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Dynamics of plant nutrient uptake as affected by biopore-associated root growth in arable subsoil

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Abstract

Aims Soil biopores facilitate root growth in arable subsoil, thus improve resource acquisition potential. We aimed at determining the dynamic relationship between soil biopores and performance of two winter crops in field condition considering different biopore size classes, root characteristics and crop growth parameters.

Methods Chicory with dominant taproot system and tall fescue with limited taproots were grown for two consecutive years as precrops. Density of soil biopores larger than 2 mm and smaller than 2 mm in diameter was measured at 45 cm of soil depth. Destructive samplings were carried out for investigation on following barley and canola roots. Shoot biomass production, nutrient uptake and final yield of the following crops were determined throughout the growth seasons.

Results Higher shares of large or small-sized bipoores were observed after chicory (23 %) or tall fescue (20 %) precrops, respectively. On average root diameter and root dry mass of following crops were greater by 11 and 15 % after chicory than tall fescue. At anthesis chicory-barley treatment accumulated 10 % more K in comparison to tall fescue-barley treatment. P uptake of canola was greater (7 %) after tall fescue compared with chicory at the stage of fruit development.

Conclusions Our results suggest that the subsoil heterogenization by altered soil biopores hold relevance for plant root growth and overall crop performance. However, the effects depended on biopore size classes, root characteristics and crop species. Development of direct methods that can quantify biopore-root-shoot processes, detailed investigation on drilosphere, root phenotyping for detection of the genetic variation in response to biopore systems have to be followed in the future.

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Introduction

Root growth in the subsoil, viz., below tilled layers, is an essential process for efficient utilization of the limited plant resources in arable lands (Lynch and Wojciechowski 2015; Köpke et al. 2015), which, however, can be restricted by mechanical resistance present in the soil (Bengough 2006). Soil compaction, which often occurs as a result of a long-term applied

compressive forces, especially of heavy machinery (Batey 2009), is one of the major physical factors hindering root penetration into the deep soil horizons (Materechera et al. 1992; Valentine et al. 2012).

Biopores are round-shaped voids in the soil formed by 'biological activity' (Kautz 2015). The biological activity mainly refers to plant root penetration (McCallum et al. 2004; Głąb et al. 2013; Bodner et al. 2014) and earthworm movement (Ehlers 1975; Lamandé et al. 2003; van Schaik et al. 2014). One of the crucial notions regarding the soil biopores in relation to plant growth is that roots tend to grow towards the least mechanistic resistance, especially under high soil strength (Lynch and Wojciechowski 2015). Since nutrient absorption is often a function of rooting density (Köpke 1995; Jungk and Claassen 1997), enhanced root establishment assisted by the preferential root growth via the soil biopore channels can be beneficial.

In arable fields, biopore formation is strongly affected by plant root penetration capacity (Materechera et al. 1992). With large root diameter, perennial fodder crops such as lucerne (Medicago sativa) have been found to be capable of generating biopores on the top of B horizon of Sodosol (McCallum et al. 2004). Chicory (Cichorium intybus) was also capable of creating circular-shaped biopores larger than 2 mm in diameter under 45 cm of Haplic Luvisol (Kautz et al. 2014). Similar results were found in Molic Fluvisol where beet (Beta vulgaris) demonstrated greater impacts on biopore density (50–2000 μm in diameter) in comparison to Triticale spp. (Głąb et al. 2013).

Reports on the preferential root growth through large-sized pore channels are numerous. For instances, with less than 1 % of biopore volume in a grey brown podzolic soil, weekly observed root growth of oat (Avena sativa) was closely related to the presence of earthworm channels, especially in untilled soil (Ehlers et al. 1983). Previously discovered preferential location of blue grass (Dichanthium sericeum) and tall oat grass (Themedia avenace) roots adjacent to soil macropores in two vertisols (Stewart et al. 1999), and also of maize (Zea mays) roots in Brown Lowland soil, Pseudogley and Ordinary Andosol (Hatano et al. 1988) also demonstrated roots' tendency to grow in zones with less mechanical resistance (Bengough 2006).

Recently, effects of the increased large-sized biopore density on the following crops were clearly shown in Haplic Luvisol. The increase in the number of large-sized biopores (>2 mm) enhanced rooting density of subsequently grown barley (Hordeum vulgare) and canola (Brassica napus), especially under 105 cm of soil depth (Perkons et al. 2014). Given the soil condition on site, the extended root system in the subsoil was assumed to be caused by the 're- entry' of the fine roots from biopores to the bulk soil (Athmann et al. 2013), which was further confirmed by the relatively smaller proportion of roots present inside biopores in the subsoil (25 %; Kautz et al. 2013b). Rooting density of spring wheat (Triticum aestivum) inside as well as outside the large-sized biopores significantly increased 300 and 46 %, respectively (Han et al. 2015b). The biopore-associated root growth of barley depended on the root size classes (Han et al. 2016). Specifically saying, rooting density of fine roots (<0.2 mm) were significantly increased in fine pore dominated soil created by fine rooted plant species. On the other hand, large-sized pores created by the taproot-dominated plants promoted the growth of medium (2–5 mm) and coarse roots (>5 mm).

Originally, Schultz-Lupitz (1895) reported a higher tuber yield of potato (Solanum tuberosum) after cultivating lupin (Lupinus albus) as a precrop on very poor sandy soils; the effects were not based on residual N but enhanced root growth of the following crop via biopores created by lupin taproots. Since then, several efforts have been made to relate the biopore availability and crop yield. When wheat was grown over 70 h on experimental pots filled with a clay loamy soil collected from B horizon, Volkmar (1996) found significant correlations coefficients (r^2) between biopore-associated root growth and shoot ^{15}N uptake at the moisture levels of −0.10 and −1.50 MPa, respectively. Leaf area of barley and pea (Pisum sativum) increased by formation of artificial channels of 3.2 mm in size and biopores created by roots of lucerne, ryegrass (Lolium rigidum), canola and clover (Trifolium subterraneum) in hard soil in low moisture condition (Stirzaker et al. 1996). McKenzie et al. (2009) demonstrated an improved access to subsoil water of five barley genotypes when grown with artificially created 2 mm pores in Stagnic Cambisol with increased leaf area index, plant height and Normalized Difference Vegetative Index (NDVI), especially at 55 days after sowing.

Despite the novel findings above, further extension of our knowledge, on the patterns of biopore formation in arable fields and its influence on root growth in the subsoil as well as on the overall crop performance is necessary. While the previous studies mainly focused on

the impacts of biopore system of large-size classes (e.g. 2–5 mm and >5 mm) on the root growth of following crops, only limited attention has been given to the small-sized biopores (e.g. <2 mm) and their relevance to root development. Moreover, root morphological aspects have not been considered in terms of biopore-root relationship, especially in situ, despite its potentially significant implication for root biology and nutrient/water uptake potential. In order to make a firm conclusion on the positive influence of the extended biopore system in arable subsoil, the dynamics of root and shoot growth patterns of the following crops during the complete cropping season should be better understood. Finally, the varying degree and patterns of biopore effects on different crop species should be compared in order to plan and formulate more efficient cropping system.

Therefore, the aim of this study was to determine the effects of increased proportion of the soil biopores on the two different field crop species with special focuses on the dynamics of rooting density and root morphological changes in the subsoil and shoot growth parameters during a complete growing season. We hypothesize that (a) plant roots respond differently to the altered shares of biopore density of different size classes, i.e., >2 mm and <2 mm in diameter, hence the shoot growth, of which (b) the degree and pattern vary depending on crop growth stages, root/shoot traits and crop species.

Materials and methods

Experimental site

The field experiment was conducted at the Campus Klein-Altendorf research station (50°37'9″ N, 6°59' 29″ E) located in Rheinbach, Germany from 2010 to 2013. Monthly recorded air temperature (°C), soil temperature (°C; measured at 20 cm of soil depth) and precipitation (mm) from 2010 to 2013 at the experimental station are shown in Table 1. The soil at the study site was classified as Haplic Luvisol (Hypereutric, Siltic) developed from loess (IUSS Working Group WRB 2006). The detailed information on soil properties at seven distinct horizons (0–140 cm of soil depth) is available in Table 2.

Treatments

Two fodder crops, viz., chicory (*C. intybus* L. 'Puna') with a taproot-dominated root system and tall fescue (*Festuca arundinacea* Schreb. 'Hykor') with a limited taproot system (Zobel and Waisel 2010) were grown for two consecutive years (2010–2012) as precrops (factor: PRE). Chicory and tall fescue were sown in April 2010 with sowing densities of 5 kg ha^{-1} (385 seeds m^{-2}) and 30 kg ha^{-1} (1250 seeds m^{-2}). Both species were cut three and five times during growing seasons in 2010 and 2011, respectively. Shoot materials remained as mulch on site.

Table 1 Monthly means of air/soil temperature and precipitation in 2010–2013 at the study site

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Air temperature (°C)												
2010	-1.61	1.37	5.64	9.45	10.66	16.70	20.31	16.97	13.02	9.24	6.01	-1.94
2011	2.73	3.75	6.52	12.55	14.50	16.54	16.04	17.78	16.18	10.71	6.67	5.45
2012	4.00	-0.56	8.15	8.67	14.49	15.34	17.19	18.97	13.62	9.89	6.33	3.80
2013	1.64	0.43	1.66	8.82	11.57	15.59	19.35	17.89	13.99	11.67	5.45	5.09
Soil temperature (°C)*												
2010	1.98	2.97	6.23	11.10	14.28	20.43	24.57	20.59	16.74	12.48	9.14	3.20
2011	4.30	4.58	7.08	13.59	17.78	19.85	20.22	20.57	18.22	13.00	8.44	5.92
2012	5.30	1.12	8.72	10.51	16.80	18.52	20.75	21.71	17.22	12.48	8.13	5.32
2013	4.72	3.12	4.26	9.68	14.34	18.22	22.05	21.15	17.34	13.65	8.72	6.04
Precipitation (mm)												
2010	22.77	20.59	40.48	7.94	55.64	37.38	65.09	157.90	53.70	35.60	59.30	51.10
2011	35.90	18.40	7.90	22.00	30.10	123.30	31.50	89.60	25.80	41.80	1.50	116.80
2012	86.00	19.20	10.50	33.90	49.20	58.50	89.30	46.80	18.00	99.90	22.10	68.70
2013	17.70	29.50	26.16	42.12	92.70	89.60	42.40	42.70	81.40	65.70	54.90	22.30

*Measured at 20 cm of soil depth

Table 2 Soil profile classification at the study site

Depth (cm)	Horizons*	Sand (%)	Silt (%)	Clay (%)	Bulk density (g cm^{-3})	SOC (g kg^{-1})	N_{tot} (g kg^{-1})	CaCo$_3$ (g kg^{-1})	CEC (cmolc kg^{-1})
0–27	Ap	8	77	15	1.29	10.0	1.02	<1	12.01
27–41	E/B	5	74	20	1.32	4.6	0.55	<1	11.91
41–75	Bt1	4	69	27	1.42	4.5	0.51	<1	15.68
75–87	Bt2	4	65	30	1.52	3.9	0.50	<1	18.48
87–115	Bt3	5	70	25	1.52	2.5	0.34	<1	15.49
115–127	Bw	5	72	23	1.46	2.6	0.34	<1	14.35
127–140+	C	8	79	13	1.47	–	>0.00	127	–

Source: Vetterlein et al. (2013)

*World Reference Base for Soil Resources (WRB 2006)

Additional fertilization and tillage operation were not carried out during the biopore generating phase. Prior to cultivation of the arable species, the mulched residues were incorporated into the soil (30 cm soil depth) with a mouldboard plough. From 2012 to 2013 two winter crops, namely, barley (*H. vulgare* L. 'Highlight') and canola (*B. napus* L. 'Visby') were cultivated as following crops resulting in four crop sequences. Barley and canola were sown on August 30, 2012 and October 4, 2012, with sowing densities of 330 and 100 grains m^{-2}. Both crops were sown with 12 cm row width and received 40 kg N ha^{-1} as calcium ammonium nitrate per growing season. Barley and canola were harvested July 18 and 23, 2013, respectively. The experimental plot size was 6 m × 10 m.

Soil biopore density measurement

Prior to the sowing of barley and canola biopore density (number of biopores per unit area) was measured in April 2012. Rectangular trenches were formed to the soil depth of 45 cm inside the plots where chicory and tall fescue were previously grown. At the depth, the surface area (50 cm × 50 cm) was flattened horizontally, then the soil biopores were revealed by cleaning the area with vacuum cleaner. Round-shaped and enclosed biopores larger than 2 mm (large-sized biopores) and smaller than 2 mm (small-sized biopores) were recorded on a transparent sheet, and their densities were calculated as the number of biopores per m^{-2}.

Seasonal root and shoot growth measurements

Root and shoot growth parameters were measured during four crop growth stages (BBCH: phenological development stages of a plant, factor: STAGE; Table 3) of barley at tillering, stem elongation, booting and anthesis (BBCH-scale: 25, 31, 41 and 61) and of canola at stem elongation, flowering, development of fruit and ripening (BBCH-scale: 35, 60, 71 and 80) based on Lancashire et al. (1991). Investigation on the temporal root development of barley and canola were done using the profile wall method (Böhm 1979b). Two-meter-deep soil profile wall was formed inside the plots with the crop standing. The roots projected from the vertically flattened wall were then cut to the surface. After that, the surface was jet-sprayed with pressure of 300 kpa until approximately 0.5 cm-thick soil was washed away, which was intended to reveal the roots for measurement. Onto the prepared wall surface, a rectangular frame (1 m × 2 m) consisting of grids (5 cm × 5 cm) was placed, and visual observation on the root was carried out. Visible roots inside each grids were recorded with

Table 3 Sampling dates for root and shoot growth parameters during four growth stages of barley and canola in 2013

Plant species	Sampling date (days after sowing)	Growth stage (BBCH-scale)
Barley	27 Mar (174)	Tillering (25)
	17 Apr (195)	Stem elongation (31)
	10 May (218)	Booting (41)
	03 Jun (242)*	Anthesis (61)
Canola	27 Mar (209)	Stem elongation (35)
	17 Apr (230)	Flowering (60)
	02 May (245)*	Seed development (71)
	11 Jun (285)	Ripening (80)

* Dates for soil monolith sampling

root-length unit (1 RLU = 5 mm), then converted to root length (RL; km m^{-2}) afterwards. In this paper, RL was calculated with the data acquired beneath 45-cm soil depth only. The investigation was carried out in two-replicated plots.

Seasonal plant biomass production of barley and canola was determined at four growth stages (Table 3). Two areas of 0.5 m × 0.5 m size located 1 m apart from the left and right plot border were dedicated for sampling, after which three other samplings were carried out along the border with approximately 0.5 m distance. Final yield of both crops were determined by harvesting the grains from central part of each plots. Four replicated samples were collected from each treatment. Chlorophyll content in plant leaves (SPAD-value) was determined using SPAD-502Plus (Konica Minolta). Shoot biomass was determined as dry matter (DM t ha^{-1}) after oven drying (105 °C). Prior to the oven drying, leaf area index (LAI) and shoot length (cm) were determined. For both shoot and grain samples, Dumas method was used for N determination (%) and P and K contents (%) were measured using atomic absorption spectrometry (AAS). The nutrient contents of shoot and grain were converted to shoot and grain N, P and K uptake (kg ha^{-1}).

Soil monolith sampling

Based on the principle suggested by Böhm (1979a) four replicated soil monolith samples (25 cm × 10 cm × 10 cm) from each two plots were collected for the root measurements of chicory and tall fescue from the six levels of soil depth at 10 cm interval (factor: DEPTH; 45 to 105 cm) in 2011. In 2013 at the growth stages of anthesis (BBCH-scale 61) and seed development (BBCH-scale 71) of barley and canola, respectively, six soil monolith samples (12 cm × 12 cm × 10 cm) from two plots of each treatment were taken from the profile walls from 45 to 155 cm of soil depth (factor: DEPTH; 11 depth levels). Both categories of monolith samples were carefully rinsed with tap water until the soil was washed away. The remaining parts of the samples were sorted by removing debris and dead roots. The clean root samples were photo-scanned (Epson Perfection V700) and the resulting images (400 dots per inch: DPI) were analyzed for root diameter (mm) and root-length density (RLD; cm cm^{-3}) with the software 'WinRHIZO Pro' (Version 2009c, 32 Bit). Minimum surface area and length to width ratio of the root objects considered for analysis were 2 cm^2 and 4, respectively.

Image smoothening was adjusted for 'low' for noise removal. After scanning, barley and canola roots were transferred to pre-weighted glass vials and oven dried at 65 °C for two consecutive days. Finally, the root dry mass (mg cm^{-3}) and specific root-length (SRL; m g^{-1}) were calculated. For canola, RLD was calculated for four diameter classes, viz., very fine (≤0.1 mm), fine (0.1–0.2 mm), medium (0.2–0.5 mm) and coarse (≥0.5 mm) roots (root classes were derived from Reinhardt et al. (1990) with a slight modification).

Statistical analysis

Statistical analysis of data was done with R version 3.1.0 (R Core Team 2014). Prior to statistic tests, the variables were checked for normality (Shapiro-Wilk test, $P \leq 0.05$), which suggested transformation of the root data (log-transformation) for further univariate analysis. Linear mixed-effects models (Pinheiro and Bates 2000) were used for further univariate analysis of the data. Repeated measures, viz., soil depths for root measurements and crop growth stages for root and shoot measurements were included in the models based on the suggestion by Piepho et al. (2004). The mixed-effects models were fitted for making no allowance for correlation structure potentially caused by the repeated measures (Pinheiro and Bates 2000). The fitted models were compared for Akaike information criterion (AIC: Akaike 1974), among which the final model with lowest AIC value was chosen. If required independent t tests ($P \leq 0.05$) were performed to compare mean values between the treatments.

Results

Root system and soil biopore density

Roots smaller than 1 mm in diameter showed significant interactions in RLD between the fodder crop species (factor: PRE) and soil depth (factor: DEPTH; Table 4). Tall fescue had higher RLD at upper horizons of the subsoil (45–65 cm), whereas chicory's RLD was higher at 85–105 cm of soil depth (Fig. 1a). Across the soil depths, RLD of chicory (0.009 cm cm^{-3}) and tall fescue (0.001 cm cm^{-3}) significantly differed for the root size classes of 1–2 mm and >2 mm (Fig. 1b and c). Proportional distribution of chicory roots smaller than 1 mm, 1–2 mm and larger than 2 mm in diameter was 97.83,

Table 4 Univariate analysis on root-length density (RLD) of chicory and tall fescue (factor: PRE) measured from 45 to 105 cm of soil depth (factor: DEPTH 45–105 cm) in 2011

Factor	df	<1 mm	1–2 mm	>2 mm
PRE	1	2.356 (0.134)	**77.985 (≤0.001)**	**13.597 (≤0.001)**
DEPTH	5	**18.353 (≤0.001)**	2.148 (0.084)	1.560 (0.229)
PRE x DEPTH	5	**5.874 (≤0.001)**	1.112 (0.373)	1.120 (0.369)

F values are shown with their probability levels in parentheses. Bold *p*-values indicate significant effects

1.95 and 0.22 %, respectively. Tall fescue roots mainly consisted of roots smaller than 1 mm (99.90 %) followed by roots sized 1–2 mm (0.097 %) and >2 mm (0.002 %). At 45 cm of soil depth, density of small-sized biopores (<2 mm in diameter) was significantly higher (*t test*; $P \leq 0.05$) after cultivating tall fescue (888 m^{-2}) than chicory precrop (592 m^{-2}). On the other hand, chicory (391 m^{-2}) created more number of large-sized biopores (>2 mm in diameter) compared with tall fescue (245 m^{-2}; Fig. 2b).

Root morphological traits at different soil depths

Effects of crop sequence (factor: PRE) on root diameter, root dry mass and SRL of barley measured at the time of anthesis depended on the soil depth (factor: DEPTH; Table 5). Barley roots revealed an overall increase in root diameter when grown after chicory except at 55–65 cm of soil depth (Fig. 3a). Root dry mass of barley when grown after tall fescue was higher than chicory at the upper parts of soil depth (45–55 cm, 55–65 cm and 65–75 cm; Fig. 3b). In contrast, chicory-barley treatment resulted in higher root dry mass than tall fescue-barley sequence at the deeper soil layers (95–105 cm and 105–115 cm). SRL of barley was significantly

higher after tall fescue as compared to chicory except at 55–65 cm and 65–75 cm of soil depth (Fig. 3c).

Root diameter and SRL of canola showed significant interactions between PRE and DEPTH (Table 5). Root dry mass showed the overall effects of PRE. Root diameter of the chicory-canola treatment was higher than tall fescue-canola at 115–125 cm, 125–135 cm, 135–145 cm and 145–155 cm of soil depth (Fig. 3d). On average, root dry mass of canola grown after chicory and tall fescue was 0.030 and 0.020 mg cm^{-1}, respectively (Fig. 3e). Chicory-canola treatment resulted in higher SRL compared with tall fescue-canola treatment at 85–95 cm and 95–105 cm of soil depth. Whereas the pattern was reversed at the soil depths at 135–145 cm and 145–155 cm (Fig. 3f).

RLD of the very fine, fine and medium roots of canola was higher when grown after chicory precrop compared with tall fescue (Fig. 4a–c). The differences were most vividly shown with the coarse roots (>0.5 mm), especially at 125–135 cm, 135–145 cm and 145–155 cm of soil depths (Fig. 4d). The proportion of roots having larger diameter, viz., medium (0.2–0.5 mm) and coarse roots (>0.5 mm), increased by approximately 15 % under higher share of large-sized biopores, especially in deeper soil layers (≥105 cm).
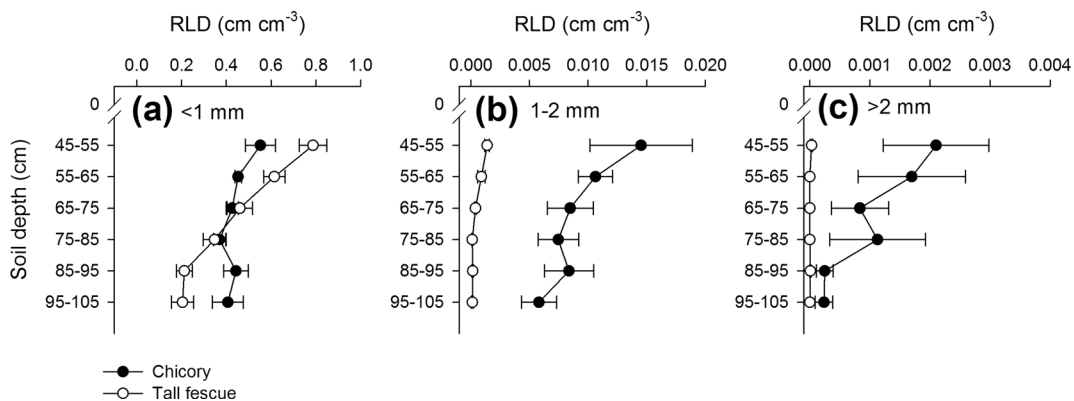
Fig. 1 Root-length density (RLD; cm cm^{-3}) of chicory and tall fescue within <1 mm (a), 1–2 mm (b) and >2 mm (c) root size classes measured in 2011. The data were transformed for the analysis but mean values (± SE) are shown. For significant effects, see Table 4

Fig. 2 Density of small-sized (<2 mm; **a**) and large-sized biopores (>2 mm; **b**) measured in 2012 after growing chicory and tall fescue for two consecutive years in 2010 and 2011. Small letters indicate significant differences between the treatments within the soil depth (*t test*; $P \leq 0.05$). Error bars represent standard error (SE) of means
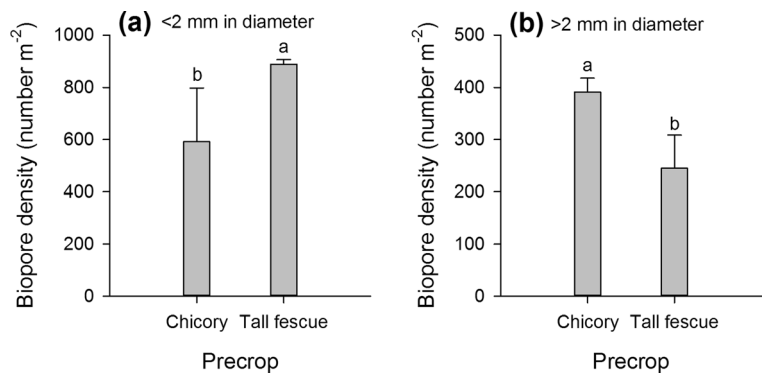
From the total RL, proportional allocations of smaller roots of canola, viz., very fine (<0.1 mm) and fine roots (0.1–0.2 mm), on average, were 62 and 48 % after growing tall fescue and chicory precrops, respectively.

Root growth dynamics inside and outside soil biopores

Interactions between PRE and STAGE were found to be significant for RL in bulk soil of barley and canola (Table 6). RL inside biopores of both crops was not affected by PRE. Further tests suggested that RL in bulk soil of barley grown after tall fescue (1.287 km m^{-2}) was higher compared with chicory (0.926 km m^{-2}) at the stage of anthesis (BBCH-scale 61). RL inside biopores of chicory-barley and tall fescue-barley treatments was highest at the times of booting (BBCH-scale 41: 0.642 km m^{-2}) and anthesis (BBCH-scale 61: 0.456 km m^{-2}), respectively. RL in bulk soil when grown after chicory (1.488 km m^{-2}) was higher compared with tall fescue (1.159 km m^{-2}) at the time of ripening of canola (Fig. 5b). Across the growth stages, RL inside biopores of chicory-canola and tall fescue-canola was 0.736 and 0.654 km m^{-2}, respectively.

Crop performance of barley and canola

SPAD-value, LAI and plant height of barley and canola measured during the four growth stages did not reveal significant effects of PRE but STAGE (Table 6). PRE did not affect shoot biomass production of both crops but STAGE. Shoot K uptake of barley revealed significant effects of PRE and STAGE. PRE did not affect shoot biomass, N and P uptake of barley. Shoot N and P uptake of canola were affected by PRE and STAGE but shoot biomass and K uptake were only affected by the latter.

The average biomass production of barley grown after chicory and tall fescue was 3.8 and 3.7 t ha^{-1}, respectively (Fig. 6a). Similarly, shoot N and P uptake showed slight increases of 3 and 5 %, respectively, from barley-tall fescue (Fig. 6b) to barley-chicory treatments (Fig. 6c). The average shoot K uptake of barley grown after chicory and tall fescue was 109 and 96 kg ha^{-1}, respectively (Fig. 6d). Tall fescue-canola treatment (4.94 t ha^{-1}) resulted in relatively higher biomass production compared with the treatment of chicory-canola (4.82 t ha^{-1}) across the growth stages (Fig. 6e). Shoot N and P uptake from chicory-canola to tall fescue-canola treatments decreased by 11 and 7 % (Fig. 6f). Shoot K uptake of canola

Table 5 Univariate analysis on root diameter, root dry mass and specific root-length (SRL) of barley and canola at the stages of anthesis and seed development, respectively, as affected by crop sequence (factor: PRE) and soil depth (45–155 cm; factor: DEPTH) in 2013

Plant species	Factor	df	Root diameter	Root dry mass	Specific root-length (SRL)
Barley	PRE	1	**124.282 (0.008)**	**62.572 (≤0.001)**	3.381 (0.207)
	DEPTH	10	**2.509 (0.010)**	**11.369 (≤0.001)**	1.912 (0.052)
	PRE x DEPTH	10	**3.807 (≤0.001)**	**7.945 (≤0.001)**	**2.657 (0.007)**
Canola	PRE	1	4.084 (0.181)	**6.881 (0.010)**	0.514 (0.548)
	DEPTH	10	**3.919 (≤0.001)**	**5.029 (≤0.001)**	**4.406 (≤0.001)**
	PRE x DEPTH	10	**5.110 (≤0.001)**	0.856 (0.577)	**3.658 (≤0.001)**

F values are shown with their probability levels in parentheses. Bold *p*-values indicate significant effects

Barley
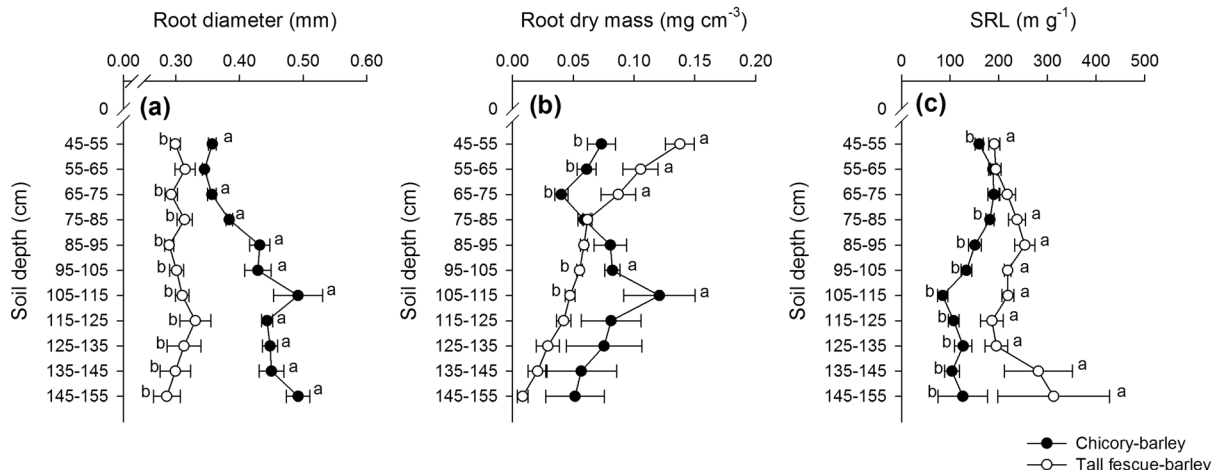
Canola
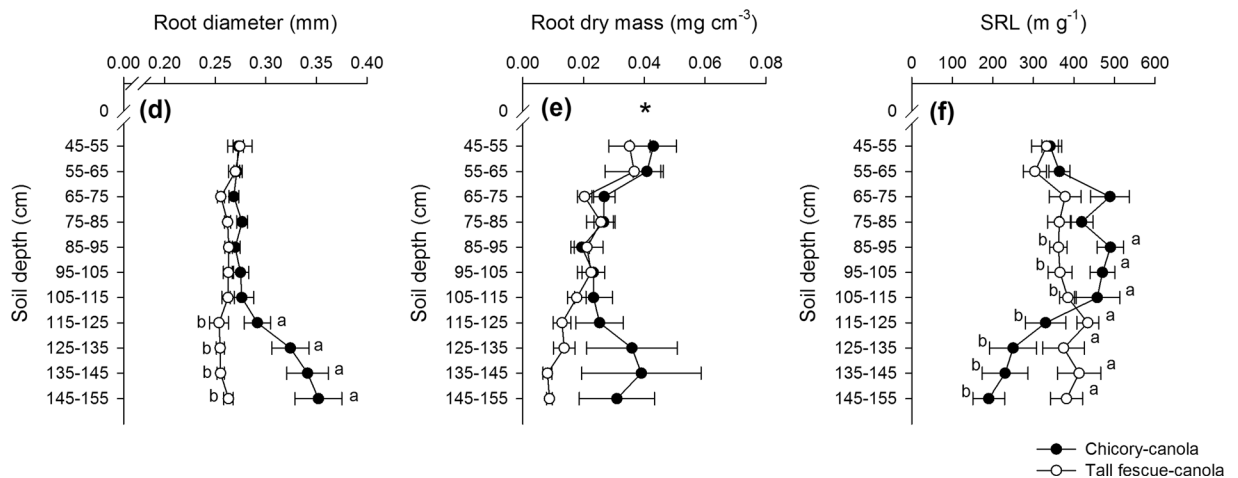
Fig. 3 Root diameter (mm), root dry mass (mg cm^{-3}) and specific root-length (SRL; m g^{-1}) of barley at anthesis (**a**, **b** and **c**) and canola at seed development (**d**, **e** and **f**) measured in 2013 after growing chicory and tall fescue for two consecutive years in 2010–2011. Small letters indicate significant differences between the treatments within the soil depth (*t test*; $P \leq 0.05$). The asterisk indicates the significant effects of PRE. The data were transformed for the analysis but mean values (± SE) are shown. For significant effects, see Table 5

(Fig. 6g) was slightly higher when grown after tall fescue (126 kg ha^{-1}) than chicory (119 kg ha^{-1}).

Final grain yields, N, P and K uptakes of both crops did not show significant effects of the treatments (Table 7). Final yield of chicory-barley treatment (5.7 t ha^{-1}) was relatively higher compared with tall fescue-barley treatment (5.4 t ha^{-1}) of grain yield. Canola yielded 3 % more when grown after tall fescue than chicory. In comparison to tall fescue-treatments, when grown after chicory, grain N, P and K uptake of barley showed increases of 7, 7 and 8 %, whereas canola showed decreases of 6, 3 and 23 %, respectively. Root

to shoot ratio did not differ between the chicory (0.098) and tall fescue treatments (0.071) of both barley and canola (Table 7) although it tended to decrease as the share of small-sized biopores increased.

Discussion

Root-induced soil biopores

The elevated share of large-sized biopores after growing deep-rooted crop plants with larger root diameter has

Fig. 4 Root-length density (RLD, cm cm^{-3}) of very fine (**a**; <0.1 mm), fine (**b**; 0.1–0.2 mm), medium (**c**; 0.2–0.5 mm) and coarse (**d**; >0.5 mm) roots of canola in 2013 subsequently grown after a 2-year cultivation of chicory and tall fescue. Small letters indicate significant differences between the crop sequence (t test; $P \leq 0.05$). The data were transformed for the analysis but mean values (±SE) are shown
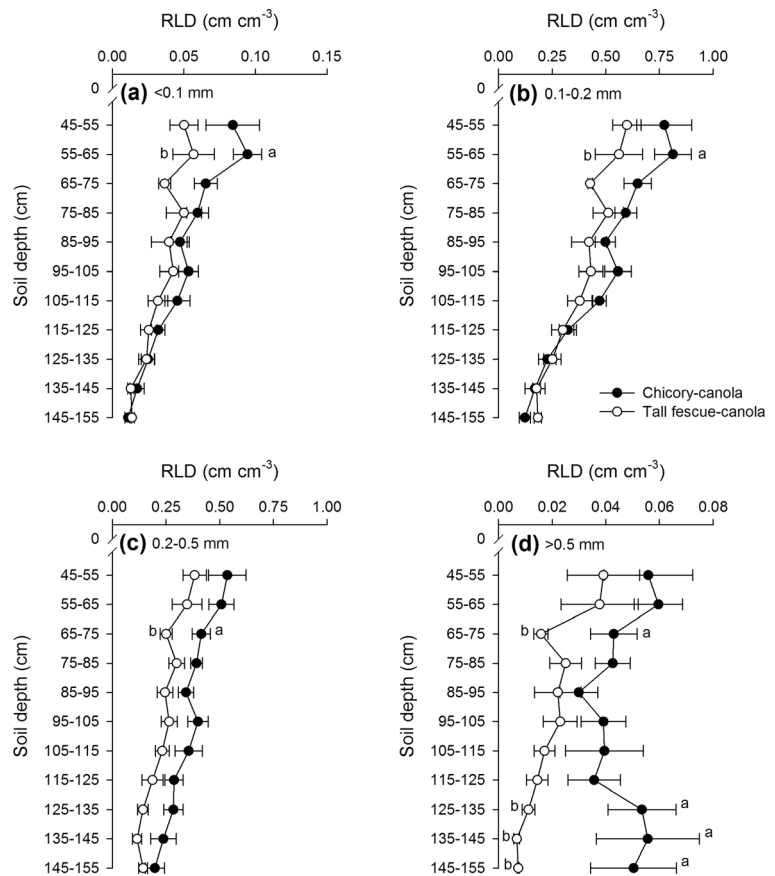
been reported previously (e.g. McCallum et al. 2004; Kautz et al. 2014). A novel finding of this study is the quantitative evidence of the increased density of small-sized biopores caused by the extensive rooting habit of tall fescue with smaller root size (Huang and Gao 2000). To our knowledge, apart from earlier studies based on model simulation (e.g. Bodner et al. 2014), no field measurement was made with such small biopore classes, i.e., <2 mm, in relation with cropping system.

It should be acknowledged that the other biological activity for biopore formation, i.e., earthworm movement was not considered in this study. Earlier investigations on the subsoil of Haplic Luvisol at the same site have shown no clear relationship between the abundance of an anecic earthworm species (*Lumbricus terrestris*) and the large-sized soil biopore density (e.g. Kautz et al. 2014; Han et al. 2015a). The roles of soil burrowers might be important rather for stabilization of biopores and altering chemical properties of pore walls (Pagenkemper et al. 2014). This indicates that the biopore formation process should be regarded as a continuous process which might require long-term investigations (Han et al. 2015a).

Preferential root growth and overall rooting density

The proportion of rooting density inside large-sized biopores (approximately 47 %) demonstrated the preferential root growth into the zones of less mechanical impedance (Bengough 2006). The high share of roots located inside the biopore channels agrees with the study of Ehlers et al. (1983), meanwhile it is relatively higher than the results from other studies (e.g. 33 % of maize roots inside artificially created biopores; Nakamoto 1997) and even previous studies done at the same site (e.g. 20 % of barley roots inside biopore channels; Perkons et al. 2014). This might be due the longer growing period and subsequent deeper rooting capacity of the winter crops, which were reported with even double the rooting depth (e.g. winter wheat vs. spring wheat; Thorup-Kristensen et al. 2009).

Table 6 Univariate analysis on root and shoot traits as affected by crop sequence (PRE: chicory-barley, tall fescue-barley, chicory-canola and tall fescue-canola) and growth stages (STAGE: 4 stages of barley and canola) of barley and canola in 2013

Plant species	Variable	PRE (df = 1)	STAGE (df = 3)	PRE x STAGE (df = 3)
Barley	Root length (RL) in bulk soil	2.995 (0.085)	**133.777 (≤0.001)**	**3.652 (0.013)**
	Root length (RL) inside biopores	0.664 (0.416)	**6.463 (≤0.001)**	1.001 (0.393)
	SPAD-value	1.783 (0.196)	**21.349 (≤0.001)**	0.691 (0.568)
	Leaf area index (LAI)	1.780 (0.197)	**17.663 (≤0.001)**	0.228 (0.876)
	Plant height	0.196 (0.663)	**2441.134 (≤0.001)**	0.590 (0.663)
	Shoot biomass	0.371 (0.549)	**266.897 (≤0.001)**	0.337 (0.799)
	Shoot N uptake	0.283 (0.600)	**105.204 (≤0.001)**	0.234 (0.872)
	Shoot P uptake	0.716 (0.407)	**261.205 (≤0.001)**	0.225 (0.878)
	Shoot K uptake	**6.831 (0.017)**	**151.042 (≤0.001)**	1.498 (0.246)
Canola	Root length (RL) in bulk soil	0.097 (0.756)	**69.373 (≤0.001)**	**4.868 (0.003)**
	Root length (RL) inside biopores	2.596 (0.108)	1.004 (0.392)	1.931 (0.125)
	SPAD value	0.118 (0.735)	**82.097 (≤0.001)**	0.913 (0.451)
	Leaf area index (LAI)	2.470 (0.131)	**5.575 (0.006)**	0.488 (0.694)
	Plant height	0.441 (0.514)	**1964.278 (≤0.001)**	0.412 (0.746)
	Shoot biomass	0.097 (0.759)	**93.672 (≤0.001)**	0.245 (0.864)
	Shoot N uptake	**11.090 (0.003)**	**8.984 (≤0.001)**	0.837 (0.489)
	Shoot P uptake	**9.011 (0.007)**	**81.131 (≤0.001)**	1.179 (0.342)
	Shoot K uptake	3.807 (0.065)	**24.873 (≤0.001)**	0.381 (0.768)

F values are shown with their probability levels in parentheses. Bold p-values indicate significant effects

In contrast to the earlier study with spring barley (Han et al. 2015b), the preferential root growth followed by the presumed 're-entry' back to the bulk soil did not influence the root growth in soil matrix at earlier growth stages but at final growth stages of barley and canola. Given that the soil temperature at the study site during winter season of 2012 did not fall below zero (see Table 1), the root systems of the winter crops may not have been completely dormant, hence the continuous
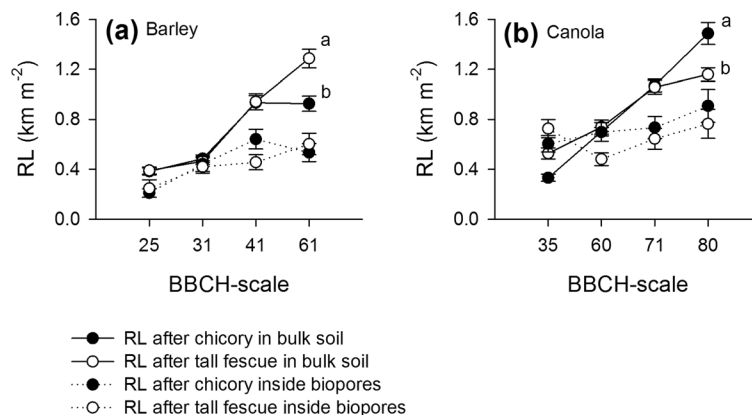
Fig. 5 Root length (RL; km m^{-2}) of barley (**a** and **b**) and canola (**c** and **d**) measured beneath 45 cm of soil depth in bulk soil and inside biopores in 2013 after growing chicory and tall fescue for two consecutive years in 2010–2011. The measurements were done at the growth stages of tillering, stem elongation, booting and anthesis (BBCH-scale: 25, 31, 41 and 61) of barley, and stem elongation, flowering, seed development and ripening of canola (BBCH-scale: 35, 60, 71 and 80). Small letters indicate significant differences between the treatments (*t test*; $P ≤ 0.05$). The data were transformed for the analysis but mean values (± SE) are shown. For significant effects, see Table 6
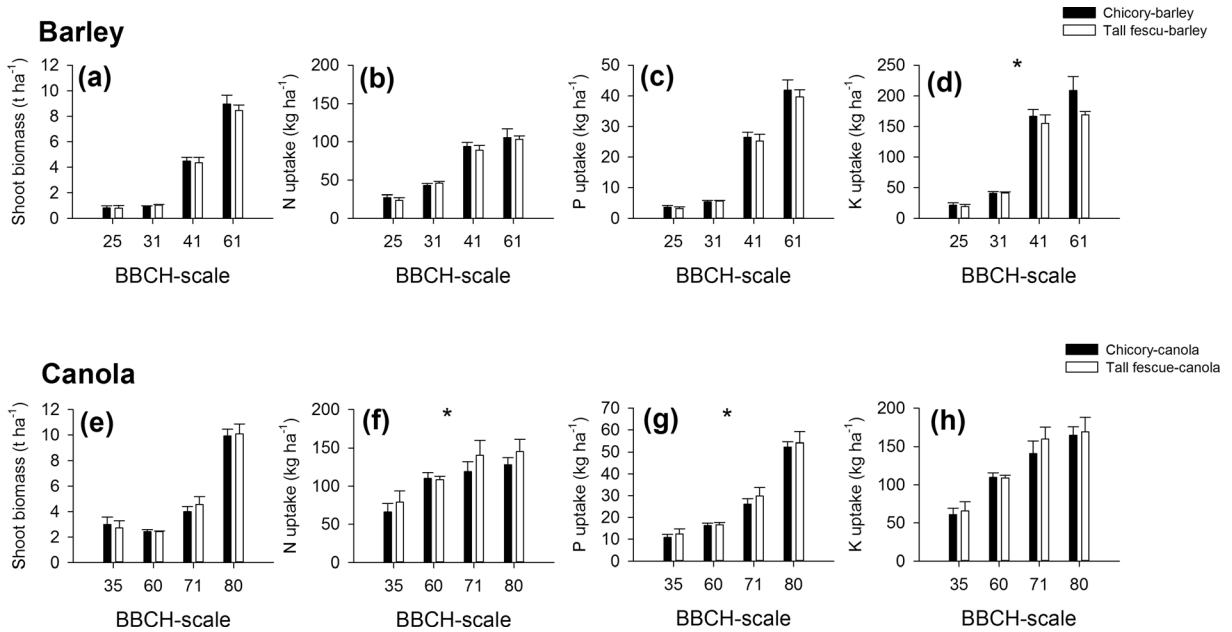
Barley

Canola

Fig. 6 Shoot biomass (t ha^{-1}), N, P and K uptake (kg ha^{-1}) of barley (**a-d**) and canola (**e-h**) in 2013 after growing chicory and tall fescue for two consecutive years in 2010–2011. The measurements were done at the growth stages of tillering, stem elongation, booting and anthesis (BBCH-scale: 25, 31, 41 and 61) of barley, and stem elongation, flowering, seed development and ripening of canola (BBCH-scale: 35, 60, 71 and 80). Error bars represent standard error (SE) of means. Figures with asterisks indicate significant effects of PRE. For detailed information on univariate analysis, see Table 6

increment in rooting density (Fernandez and Caldwell 1975). This also explains the undetected 'rapid root growth' as influenced by large-sized biopores.

Another novel finding of this study was the varying response of barley and canola towards the altered large-sized biopore systems in terms of rooting density at the growth stages of anthesis and ripening, respectively. It might be due to their different rooting patterns inside soil biopores (Athmann et al. 2013), capacity for re-entering back to bulk soil (Stirzaker et al. 1996), contrasting root growth patterns (Pietola and Alakukku 2005), more importantly, root system architecture (Fitter 1987) might have played important roles.

Table 7 Univariate analysis on grain yield, N/P/K uptake of barley and canola in 2013

Plant species	Variable	Main effect		Block effect	
		F-statistics	*p-value*	*F-statistics*	*p-value*
Barley	Grain yield	0.331	0.623	2.169	0.316
	Grain N uptake	0.638	0.508	0.737	0.576
	Grain P uptake	0.682	0.496	0.953	0.512
	Grain K uptake	0.671	0.499	1.652	0.377
	Root:shoot ratio	0.004	0.952	0.048	0.836
Canola	Grain yield	0.380	0.582	1.486	0.376
	Grain N uptake	1.426	0.318	3.189	0.183
	Grain P uptake	0.644	0.481	5.003	0.110
	Grain K uptake	3.347	0.165	1.650	0.345
	Root:shoot ratio	1.341	0.299	0.102	0.762

Root morphological changes

Our results indicate that both large-and small-sized biopores hold relevance for determining root morphology of the field crops in the subsoil. Considering only the soil physical aspects, root elongation and expansion inside soil pores would depend on the balance between radial and axial pressure exerted by the pore structure (Bengough 2012). Therefore, the smaller root diameter of barley and canola under higher share of small-sized biopores shown in this study can be explained by the presence of radial pressure inside the narrow pores (Kolb et al. 2012; Han et al. 2016). Roots growing within a structure narrower than the normal root diameter can be flattened and distorted, especially under hard soils, e.g., red Kandosol with a bulk density higher than 1.6 g cm^{-3} (White and Kirkegaard 2010). It is, however, uncertain to which extent the sandy loamy soil at the study site with the maximum bulk density of 1.52 g cm^{-3}, compressed the barley and canola roots in deep soil horizons, especially considering the assumed capacity of plant roots to cross the pore walls (Stirzaker et al. 1996).

Another explanation for the increased root diameter might be due to the presence of axial pressure inside the large-sized biopores (Bengough and Mackenzie 1994). Also, in general, an acute increase in root weight occurs with relatively older roots than young roots due to thickening. Although it was not directly observed in this study, it is possible that more rapid root growth via larger soil biopores (Han et al. 2015b) might have resulted in higher proportion of older roots, hence the thicker roots. This also explains both the larger root size and relatively less correlations coefficients between RLD and root weight under higher share of large-sized biopores.

The proportional dynamics of root size classes in the subsoil might be also related with soil strength. The thinner roots were reported for their preference to grow in the denser soil matrix, whereas the thicker roots tended to follow the less mechanical resistance in the large-sized pores as claimed by the X-ray-based measurements (e.g. Moran et al. 2000; Pierret et al. 2005).

Precrop root systems might have been involved in the dynamic biochemical processes within rhizosphere level (see York et al. 2016), which could influence the root systems of the subsequent crops. For example, root respiration and exudation was reported to elevate or decrease soil pH in rhizosphere to 1–2 pH units (Hinsinger et al. 2009). Also considering that the pore

environment often consists of remnant roots (White and Kirkegaard 2010) and high degree of microbial activity (Stewart et al. 1999), root growth might have been affected by the attracted pathogenic and even growth inhibitory microbes (Smucker 1993; Watt et al. 2005).

Biopore-root-shoot relationship

The proportional increase in smaller roots in deeper soil layers under higher share of small-sized biopores might have increased shoot N and P uptake of canola. It suggests the elevated nutrient acquisition potential from the subsoil by establishing more intensive root-soil contacts by promoting the fine and active roots (Hodge et al. 1999). In fact, the greater SRL and smaller root diameter as promoted by the small-sized biopores can be considered to provide more favorable geometric conditions of diffusion to the root surface because delivering soil volume is proportional to reciprocal root radius (Jungk and Claassen 1997).

However, the aforementioned statement was not true for barley in this study. Despite the increase in root diameter and decrease in SRL, shoot K uptake of barley under higher share of large-sized biopores revealed significant increase. This was previously demonstrated at the same study site with P uptake of spring wheat (Han et al. 2015b). The winter cereal, when allowed to penetrate into the large-sized biopores, might have been able to draw a higher amount of P and K from the nutrient-rich zones of biopore channels, otherwise called 'drilosphere' (Bouché 1975) or 'macropore sheath' (MPS; Pierret et al. 1999). In fact, substantial differences in microbial and chemical conditions between the bulk soil and the drilosphere have been reported (Pankhurst et al. 2002; Barej et al. 2014; Uksa et al. 2015). The thicker roots of barley in this study might have been more desirable to bear more number of laterals and also to increase the root length (Wu et al. 2016). It might have established more intensive root-soil interface for nutrient uptake. Also the resulted thicker roots under higher share of large-sized biopores might have been beneficial for plant growth if it aided in enhancement the internal transport (Lauenroth and Gill 2003) or capture of soil resources associated with formation of root cortical aerenchyma (RCA; Zhu et al. 2010; Chimungu et al. 2015).

The contrasting biopore-effects between barley and canola might have occurred due to, firstly, the varying effects of biopore system on root growth dynamics (in terms of seasonal RL), secondly, different nutrient

requirement between their growth stages (Neukirchen et al. 1999; Peng et al. 2012; Girma et al. 2014). Also the actual efficiency for nutrient uptake depends on root hair geometry (Föhse et al. 1991; Bates and Lynch 2001), which often shows genotypic variation (Lynch and Wojciechowski 2015).

The limited effects of biopore-associated root growth on the shoot growth parameters and final yield shown in this study suggest that the biopore-root-shoot relationship might not be distinctively shown in the relatively optimum soil environment at the study site but rather under stress condition (Gaiser et al. 2012). Also it should be considered that the cropping system adopted for current experiment involved a series of mulching of the precrop shoot biomass 3–5 times a year on the soil surface. Thus, accumulation of nutrients, which might have been subsoil-drawn (Kautz et al. 2013a), would have also influenced the plant nutrient uptake process at the study site (see Han et al. 2015b). Also other important factors such as mycorrhizal association (Reinhardt and Miller 1990; Pii et al. 2015) and root age (Engels et al. 2000; Loades et al. 2015) might have played important roles determining the crop growth.

All in all, a firm conclusion on the relationship between biopores and plant growth should be made with a caution due to its complexity with myriad factors involved (Kautz et al. 2013a). Often simulation of mathematical models has been found to be helpful. With a model simulation, Jakobsen and Dexter (1988) have predicted an increase in wheat grain yield along with the changes in biopore density from 2000 to 6000 m^{-2} based on Australian site conditions. A model simulation with SIMPLACE (Scientific Impact Assessment and Modelling Platform for Advanced Crop and Ecosystem management) predicted increased root elongation rate, water and N uptake of spring wheat corresponding to the elevated pore volumes in soils with clay accumulation (Gaiser et al. 2013).

Controversy and the future scope

There have been contradicting notions for biopore utilization by plants (see Cresswell and Kirkegaard 1995). Among all, the 'clumping model' (Passioura 1991) referring to a restricted root growth inside the pore channels should be acknowledged as a detrimental type of biopore-associated root growth since it can result in the poor root-soil contact. Also using a thin section technique, Veen et al. (1992) measured the effects of root-

soil contact on shoot growth and water uptake of maize under artificially formulated compact condition, in which soil porosity from 60 % onwards decreased shoot growth and the rate of water uptake increased with higher degree of soil compaction. Some of the earlier reports also suggest that fine roots do not necessarily utilize the pore channels (e.g. Moran et al. 2000; Pierret et al. 2005) as mentioned earlier. On the other hand, more intensive root-soil contacts as influenced by the increased biopore density were also claimed. In Haplic Luvisol, more than 80 % of barley and canola roots had direct contacts to the pore wall either by vertical roots or laterals by the in situ endoscopy method (Athmann et al. 2013), which was also shown with the root hairs in Australian site conditions (e.g. White and Kirkegaard 2010).

The results of this study and the controversial claims indicate the need for the future study, which should allow exchanging our current understanding on soil biopore-plant relationship between the research platforms and agronomic contexts. In doing so, especially, the development of more precise methods that can directly quantify the processes from soil/root interplay to the plant nutrient uptake potential is necessary (e.g. tracer-based determination). Properties of the nutrient-rich drilosphere and their relationship with root functioning, especially of the root hairs (White and Kirkegaard 2010) and fine-root classes (McCormack et al. 2015) should be investigated in detail as they might hold great relevance for subsoil resource acquisition potential (Kautz et al. 2013a; Köpke et al. 2015). Species-specific response towards the altered biopores system shown in this study and elsewhere (Stirzaker et al. 1996; Athmann et al. 2013) should be considered as an important implication for genetic variation hence the breeding strategy. Intensive phenotyping on the biopore-associated roots using advanced technique such as X-ray computed tomography (CT) can be helpful.

Conclusions

Crop growth is strongly influenced by the heterogenized subsoil structure with increased biopore density. Our results suggested that the effects, however, largely depend on biopore size classes, root traits, shoot growth parameters and crop species. It was clearly shown that root size decreased under high share of small-sized biopores, whereas dynamics of rooting density revealed

variation between the crop species. Nutrient acquisition of following crops was significantly affected by the crop sequence, and presumably, also by the altered root growth pattern in the subsoil. Development of direct methods that can quantify biopore-root-shoot processes, detailed investigation on drilosphere, root phenotyping for detection of the genetic variation in response to biopore systems have to be followed in the future.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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