, and Buczko 2009). The detected roots were stained with a blue dye solution by dripping a methylene-violet solution (1 g in 100 mL of 95% ethanol solution) and leaving in contact for 2 d such that the visibility of roots was increased for the following quantitative steps. Then roots were rinsed and counted. The elutriated roots were stored in 60% (volume %) aqueous ethanol solution until RL was determined using the modified Newman line intersect method (Tennant 1975). During the counting of intersections on the grid, roots were separated according to morphology and approximate diameter (with the help of a microscale) into five classes (pictured exemplarily in Figure 2):

1. large, diameter > 3 mm;
2. coarse, diameter 1–3 mm;
3. fine 0.35–1 mm coarse, diameter < 1 mm;
4. fine 0.35–1 mm fine, diameter < 1 mm;
5. fine < 0.35 mm, diameter < 0.35 mm.

In contrast with studies that used image analysis of scanned roots and fixed root diameter classes, for instance, with 0.2-mm steps between <0.2 and 3.2 mm as in Chassot,

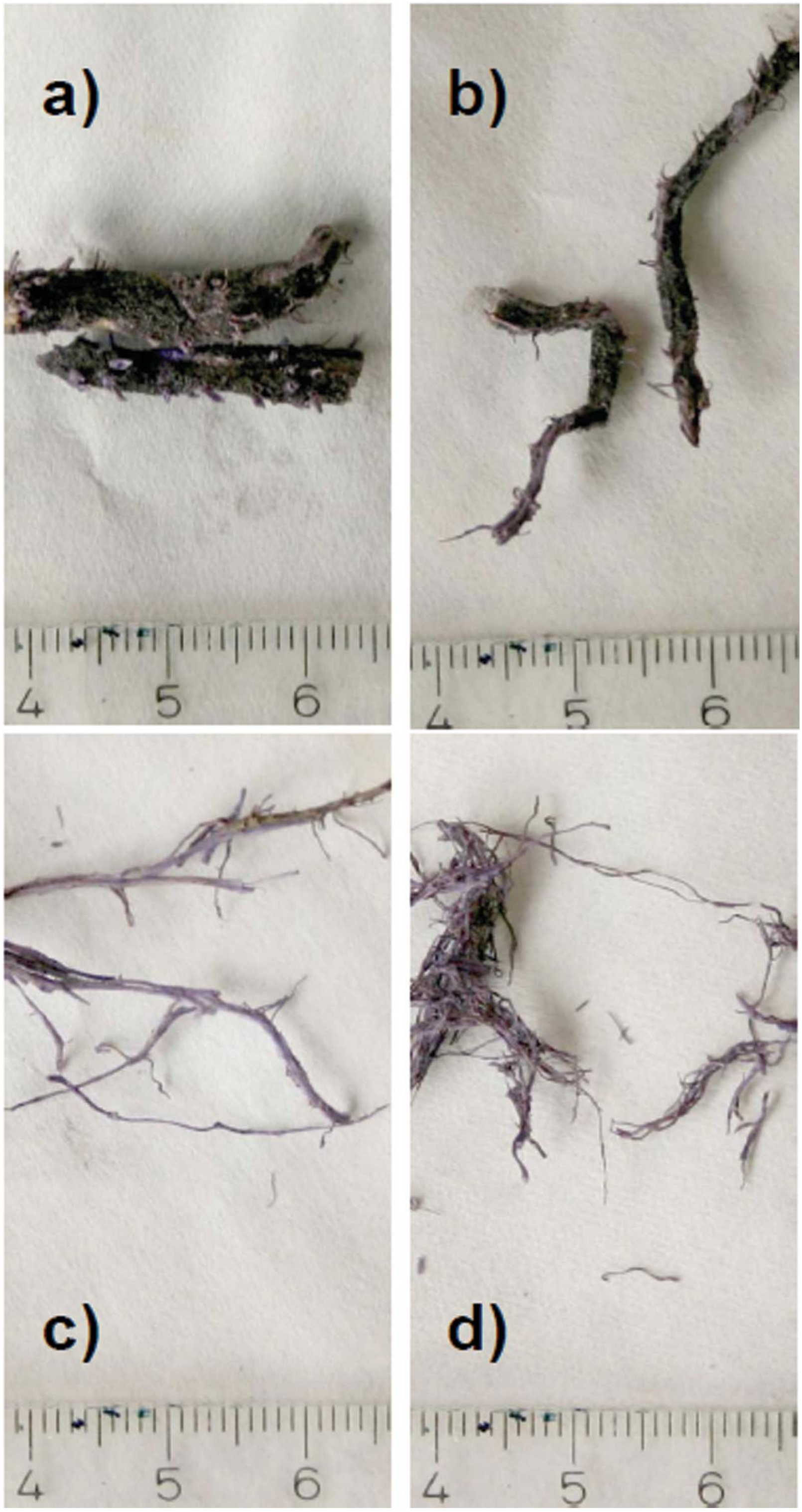

Figure 2. Photographs of roots of different diameter classes: (a) large, (b) coarse, (c) 0.35–1 mm, and (d) fine; all are of the same scale (color figure available online).

Stamp, and Richner (2001) or Qin, Stamp, and Richner (2005), in the visual assessment employed here we attempted to distinguish between visually and morphologically distinct root classes, where the three "fine" classes corresponded obviously to branch roots and the coarse and large roots to nodal and seminal axile roots.

The fresh RM was determined after removing water adhering to the roots by carefully using an absorbent paper towel. The separated root fractions were weighed and root lengths were estimated by counting the number of intersections of roots with mesh grid sizes ranging between 0.5 and 3 cm (depending on the estimated RLD), using the modified Newman line intersect method (Tennant 1975).

Root length density (RLD) for each root size class was calculated by dividing the root length by the known volume of soil samples. Root bulk densities were obtained as described in Gerke and Kuchenbuch (2007).

Photographs of the three root size classes show that samples consist of roots of several diameters within each of the visual classes (Figure 2). In a given sample, the three different fine root classes were mutually exclusive (i.e., when roots pertaining to one of the fractions were determined for a given sample, the other fraction was absent). Thus root diameters of the root size fractions were re-evaluated based on root mass and root length: For each sample (of 1000 cm^3) and RD class, a mean RD was calculated from measured fresh RM and RL (Anderson 1987), assuming a cylindrical shape and measured root bulk density (RBD) values (Gerke and Kuchenbuch 2007) (1.15 g cm^{-3} for fine roots; 1.06 g cm^{-3} for coarse and large roots; 1.12 g cm^{-3} for all roots bulked):

$$RD = 2\sqrt{\frac{RM}{\pi \cdot RL \cdot RBD}} \tag{1}$$

Histograms of the resulting RDs for each RD class and all samples (2×84) (Figure 3) show that calculated RDs for the three fine RD classes overlap over a wide range (although overall mean values are different). On the other hand, there is no overlap between the three

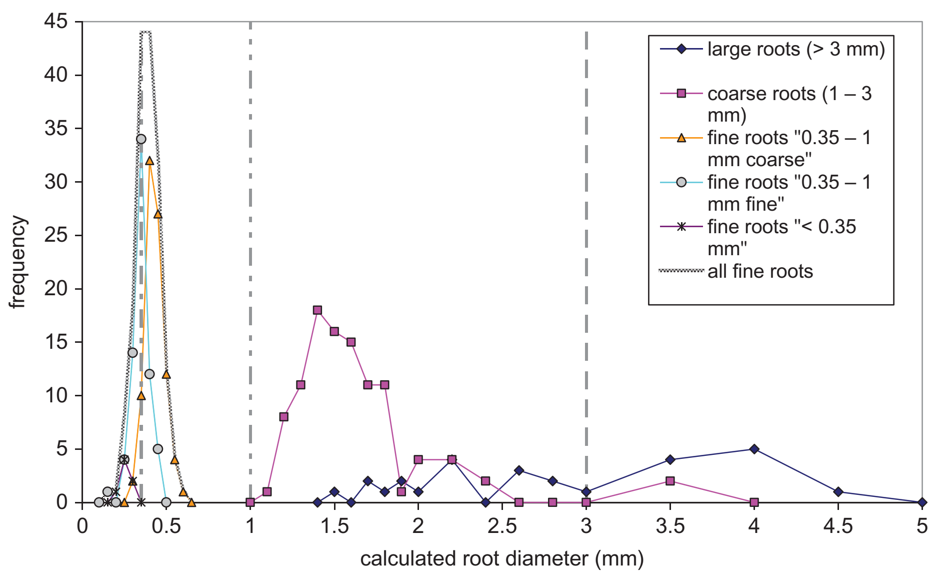

Figure 3. Histograms of calculated root diameters of visual root diameter classes (color figure available online).

fine root classes on the one hand and the two coarser diameter classes on the other hand (Figure 3).

A similar bimodal distribution of root diameters as observed here was reported by Cahn, Zobel, and Bouldin (1989) with a minimum frequency of 0.6-mm diameter roots, which can be interpreted as the threshold diameter between axile and lateral roots. Similarly, Varney et al. (1991) described four distinct diameter classes of maize lateral roots.

Because of the thorough overlap of root diameters of the three fine root classes and the mutual exclusiveness of these three classes within one given sample, we lumped these three classes in the following into one “fine” root class. The calculated RD values corroborate the assumption that roots of this class represent branch roots, whereas the coarse and large classes represent (nodal and seminal) axile roots.

Statistical Analyses

Multiple regression analysis of RMD, distance to plant row, soil depth, row width, SBD, and SWC as independent variables and RLD, proportion of fine roots, and RD as dependent variables was conducted using the software SPSS version 15.0 (SPSS Inc., Chicago, Ill.).

Results

General data about root and shoot parameters of this sampling trial are given in Kuchenbuch, Gerke, and Buczko (2009). For the sampling date considered here, the root/shoot (mass) ratio was 0.22 for wide row spacing (wrs) and 0.21 for narrow row spacing (nrs). The root biomass (dry mass) per plant was 28.6 g for wrs and 32.5 g for nrs. This is well within the normal range for maize plants of this growth stage (Amos and Walters 2006).

For the whole sampled soil monolith, the overall average RLD is 769 cm per 1000 cm^3 soil volume for wrs and 741 for nrs, whereas the average RMD is 2.6 g per 1000 cm^3 soil volume for wrs and 3.0 g per 1000 cm^3 soil volume for nrs (the differences between row spacing treatments are statistically not significant).

However, for individual samples, both RLD and RMD values vary over an order of magnitude within the total monolith. Overall, RL is dominated by fine roots (97.1% for wrs, Table 1; 96.4% for nrs, Table 2). The greatest RLD values are observed at the locations of plant rows (“vertical slice parallel to plant row,” no. 2 for wrs, Table 1, and nos. 2 and 6 for nrs, Table 2). On the other hand, the locations of the plant rows exhibit the greatest proportions of the “large” and “coarse” root diameter classes, and correspondingly a lower proportion of fine roots (for proportions of RL), both for wrs (Table 1) and nrs (Table 2). Overall, RLD decreases distinctly with depth, by a factor of about 2 between the 0- to 10-cm layer and the 20- to 30-cm depth layer (Tables 1 and 2).

Compared to the proportions of RD classes when RL is considered, a less distinct preponderance of fine roots is observed overall in terms of root mass (71% for wrs, Table 3; 63.8% for nrs, Table 4). Even more than for RLD, the greatest RMD values are observed at the locations of plant rows: Mean RM contents of the slices within the rows are greater by a factor of more than 10 than those between the rows (Tables 3 and 4). On the other hand, the decrease of RM with depth is somewhat more pronounced than the decrease of RL with depth, by a factor of about 5–7, between the upper and the lowest layers (Tables 3 and 4). The proportion of the “large” root diameter class decreases distinctly with depth (at 20–30 cm deep, no roots of this diameter class were observed).

Table 1
Root length and corresponding proportions of root diameter classes for vertical slices perpendicular to plant rows (x–z plane), parallel to plant rows (y–z plane), and horizontal layers; wide row spacing

	Root length		Percentage of root diameter classes [mean (min–max)]		
Parameter	Sum (cm)	Mean (cm / 1000 cm ^{3}) (min–max)	Large (>3 mm)	Coarse (1–3 mm)	Fine (<1 mm)
Vertical slice perpendicular to plant rows					
1	17182	818 (318 – 1979)	1.0 (0 – 9.4)	1.5 (0 – 4.6)	97.5 (89.8 – 100)
2	13398	705 (227 – 1199)	0.9 (0 – 8.0)	1.6 (0 – 12.6)	97.5 (87.4 – 100)
3	16568	789 (227 – 1878)	1.2 (0 – 13.0)	3.0 (0 – 8.7)	95.8 (87.0 – 100)
4	15944	759 (351 – 2346)	0.6 (0 – 6.5)	1.9 (0 – 7.7)	97.5 (92.3 – 100)
Vertical slice parallel to plant rows[a]					
1	8958	746 (346 – 1362)	1.6 (0 – 5.6)	2.1 (0 – 7.7)	96.3 (92.3 – 100)
2	13714	1143 (430 – 2346)	2.9 (0 – 13.0)	2.7 (0 – 6.1)	94.4 (87.0 – 98.7)
3	10040	837 (411 – 1979)	1.8 (0 – 9.4)	4.2 (0 – 12.6)	94.0 (87.4 – 98.5)
4	8454	705 (233 – 1252)	0 (0 – 0)	1.7 (0 – 7.5)	98.3 (92.5 – 100)
5	7571	688 (297 – 1236)	0 (0 – 0)	0.3 (0 – 3.0)	99.7 (97.0 – 100)
6	7080	644 (295 – 998)	0 (0 – 0)	0.9 (0 – 3.4)	99.1 (96.6 – 100)
7	7275	606 (227 – 1199)	0.1 (0 – 1.5)	1.8 (0 – 8.1)	98.1 (91.9 – 100)
Horizontal planes					
0–10 cm	30090	1075 (468 – 2346)	1.3 (0 – 13.0)	0.3 (0 – 3.7)	98.3 (87.0 – 100)
10–20 cm	20171	776 (410 – 1382)	1.5 (0 – 8.0)	1.7 (0 – 12.6)	96.8 (87.4 – 100)
20–30 cm	12830	458 (227 – 968)	0 (0 – 0)	3.9 (0 – 8.7)	96.1 (91.3 – 100)
Whole soil block	63092	769 (227 – 2346)	0.9 (0 – 13.0)	2.0 (0 – 12.6)	97.1 (87.0 – 100)

[a]Position of plant row is in no. 2.

Table 2

Root length and corresponding proportions of root diameter classes for vertical slices perpendicular to plant rows (x–z plane), parallel to plant rows (y–z plane), and horizontal layers; narrow row spacing

	Root length		Percentage of root diameter classes [mean (min–max)]		
Parameter	Sum (cm)	Mean (cm / 1000 cm ^{3}) (min–max)	Large (>3 mm)	Coarse (1–3 mm)	Fine (<1 mm)
Vertical slices perpendicular to plant rows					
1	17575	837 (310−2607)	0.9 (0−9.1)	3.1 (0−9.2)	96.0 (90.8−100)
2	12413	591 (415−1110)	0.1 (0−1.6)	2.6 (0−8.2)	97.2 (91.8−100)
3	15895	757 (241−2176)	1.1 (0−10.3)	3.1 (0−9.7)	95.8 (89.7−100)
4	16389	780 (369−2965)	0.3 (0−4.4)	2.9 (0−9.5)	96.7 (90.5−100)
Vertical slices parallel to plant rows[a]					
1	7107	592 (299−899)	0 (0−0.3)	2.1 (0−6.3)	97.9 (93.7−100)
2	12626	1052 (445−2965)	1.6 (0−9.1)	3.8 (0−8.8)	94.5 (90.9−97.3)
3	8805	734 (369−1645)	0 (0−0)	2.8 (0−9.5)	97.2 (90.5−100)
4	6557	546 (406−856)	0.1 (0−0.6)	2.2 (0−5.5)	97.7 (93.9−100)
5	10101	842 (443−1804)	1.4 (0−9.8)	4.0 (0−7.1)	94.6 (90.2−97.9)
6	10147	846 (445−2176)	1.4 (0−10.3)	4.3 (0−9.7)	94.3 (89.7−99.6)
7	6927	577 (241−988)	0 (0−0)	1.3 (0−4.3)	98.7 (95.7−100)
Horizontal planes					
0–10 cm	31239	1116 (391−2965)	1.8 (0−10.3)	0.5 (0−2.3)	97.7 (89.7−100)
10–20 cm	17436	623 (369−897)	0.1 (0−1.6)	4.7 (0−9.7)	95.3 (90.3−100)
20–30 cm	13596	486 (241−686)	0 (0−0)	3.6 (0−8.2)	96.4 (91.8−100)
Whole soil block	62271	741 (241−2965)	0.6 (0−10.3)	2.9 (0−9.7)	96.4 (89.7−100)

[a]Plant rows are in no. 2 and 6.

Table 3

Root fresh mass and corresponding proportions of root diameter classes for vertical slices perpendicular to plant rows (x–z plane), parallel to plant rows (y–z plane), and horizontal layers; wide row spacing

	Root fresh mass		Percentage of root diameter classes [mean (min–max)]		
Parameter	Sum (g)	Mean (min–max) (g / 1000 cm ^{3})	Large (>3 mm)	Coarse (1–3 mm)	Fine (<1 mm)
Vertical slices perpendicular to plant rows					
1	59.0	2.8 (0.34 – 28.7)	13.7 (0 – 86.5)	16.3 (0 – 76.8)	70 (11.9 – 100)
2	31.6	1.8 (0.42 – 8.6)	15.1 (0 – 79.5)	12.0 (0 – 63.6)	72.8 (15.3 – 100)
3	62.2	3.0 (0.43 – 34.5)	11.2 (0 – 86.6)	23.3 (0 – 64.8)	65.5 (13.4 – 100)
4	62.2	3.0 (0.26 – 38.2)	9.7 (0 – 87.4)	14.5 (0 – 49.7)	75.8 (12.6 – 100)
Vertical slice parallel to plant rows					
1	17.7	1.5 (0.56 – 2.9)	19.9 (0 – 55.9)	22.8 (0 – 76.8)	57.3 (23.2 – 100)
2	109.5	9.1 (1.29 – 38.2)	32.3 (0 – 87.4)	23.2 (0 – 57.5)	44.5 (12.6 – 69.3)
3	49.9	4.2 (0.95 – 28.7)	22.6 (0 – 86.5)	29.1 (0 – 63.6)	48.3 (11.9 – 72.3)
4	14.4	1.2 (0.40 – 5.5)	7.1 (0 – 84.8)	13.9 (0 – 46.8)	79.0 (15.2 – 100)
5	7.3	0.7 (0.34 – 1.3)	—	3.1 (0 – 23.5)	96.9 (76.5 – 100)
6	8.3	0.8 (0.26 – 1.8)	—	10.5 (0 – 30)	89.5 (70 – 100)
7	7.9	0.7 (0.39 – 1.1)	1.7 (0 – 18.3)	12.0 (0 – 51.2)	86.3 (48.8 – 100)
Horizontal planes					
0–10 cm	140.4	5.0 (0.26 – 38.2)	22.7 (0 – 87.4)	6.4 (0 – 76.8)	70.9 (11.9 – 100)
10–20 cm	44.7	1.6 (0.60 – 5.4)	14.7 (0 – 60.6)	13.8 (0 – 63.6)	71.6 (30.9 – 100)
20–30 cm	29.9	1.1 (0.43 – 3.4)	—	29.5 (0 – 64.8)	70.5 (35.2 – 100)
Whole soil block	215.0	2.6 (0.26 – 38.2)	12.4 (0 – 87.4)	16.7 (0 – 76.8)	71.0 (11.9 – 100)

Table 4
Root fresh mass and corresponding proportions of root diameter classes for vertical slices perpendicular to plant rows (x–z plane), parallel to plant rows (y–z plane), and horizontal layers; narrow row spacing

Parameter	Root fresh mass		Percentage of root diameter classes [mean (min–max)]		
	Sum (g)	Mean (min–max) (g / 1000 cm^3)	Large (>3 mm)	Coarse (1–3 mm)	Fine (<1 mm)
Vertical slices perpendicular to plant rows					
1	82.8	3.9 (0.3 − 40.8)	11.2 (0 − 88.0)	29.7 (0 − 64.8)	59.0 (12.0 − 100)
2	19.9	0.9 (0.4 − 3.8)	3.7 (0 − 45.7)	24.4 (0 − 67.5)	71.9 (32.5 − 100)
3	84.1	4.0 (0.3 − 29.0)	15.1 (0 − 86.8)	24.6 (0 − 61.9)	60.4 (7.6 − 100)
4	61.0	2.9 (0.4 − 37.5)	8.1 (0 − 80.6)	28.1 (0 − 61.3)	63.8 (12.8 − 100)
Vertical slices parallel to plant rows					
1	8.7	0.7 (0.3 − 1.2)	1.4 (0 − 16.4)	19.4 (0 − 55.2)	79.3 (44.8 − 100)
2	99.8	8.3 (0.8 − 40.8)	25.5 (0 − 88.0)	32.0 (0 − 62.0)	42.5 (12.0 − 65.9)
3	12.4	1.0 (0.5 − 2.2)	0 (0 − 0)	26.4 (0 − 61.3)	73.6 (38.7 − 100)
4	13.2	1.1 (0.4 − 5.0)	7.0 (0 − 83.9)	22.7 (0 − 46.2)	70.3 (7.6 − 100)
5	51.2	4.3 (0.8 − 25.6)	17.7 (0 − 86.1)	37.1 (0 − 67.5)	45.2 (13.9 − 66.9)
6	56.0	4.7 (0.5 − 29.0)	15.1 (0 − 86.8)	35.4 (0 − 64.6)	49.5 (13.2 − 96.2)
7	6.6	0.5 (0.3 − 0.8)	0 (0 − 0)	13.9 (0 − 40.6)	86.1 (59.4 − 100)
Horizontal planes					
0–10 cm	182.9	6.5 (0.3 − 40.8)	24.4 (0 − 88.0)	7.1 (0 − 40.7)	68.5 (12.0 − 100)
10–20 cm	40	1.4 (0.5 − 5.0)	4.1 (0 − 83.9)	41.0 (0 − 67.5)	54.9 (7.6 − 100)
20–30 cm	25.0	0.9 (0.3 − 1.7)	0 (0 − 0)	32.0 (0 − 63.4)	68.0 (36.6 − 100)
Whole soil block	247.9	3.0 (0.3 − 40.8)	9.5 (0 − 88.0)	26.7 (0 − 67.5)	63.8 (7.6 − 100)

The average calculated RDs for lumped roots is 0.48 mm for wrs (Table 5) and 0.49 mm for nrs (Table 6). Also, values for individual samples within the monolith vary by an order of magnitude. For the three separate RD classes, calculated RD values are clearly different with little overlap between "large" and "coarse" roots, and no overlap and even a gap in diameters between fine roots and the coarser diameter classes (as already demonstrated in the histograms, cf. Figure 3).

Calculated root diameters are greatest overall at the intrarow positions and lower at the interrow positions (Tables 5 and 6). This holds true not only for RD for lumped roots but also for calculated root diameters of the separate RD classes.

Figures 4 and 5 show that the differences in the proportions of fine roots between intra- and interrow positions are more pronounced in the upper soil layer compared with lower soil depths, both for wrs (Figure 4) and for nrs (Figure 5), but the pattern is visible also at 20–30 cm deep. On the other hand, the differences in calculated root diameters between intrarow and interrow positions are much more distinct for the upper soil layer than for deeper soil layers (Figures 4 and 5). Figures 4 and 5 suggest that variation of fine root proportions is more dependent on row position than on depth, because the characteristic horizontal patterns of fine root proportions are similar for all three depths, although more pronounced in the upper soil layer than in the lower soil layer. Also, calculated RD values depend strongly on position with respect to plant row, both for wrs (Figure 4) and nrs (Figure 5). The dependence of calculated RD on the horizontal position relative to the plant row is observed in all investigated soil depths, although most pronounced in the upper 0- to 10-cm layer.

Simple regressions of RMD vs RLD, proportion of fine roots, or root diameter (Figure 6) show relatively high R^2 values only for regression of RMD vs RLD but not for the regression of RMD vs proportion of fine roots or root diameters. However, without the few (8 data points) RMD values > 10 g / 1000 cm^3, the simple linear regression of RMD vs RLD yielded only $R^2 = 0.26$ (not shown here in detail).

On the other hand, multiple regression with the additional independent variables distance to plant row (or to next plant in case of nrs), soil depth, row width, SBD, and SWC improved the R^2 values compared with simple regression, in some cases substantially (Table 7). However, in these multiple regressions, RMD shows in almost all cases (except percentage of fine roots RL) the greatest values of standardized coefficients among the independent variables (suggesting the largest influence of RMD among the independent variables) and is highly significant ($P < 0.001$). Also, distance to next plant and soil depth had relatively high standardized coefficients and were highly significant in most cases. On the other hand, the soil physical parameters SBD and SWC were mostly not significant in the multiple regressions.

Discussion

Specificity of the Study Site

When interpreting the results of this sampling trial, it is important to bear in mind that this is not a "typical" maize site, because of the shallow groundwater table, the sharp contrast between the cultivated humic topsoil and the subsoil, and redoximorphic soil patterns already at 30–40 cm deep (and below). Moreover, climatic conditions are relatively cool for maize growth. Consequently, root growth at Paulinenaue is largely restricted to the topsoil, and the major part of the root system was captured by sampling only the upper 0–30 cm of the soil (cf., Kuchenbuch, Gerke, and Buczko 2009). Under better drained conditions

Table 5

Calculated root diameters for vertical slices perpendicular to plant rows (x–z plane), parallel to plant rows (y–z plane), and horizontal layers; wide row spacing

	Root diameter (mm) [mean (min–max)]			
Parameter	Total	Large (>3 mm)	Coarse (1–3 mm)	Fine (<1 mm)
Vertical slices perpendicular to plant rows				
1	0.48 (0.20 – 1.28)	2.16 (1.47 – 4.00)	1.55 (1.18 – 1.99)	0.36 (0.13 – 0.53)
2	0.48 (0.24 – 1.00)	3.80 (1.67 – 10.84)	1.72 (1.13 – 3.00)	0.37 (0.23 – 0.52)
3	0.51 (0.25 – 1.44)	2.62 (2.13 – 3.83)	1.57 (1.20 – 2.30)	0.37 (0.24 – 0.56)
4	0.48 (0.24 – 1.36)	3.33 (1.82 – 6.64)	1.49 (1.11 – 1.73)	0.38 (0.24 – 0.51)
Vertical slices parallel to plant rows				
1	0.48 (0.27 – 0.64)	2.05 (1.82 – 2.48)	1.61 (1.24 – 1.96)	0.35 (0.13 – 0.46)
2	0.77 (0.53 – 1.44)	4.52 (1.70 – 10.84)	1.86 (1.44 – 3.00)	0.46 (0.38 – 0.56)
3	0.61 (0.35 – 1.28)	2.46 (1.67 – 4.00)	1.57 (1.13 – 1.99)	0.40 (0.27 – 0.47)
4	0.42 (0.24 – 0.84)	—	1.39 (1.18 – 1.59)	0.35 (0.24 – 0.44)
5	0.34 (0.20 – 0.47)	—	1.40 (1.36 – 1.45)	0.33 (0.20 – 0.42)
6	0.37 (0.24 – 0.48)	—	1.61 (1.36 – 2.30)	0.34 (0.23 – 0.40)
7	0.36 (0.25 – 0.53)	1.47 (1.47 – 1.47)	1.18 (1.11 – 1.23)	0.35 (0.25 – 0.52)
Horizontal planes				
0–10 cm	0.48 (0.20 – 1.44)	4.06 (1.67 – 10.84)	2.06 (1.13 – 3.00)	0.31 (0.13 – 0.56)
10–20 cm	0.47 (0.32 – 0.75)	1.90 (1.47 – 2.13)	1.51 (1.23 – 1.87)	0.39 (0.31 – 0.51)
20–30 cm	0.50 (0.36 – 0.65)	–	1.48 (1.11 – 1.92)	0.41 (0.25 – 0.53)
Whole soil block	0.48 (0.20 – 1.44)	2.98 (1.47 – 10.84)	1.57 (1.11 – 3.00)	0.37 (0.13 – 0.56)

Table 6
Calculated root diameters for vertical slices perpendicular to plant rows (x–z plane), parallel to plant rows (y–z plane), and horizontal layers; narrow row spacing

	Root diameter (mm) [mean (min–max)]			
Parameter	Total	Large (>3 mm)	Coarse (1–3 mm)	Fine (<1 mm)
Vertical slices perpendicular to plant rows				
1	0.53 (0.34 – 1.33)	3.59 (3.12 – 4.25)	1.64 (1.11 – 3.30)	0.36 (0.29 – 0.48)
2	0.41 (0.27 – 0.62)	3.05 (2.50 – 3.59)	1.45 (1.17 – 2.00)	0.33 (0.25 – 0.43)
3	0.56 (0.23 – 1.27)	5.99 (3.44 – 12.98)	1.53 (1.08 – 2.27)	0.37 (0.23 – 0.49)
4	0.47 (0.27 – 1.20)	3.58 (2.76 – 5.30)	1.54 (1.24 – 2.15)	0.34 (0.27 – 0.48)
Vertical slices parallel to plant rows				
1	0.37 (0.27 – 0.48)	2.76 (2.76 – 2.76)	1.35 (1.24 – 1.62)	0.32 (0.26 – 0.38)
2	0.67 (0.42 – 1.33)	3.82 (2.50 – 5.30)	1.66 (1.39 – 2.27)	0.40 (0.30 – 0.48)
3	0.40 (0.29 – 0.61)	—	1.48 (1.08 – 2.08)	0.34 (0.28 – 0.39)
4	0.45 (0.30 – 1.08)	12.98 (12.98 – 12.98)	1.63 (1.17 – 3.30)	0.33 (0.30 – 0.38)
5	0.61 (0.43 – 1.27)	3.49 (3.12 – 3.86)	1.63 (1.36 – 2.00)	0.39 (0.25 – 0.49)
6	0.60 (0.35 – 1.23)	3.28 (2.78 – 3.67)	1.58 (1.19 – 2.14)	0.38 (0.31 – 0.47)
7	0.34 (0.23 – 0.42)	—	1.29 (1.11 – 1.39)	0.31 (0.23 – 0.39)
Horizontal planes				
0–10 cm	0.54 (0.23 – 1.33)	3.61 (2.76 – 5.30)	1.81 (1.19 – 3.30)	0.35 (0.23 – 0.49)
10–20 cm	0.49 (0.32 – 1.08)	7.74 (2.50 – 12.98)	1.52 (1.17 – 2.27)	0.34 (0.25 – 0.42)
20–30 cm	0.45 (0.34 – 0.60)	—	1.44 (1.08 – 1.76)	0.37 (0.29 – 0.48)
Whole soil block	0.49 (0.23 – 1.33)	4.24 (2.50 – 12.98)	1.54 (1.08 – 3.30)	0.35 (0.23 – 0.49)

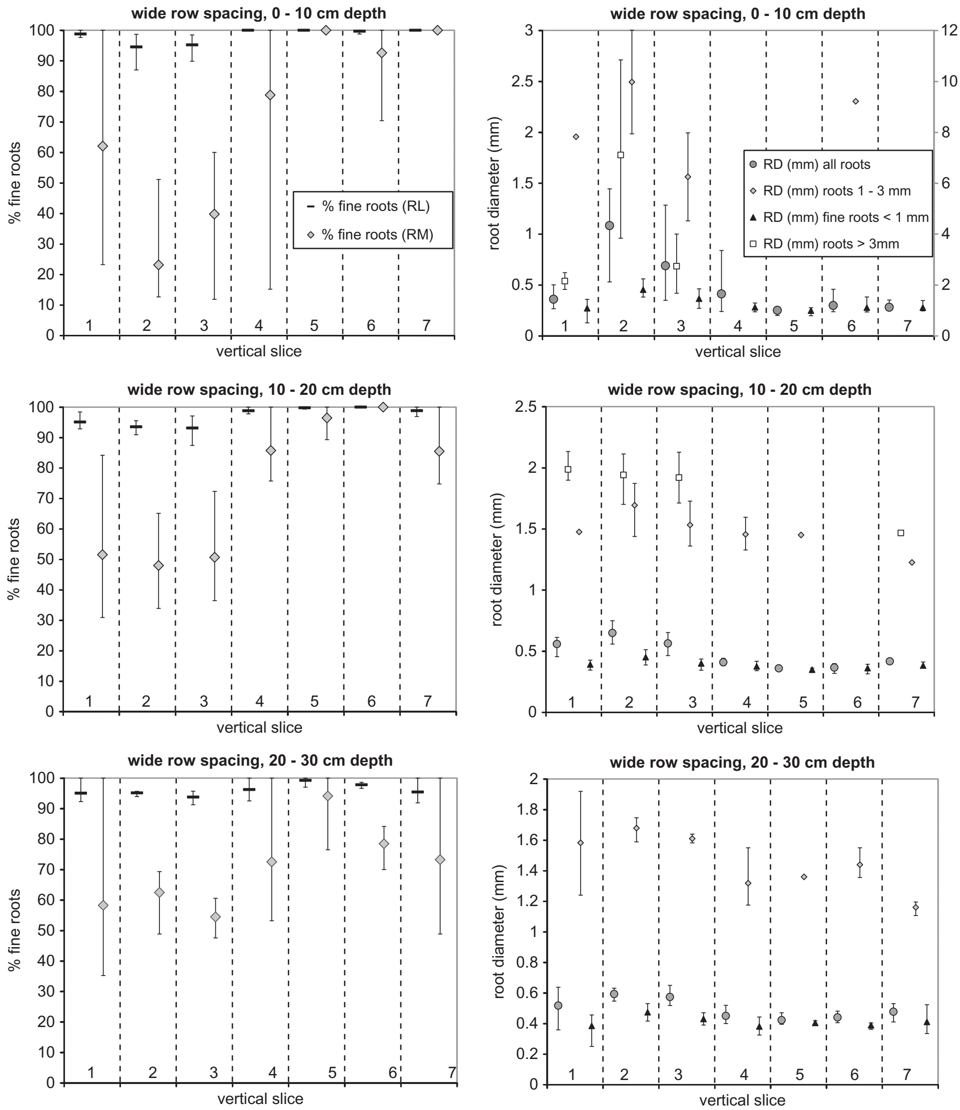

Figure 4. Distribution of proportion of fine roots (left side) and calculated root diameters (right side) for vertical soil slices normal to direction of plant rows (i.e., x-z plane) for separate soil depths; wide row spacing.

with deeper groundwater table and warmer climate, it is well known that maize roots may penetrate as deep as >2 m (Weaver 1926; Kutschera, Lichtenegger, and Sobotik 2009). For other sites in Germany, rooting depths of 150 cm have been described (e.g., Wiesler and Horst 1994). On the other hand, sites with shallow groundwater (i.e., gleysols, fen soils) are relatively widespread in the lowlands of northern Central Europe (BGR 1998) and are used commonly for agricultural purposes, including for maize. However, it seems that most studies of root distribution in the field were preferentially conducted at better drained, more typical maize sites. On the other hand, the average root biomass of 30 g and shoot biomass of 140 g per plant found here (Kuchenbuch, Gerke, and Buczko 2009) is well within the

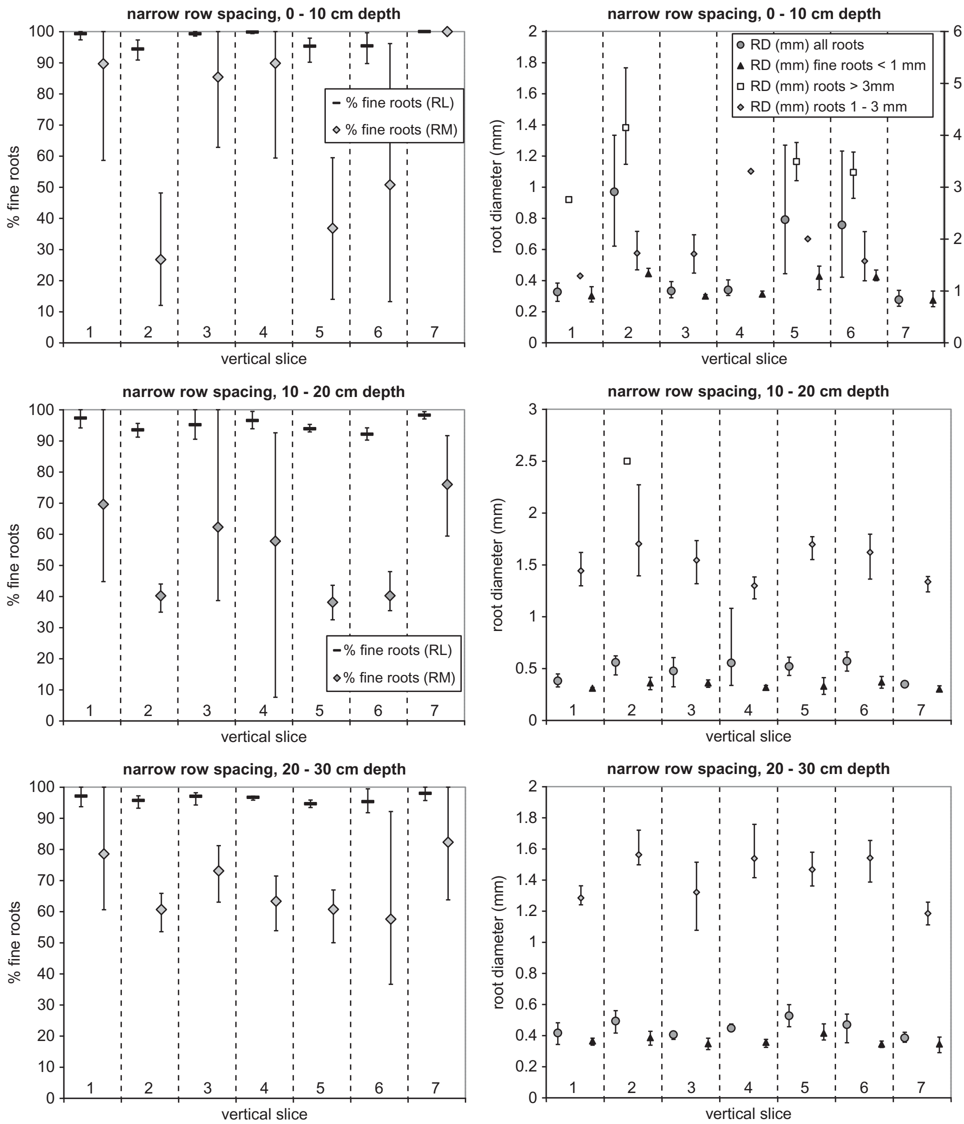

Figure 5. Distribution of proportion of fine roots (left side) and calculated root diameters (right side) for vertical soil slices normal to direction of plant rows (i.e., x-z plane) for separate soil depths; narrow row spacing.

range reported for a wide variety of maize plants of this development stage (Amos and Walters 2006).

Overall Root Diameter Distribution

Overall, root length was clearly dominated by fine roots with about 97% of total RL (Tables 1 and 2) and about 70% of total RM (Tables 3 and 4). A similar overall preponderance of fine roots as a proportion of overall RL and RM is commonly observed for maize (McCully 1999): For instance, Pagès and Pellerin (1994) describe a similar proportion of

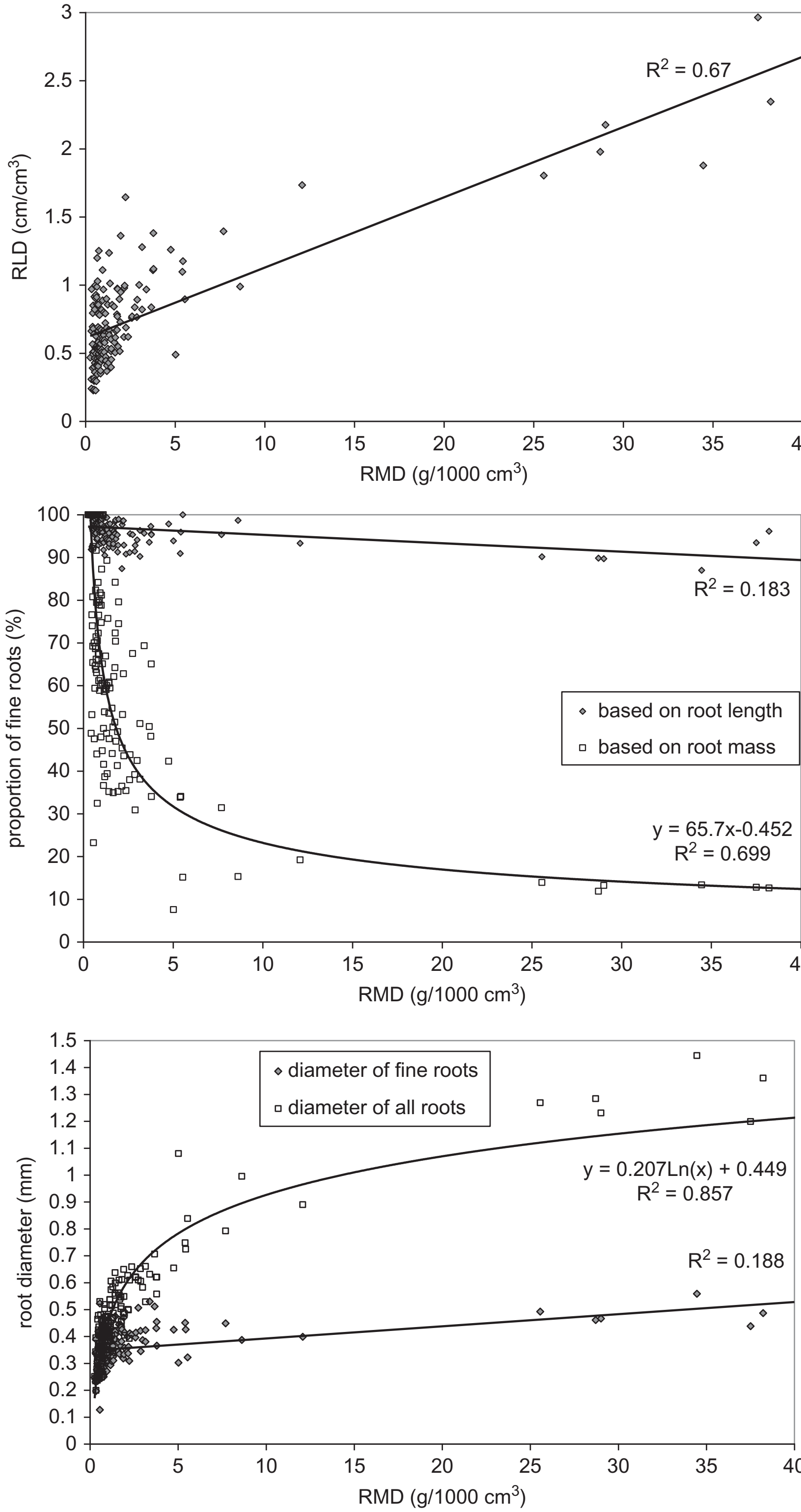

Figure 6. Correlations among root fresh mass density (RMD) and RLD (top), proportion of fine roots (middle), and root diameter (bottom).

Table 7
Results of multiple regressions to predict RLD and root morphological parameters (= dependent variable) from root fresh mass density (RMD), geometrical and soil physical parameters (= predictor variable)

Predictor variable	Dependent variable [standardized coefficient (significance)] RLD	Fine roots (%) (RL)	Fine roots (%) (RM)	RD, only fine roots	RD, total
RMD	0.661 (< 0.001)	−0.386 (< 0.001)	−0.841 (< 0.001)	0.473 (< 0.001)	0.903 (< 0.001)
Distance to next plant	−0.084 (0.04)	0.336 (< 0.001)	0.041 (0.474)	−0.221 (0.001)	−0.129 (< 0.001)
Soil depth	−0.386 (< 0.001)	−0.436 (< 0.001)	−0.048 (0.541)	0.633 (< 0.001)	0.158 (0.002)
Row width	0.076 (0.032)	0.0 (0.994)	0.096 (0.034)	0.182 (0.002)	0.046 (0.109)
SBD	−0.005 (0.926)	0.013 (0.896)	−0.043 (0.556)	−0.159 (0.1)	−0.034 (0.463)
SWC	0.054 (0.258)	−0.215 (0.008)	0.022 (0.716)	0.155 (0.055)	0.054 (0.169)
Coefficients of determination (R^2) of multiple regression compared with simple regression of RMD with the respective dependent variable					
Multiple regression	0.825	0.503	0.72	0.504	0.884
Regression only RMD	0.67	0.1834	0.699	0.188	0.8579

fine root proportion as found in Paulinenaue. Qin, Stamp, and Richner (2005) found that 99% of measured RL belonged to the diameter class $<$0.8 mm, from which 20% were in the 0.3- to 0.4-mm range and 60% in the 0.2- to 0.3-mm range. Pallant et al. (1993) found for 0–15 cm deep at 84 DAP that more than 90% of RL were composed of fine roots.

On the other hand, it seems that in several studies, roots of larger diameter are underrepresented and the maximum recorded root diameters are rather low (e.g., Costa et al. 2002), whereas in other studies, only lateral roots were investigated (Varney et al. 1991).

Generally in maize, RDs of shoot-borne nodal axile roots are greatest for the uppermost (youngest) node (phytomer), with root diameters of up to 8.5 mm under favorable growth conditions, whereas the axile roots of the first (oldest, lowest) node have diameters of 2.5–2.7 mm (Hoppe, McCully, and Wenzel 1986; Kutschera, Lichtenegger, and Sobotik 2009). Seminal axile roots have in general diameters of 0.6–1.5 mm and the diameters of lateral (branch) roots are usually in the range 0.32–0.48 mm (Kutschera, Lichtenegger, and Sobotik 2009). However, these are only average values, which may be modified by environmental and soil conditions.

Although the sampling was conducted at a rather mature stage of maize plant development, the seminal root system obviously still was of some importance. This is in line with several other field studies, which reported that although occurrence and frequency of seminal roots in maize diminish with increasing plant development stage, seminal roots are observed and functioning throughout the entire lifetime of maize roots (Fusseder 1987; McCully 1999; Kutschera, Lichtenegger, and Sobotik 2009).

It is well known that (older) nodal roots of lower order phytomers initially grow some distance horizontally before they bend downward to elongate vertically downward, whereas (younger) nodal roots of higher phytomers grow directly downward in vertical direction (Tardieu and Pellerin 1990; Feldman 1994; Pagès and Pellerin 1996). Consequently, it has to be expected that roots of the largest diameter class are restricted to the zone at and beneath the plant rows. In fact this could be observed at Paulinenaue. The "large" diameter class was only observed in the y-z slices that contained the plant rows or the adjoining slices (slice 2 for wrs, Tables 1 and 3; slices 2 and 6 for nrs, Tables 2 and 4), whereas the slices between the rows contained no roots of the "large" diameter class. This corroborates the assumption that the largest diameter class represents nodal roots of higher order phytomers. However, no roots of the "large" diameter class were observed at 20–30 cm deep (Tables 14). Possible explanations for this are that nodal roots of higher order phytomers have not yet reached this depth, or that the nodal roots become thinner with depth.

Because of the strictly soil volume-based sampling technique, the excavated roots could not be ascribed to specific maize plants. Probably, at the given plant density, the roots found in a given soil volume sample originated from several different plants, because lateral root growth of maize is appreciable and can be up to 170 cm (Weaver 1926; Kutschera, Lichtenegger, and Sobotik 2009).

The overall mean calculated root diameter found here (0.48 mm) seems rather large when compared with other studies. However, data on mean root diameters given in the literature are often not comparable to the results found here, because in some studies not the whole maize root system has been sampled (Varney et al. 1991), other sampling techniques were used (Qin, Stamp, and Richner 2005), sampling was conducted at other stages of maize plant development (Anderson 1987), experiments were under optimized controlled greenhouse conditions (Costa et al. 2002), soil conditions were different (Vamerali et al. 2003), or different cultivars/genotypes were used (Vamerali et al. 2003; Hochholdinger 2009).

Spatial Distribution of Root Parameters

As expected, the greatest RLD and RMD values were found within the plant row and lower values were found between the rows. Morever, RLD and RMD decrease distinctly with depth. Similar distributions have been described in many previous studies (e.g., Mengel and Barber 1974; Qin, Stamp, and Richner 2005; Sharratt and McWilliams 2005), although in general with larger root penetration into depth than observed here. However, within the plant row, also large differences in RLD and even more so of RMD were observed, especially for nrs. This clearly confirms the necessity of considering spatial variation in all three dimensions (cf. Kuchenbuch, Gerke, and Buczko 2009) but is in contrast to findings of some other studies: For instance, Pagès and Pellerin (1996) concluded based on simulated 2D vertical root maps of cross sections perpendicular to rows that root distribution could be reasonably well described by 2D vertical cross section (however, this conclusion was based on simulations and a row spacing of 75 cm).

On the other hand, the proportion of fine roots was lower in the vicinity of plants and greater farther away, especially lower in plant rows and greater between the rows (Figures 4 and 5). Correspondingly, overall bulk RDs were greatest in the plant rows and lower between the rows. Conspicuously, this applies not only for RD calculated for bulk roots but also for RD calculated for separate diameter classes (Tables 5 and 6).

Similar decreases of RD with increasing distance from the plant have been described previously in some studies (Anderson 1987; Holanda et al. 1998; Qin, Stamp, and Richner 2005), although for RD based on all roots lumped, which may be explained by an increase of fine roots with increasing distance, as also observed here for Paulinenaue.

The decrease of RD of specific RD classes with distance to plant row may be explained by a general decrease of RDs with increasing distance to the plant, because in general RDs of individual roots decrease as they got longer (Clowes and Wadekar 1988). A further factor could be higher soil temperatures, which probably occurred during later stages of growth when the roots farther away from the plants elongated. Moreover, soil temperatures are in general higher in the interrow positions due to less shading (Sharratt and McWilliams 2005). Soil temperature has a large influence on root growth, and higher soil temperatures cause in general reduced RDs (Kaspar and Bland 1992; McMichael and Burke 2002).

At Paulinenaue, overall RD and proportion of fine roots changed only little with depth (Tables 5 and 6). This is in line with Qin, Stamp, and Richner (2005), who described for maize at anthesis only a slight increase of RD with increasing soil depth (between 0 and 30 cm depth), though overall mean RD values range between 0.3 and 0.35 mm. Similarly, Vamerali et al. (2003) found only a slight decrease of measured RDs between 0 and 100 cm deep. On the other hand, some studies reported that the mean RD was generally larger in the topsoil and decreases with depth (Schenk and Barber 1980; Holanda et al. 1998). However, this depth trend depended on position relative to the plant row: between the rows theRD was smaller near the soil surface and larger in deeper soil layers (Holanda et al. 1998).

The inconclusive depth trends of RD values, observed here and in other studies, is probably induced by the interplay of contrasting trends: the general decrease of RD with increasing distance to the plant (Clowes and Wadekar 1988), which means decreasing RD with depth, and the increase of bulk density (Kuchenbuch, Gerke, and Buczko 2009) and decreasing temperature with depth, both of which generally lead to increases in RDs (Kaspar and Bland 1992; Kuchenbuch and Ingram 2004).

However, when comparing the results obtained here at Paulinenaue, it should be considered that only soil at 0–30 cm deep was sampled, whereas in most of the cited studies, root growth extended to greater soil depths and consequently soil root samples were taken down to a further.

In summay, at Paulinenaue, the proportion of fine roots and mean RD are more dependent on the horizontal location with respect to plant row than on depth.

The similar variation of RLD and corresponding proportions of RD classes within vertical soil slices of different spatial orientation (i.e., parallel and perpendicular to the rows, Tables 1 and 2) suggest that variability of RD classes is important both perpendicularly to the plant rows and parallel to the plant rows. This applies to a lesser extent to RMD and the corresponding proportions of RD classes (Tables 3 and 4). The relative differences in heterogeneity between vertical soil slices perpendicular and parallel to the plant rows are larger for RD than for RLD or RMD (Tables 5 and 6). This is probably due to the normalization procedure when averaging RD values for a volume sample that involves both RL and RM [Eq. (1)] and could enhance the existing spatial variation.

Nevertheless, the results show that heterogeneity is important also in the direction parallel to pant row, also for RD and proportions of different RD classes.

For horizontal slices (x-y planes), the general decrease of heterogeneity with depth for all parameters in Tables 1–6 suggests a greater structural soil heterogeneity close to the soil surface, whereas at greater depth, the "fan"-like shape and overlapping of the root systems between neighboring plants may cause a more continuous distribution of roots.

However, the relatively high variation of root parameters within horizontal layers indicate that assuming simplified 1D distribution would be fraught with large errors (cf., Buczko, Kuchenbuch, and Gerke 2009). The estimation error would be greatest for the uppermost soil layer. Also for 2D vertical distributions perpendicular to the rows, the potential error induced by spatial variability parallel to the rows can be appreciable.

Concerning the differences between the two investigated row widths, the focus here was not on a rigorous quantitative study of the effect of row width on root (and shoot) growth of maize (cf., Kuchenbuch, Gerke, and Buczko 2009), which is covered extensively in the literature (e.g., Sharatt and McWilliams 2005). However, some pertinent points should be mentioned:

Both root and shoot mass per plant were greater for the nrs compared with wrs, whereas root shoot ratio was approximately equal for both row spacings (0.21–0.22). Whereas overall RLD and RMD were essentially equal for both row spacings, the proportion of fine roots was slightly greater for wrs, especially when based on RM (although statistically not significant). For both row spacings, the horizontal distribution of root parameters is governed by the location of maize plants.

For nrs, a larger variation of root parameters parallel to the rows compared with wrs should have been expected. This was partially visible in the mean RLD values for vertical slices perpendicular to plant rows, which show a larger spread for nrs (Table 2) compared with wrs (Table 1). A similar observation can be made for RMD (Tables 3 and 4) and mean RD (Tables 5 and 6). However, for vertical slices parallel to the plant rows, the range of parameters within specific slices was not larger in general for nrs compared with wrs. Summarizing, the influence of row width on spatial distribution of root parameters was inconclusive at this stage of plant development and seems largely restricted to the effect of the exact locations of specific maize plants.

Prediction of RLD and Morphological Parameters from Root Mass and Other Parameters

Root mass is easier to measure than RL and root morphological parameters (Costa et al. 2002; Amos and Walters 2006; Blouin, Barot, and Roumet 2007). Therefore, attempts to predict RL and root morphological parameters from RM and other parameters are warranted. Moreover, with the sampling procedure applied here, the geometrical parameters distance to plant row and soil depth and the soil physical parameters SWC and SBD were measured without much additional effort. Whereas simple regression of RMD vs RLD proportion of fine roots and RD gave no satisfactory prediction (Figure 6), multiple regressions incorporating the additional geometrical and soil physical parameters clearly enhanced the quality of prediction (Table 7). On the one hand, the geometrical parameters had a large influence on the prediction quality, which suggests that the root system is characterized to a large degree by the architectural spatial structure. On the other hand, the soil physical parameters SBD and SWC had a conspicuously small influence. This could be due to a large degree by the (probable) temporal variability of SBD and SWC. The measured values represent only a snapshot. On the other hand, both these parameters are themselves influenced by the rooting patterns, and therefore cannot be viewed—strictly speaking—as "independent." In contrast, the spatial distribution of the root system has developed during the course of the plant development.

In summary, RLD, the proportion of fine roots and root diameters can be largely predicted with relatively high R^2 by multiple regression from RMD, soil depth, and distance to plant, whereas simple regressions with RMD as sole predictor variable yielded relatively poor predictions with low R^2 values.

In contrast, Costa et al. (2002) found that simple linear regression of RMD vs RLD gave good results with greater R^2 (0.77–0.88) than found here. However, those experiments were greenhouse pot experiments under controlled conditions, and the regressions refer to data of whole maize plants sampled at the silking stage.

Conclusions

This 3D spatially distributed monolith sampling for determination of the distribution of RL, RM, and root morphological parameters revealed variability in all three spatial dimensions. In contrast to previous findings and assumptions, variability parallel to the plant row is not negligible. In general, the proportion of fine roots and mean RD are more dependent on the horizontal location with respect to plant row than on depth. The high variation of root parameters within horizontal layers indicate that assuming simplified 1D distribution would incur large errors. RLD, the proportion of fine roots, and RDs can be predicted from RMD, soil depth, and distance to plant but not from RMD alone.

These 3D data could be useful for evaluating 3D root growth models, but further processing would be necessary, because the spatial resolution of the data is relatively coarse compared with the resolution of root architecture models.

However, the advantage of this soil-based sampling approach, compared with results from root architecture models, is that values could possibly be incorporated more directly into soil water flow and nutrient transport models.

Acknowledgments

The cooperation and support of Horst Gerke during the early stages of the experiment and discussions is highly appreciated. We thank J. Busse and E. Krüger from the ZALF Institute of Landscape Matter Dynamics for excellent assistance in soil and root analyses and R. Hypscher, ZALF Institute of Soil Landscape Research, Müncheberg, for her skilled assistance in density measurements. Financial support was provided by the Federal Ministry of Food, Agriculture, and Consumer Protection (BMVEL) and by the Ministry for Rural Development, Environment and Consumer Protection (MLUV) of Brandenburg.

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