Soil compaction modifies morphological characteristics of seminal maize roots

B. Konôpka[1,2], L. Pagès[3], C. Doussan[4]

[1]*Department of Forest Protection and Game Management, Forest Research Institute Zvolen, National Forest Centre, Zvolen, Slovak Republic*
[2]*Department of Forest Protection and Game Management, Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, Prague, Czech Republic*
[3]*Plants and Horticultural Systems Unit, INRA Research Centre of Avignon, Avignon, France*
[4]*Mediterranean Environment and Modeling of Agro-Hydrosystems Unit, INRA Research Centre of Avignon, Avignon, France*

ABSTRACT

An evaluation of the effects of soil structural heterogeneity on maize (*Zea mays* L.) root system architecture was carried out on plants grown in boxes containing fine soil and clods. The clods were prepared at two levels of moisture (0.17 and 0.20 g/g) and bulk density (ranges 1.45–1.61 g/ml and 1.63–1.79 g/ml). Soil moisture directly affected the probability of clod penetration by maize roots. Primary roots inside the clods manifested morphological deformations in the form of bends. We observed a significant increase of bends per root length at lower soil moisture ($P = 0.02$). Root diameter and branching density increased, and lateral root length decreased considerably inside the clods. However, once emerging out of the clods and into free soil, values of all three characteristics remained low. While changes in root diameter were caused mainly by clod moisture ($P < 0.05$), length of lateral roots was related to bulk density ($P < 0.01$). Branching density was modified exclusively by an interactive effect of both factors ($P < 0.05$).

Keywords: clod; penetration resistance; root morphology; water content; *Zea mays*

During most agricultural practices, mechanized cultivation disturbs the soil, causing fragmentation, compaction and displacement (Roger-Estrade et al. 2000). Consequently, two types of earth may appear within the soil profile: fine and compacted zones (most often defined as clods). The presence of a large portion of high penetration-resistant clods is one of the most serious factors limiting soil exploration by plant roots (Hoad et al. 1992). Since water content fluctuates during the growing season and clod penetration resistance is strongly linked to moisture, impedance of clods to root growth changes considerably. An additional factor closely linked to these interactions is the intensity of soil compaction, which can be readily interpreted as an increase of bulk density of a specific soil type (Goldsmith et al. 2001).

If soil becomes compacted to the level that plant growth is impaired, the compaction must be alleviated through several measures intended to returning satisfactory growth conditions. Especially, loosening and sub-soiling aim at eliminating soil compaction and preventing reduced soil-rooting depth (Carter 1988). However, it is safe to assume that even optimal techniques and excellent timings of agronomic operations cannot fully eliminate soil compaction. Thus, soil impedance remains one of the most important factors influencing crop yield (Atwell 1988, Stenitzer and Murer 2003).

Some previous studies showed that soil compaction decreased root development and delayed root colonization of deeper soil layers (e.g. Ehlers et al. 1982). Frequently, the relation between the

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relative root elongation rate and soil penetration resistance was used to demonstrate the importance of soil compaction for root growth (Bennie 1991). However, it appears that there is a lack of studies on alterations of other morphological properties of roots due to soil compaction, and hence on plant physiological processes and crop production (Bengough 2003). The relationship between soil compaction and root growth was usually studied using a homogeneous substrate (see for instance Unger and Kaspar 1994), structured soil conditions were considered very rarely (Amato and Ritchie 2002).

Attempting to fill the aforementioned gap in the present knowledge, our experiment has been designed to simulate maize root growth in the tilled layers of cultivated fields, which are usually very heterogeneous.

The main objectives of this paper are following: (i) to characterize the influence of soil moisture and bulk density on penetration resistance of the clods, (ii) to study the interaction of soil moisture and bulk density in terms of the probability for seminal roots to penetrate the clods, (iii) to analyse the effect of these soil properties on several morphological features of seminal roots.

MATERIAL AND METHODS

Soil preparation

The soil was prepared to simulate four different environments, a combination of two levels of soil moisture and two levels of clod bulk density. Fine soil was collected in the plough layer of an experimental field at the INRA, Domaine St. Paul – Avignon, Southern France. The soil used in this experiment was the topsoil of a Calcosol developed from alluvium with a silty clay loam texture. It was composed of 34.1% clay, 53.7% silt, and 12.2% sand. The soil had pH 8.3, organic N 0.2% and C/N ratio 7.8. After extraction the soil was sieved to remove particles larger than 0.5 cm in diameter. The permanent wilting point and the field capacity of sieved soil was 0.145 and 0.245 g/g, respectively.

Compacted soil fraction originated from the same field, but was prepared independently from the fine soil. First, the topsoil was compacted by four passes of backhoe loader through the field. Machine total weight was 7200 kg. Compacted soil was then manually collected with a spade as 10–30 kg blocks. Soil blocks were split into smaller pieces by a chisel and any major irregularities were removed using a knife. The diameter of the longest side in the set of clods fluctuated between 5 and 12 cm, with an average of 8 cm. Clod shape was rather irregular, from ellipsoidal to bean-like form. Bulk density was measured on a set of approximately 600 clods. The clods were packed in a thin plastic film, submerged under water to measure their volume, and subsequently dried and weighed. The mean bulk density of the clod set was 1.62 g/ml. Thus, the clods were grouped for those under 1.61 g/ml and above 1.63 g/ml. To obtain two moisture treatment levels, clods were wetted with a sprayer to the desired moistures: 0.17 g/g (dry treatment hereafter) and 0.20 g/g (wet treatment hereafter) as calculated on a weight basis.

Both fine soil and wetted clods were placed into plastic boxes 24 × 35 × 55 cm (H × W × L), forming a volume of 48 litters. The bottom layer of the soil column inside each consisted of 9–10 cm of fine soil, on top of which one layer of clods was placed. Prior to placing into the boxes, the clods were sorted into two groups according to their bulk density; making up a set of clods with 1.45–1.61 g/ml and 1.63–1.79 g/ml (low and high bulk density, respectively). The clods, circa 35–40 pieces per box, were fitted on a horizontal plane created by the fine soil, their projected area made at least 80% of the total. Spaces between the clods were filled with fine soil and a second layer of fine soil with thickness of 9–10 cm was placed on top of the clods. Each layer of fine soil was subsequently wetted to desired moisture (0.17 or 0.20 g/g). The combination of two soil moisture levels and two clod bulk density levels created four different treatments, each of which was replicated three times. Hereafter, codes L-17 and H-17 are used for dry treatments containing the clods with low and high bulk densities and codes L-20 and H-20 are used for the wet treatments containing clods with low and high bulk densities.

Growth conditions

The boxes were placed in a growth chamber in a randomised design. Air temperature was maintained at 26 ± 1°C, air moisture at 60 ± 5%, photoperiod to 15 h by day at the light intensity of 300 μmol/m/s. Pre-germinated seeds (1 day in wet peat) of the PR35Y65 maize variety were sown in the soil at a depth of 4–5 cm. Three lines with 5 plants each (i.e. 15 plants) spaced at 9 cm were established in each box. Evapo-transpiratory water losses were minimised by placing a layer of clay-stones on the soil surface and manual water-spraying of the soil surface. Plants were harvested on the 15th day after sowing (i.e. 16th day after seed germination). Then, number of roots on the stem base of each plant was recorded.

Root measurements

To enable access to the roots penetrating the clods, top layer of the fine soil was removed from the boxes. At this level, the number of roots entering the clods and those avoiding them were counted. Roots entering clods were categorised into two categories: (I) shallow-penetrating, leaving the clods in the proximity of the point of entry; (II) deep-penetrating, entering and leaving the clods throughout the opposite sides of the clod.

Several segments of the roots were then sampled from each box. First, 6 cm-long sections of primary roots located in the fine soil were separated. Then, 6-cm long segments just before entering and after exiting the clods were collected for both shallow- and deep-penetrating root categories. The clods containing the roots were subsequently stored in a deep-freezer for later analyses. The roots outside the clods were placed in a 7:3 mixture of distilled water and alcohol and stored at 4°C. The desired sampling rate in each category of roots was 4 per box, but some boxes contained less than 4 individuals of a root group. Clods were disaggregated in a water + Calgon solution and roots were separated from soil by gentle shaking. Primary root diameter, branching densities and lateral root length of all root groups were measured under an illuminated magnifying glass.

In particular, the diameter of clod-penetrating roots was measured at 5, 3 and 1 cm before as well as 1, 3 and 5 cm after the clod. Root diameter was also measured where roots entered and exited the clods as well as in the middle of the root segment growing inside the clods. The root diameter measurements thus obtained are labelled as "B", "IN" and "A" for the root segments before, inside and after clods, respectively. Labels also contain 0, 1, 3, and 5 to indicate the distance of the measurement from the clod in centimetres. The diameter of roots avoiding the clods was measured on three random locations always placed two centimetres from each other.

The branching density (number of lateral roots per cm of primary root) on the roots penetrating the clods was counted on 2-cm-long segments 0–2 cm, 2–4 cm and 4–6 cm before and 0–2 cm, 2–4 cm and 4–6 cm after the clod. Moreover, the branching density was counted on the 2-cm-long root segment excavated from the clods (both shallow- or deep-penetrating). The codes "B", "IN" and "A" are used for the roots segments before, inside and after clods, respectively. Number after the codes (i.e. 0–2, 2–4, and 4–6) indicate distance of the measured segment from the clod in centimetres. Branching density of the roots, which avoided the clods, was measured on three 2-cm-long consecutive segments.

The length of lateral roots was measured on the root segments used to measure branching density (the same coding was used as well). The measurement of length was performed on two longest lateral roots of each root segment and expressed as the average of these two values.

Soil measurements

Twenty clods were used to measure the penetration resistance according to their bulk density and moisture. These clods were selected to cover the full range of observed bulk density, i.e. between 1.45–1.79 g/ml. Prior to measurement they were wetted to moistures of 0.14, 0.15, 0.16, 0.17, 0.18, 0.19 and 0.20 g/g. Penetration resistance was measured with a spring-operated pocket penetrometer (Eijkelkamp, the Netherlands) modified to accept a needle with a cone-shaped tip. The angle of the tip was 60° and its basal diameter 3 mm. The resistance was recorded after penetration 2 cm inside the clods.

In addition, four samples of clods were taken from each replicate box at the end of the experiment. These were used for establishing moisture by the gravimetric method in order to have the initial and final moistures in the clods in each treatment.

Statistical analysis

One-way ANOVA was used for comparing root characteristics among roots avoiding clods, shallow- and deep-penetrating roots. Two-way ANOVA was implemented for testing effects of treatments on probability of roots to penetrate clods as well as on relative number of bends. Three-way ANOVA was applied in order to test the effects of treatments, i.e. soil moisture and bulk density and root segment position, on relative root parameters. *T*-test was used to assess differences in penetration resistance between the clods of different bulk density in specific moisture levels. Also, *t*-test was used for testing relative root parameters with regards to position of root segment, considering root segment 4–6 cm before clods as a reference. Results were considered significant at the 0.05 level. All analyses were performed using the statistical software R (version 2.4.1; Ihaka and Gentleman 1996).

RESULTS AND DISCUSSION

Soil moisture, bulk density, and penetration resistance

Significant differences were observed between penetration resistance of clods due to changing soil moisture and bulk density (Figure 1). While a mean value of penetration resistance for soil with moisture of 0.14 g/g was about 9.5 MPa, penetration resistance of the same set of clods with moisture of 0.20 g/g was circa 3.5 MPa. The effect of bulk density, within a range of 1.45–1.79 g/ml, was also statistically significant, but less sharp (test on R square, $P \leq 0.05$). Results indicated that bulk density is stronger in influencing penetration resistance in dry than wet clods.

It has to be pointed out that we were not able to monitor exact soil moisture of the clods during the experiment. In the wet treatments the initial and final moistures were 0.20 and 0.16 g/g, respectively. While in the dry treatment were 0.17 and 0.145 g/g at the start and at the end of the experiment, respectively. Assuming a linear decrease of soil moisture, and taking into account the time required by roots for reaching the clods, we assume that during clod-penetration by roots moisture might have been about 0.17 and 0.15 g/g for the wet and dry treatment, respectively. Accordingly, from the model fits shown in Figure 1 we estimate that the penetration resistance was 5.3, 5.9, 7.8, and 8.5 MPa for L-20, H-20, L-17 and H-17 treatments, respectively.

Morphological traits of roots

The number of roots on stem base was about 7 (specifically: 1 radicle, 2 additional seminal, and 4 nodal). Excavation of root systems showed that the mean number of roots reaching the clod level

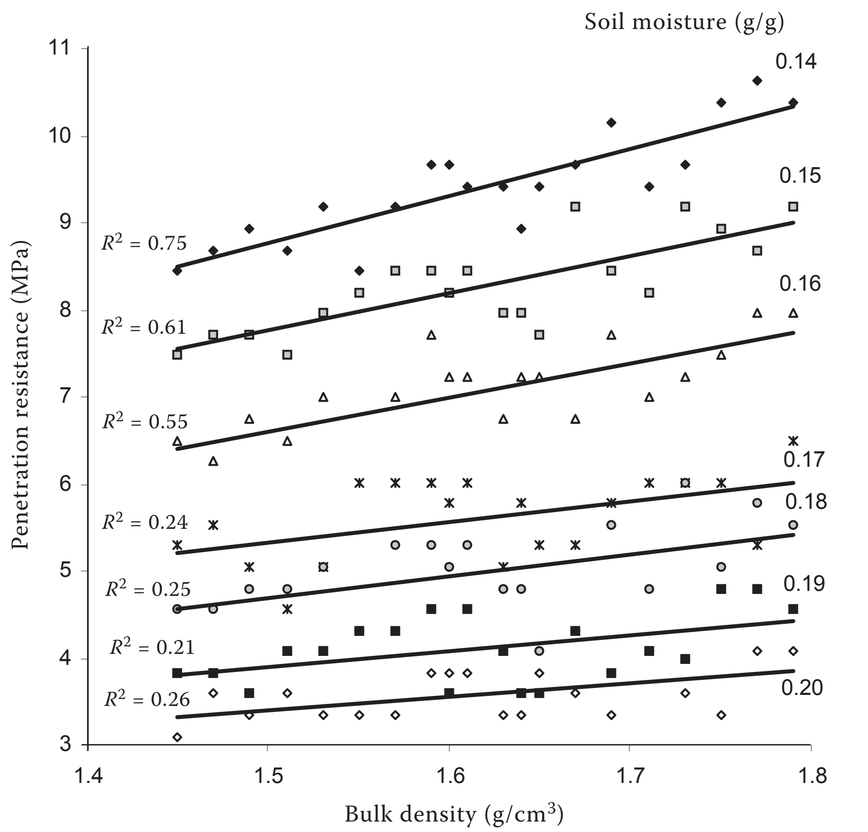

Figure 1. Penetration resistance of clods with different bulk densities and moisture gradient

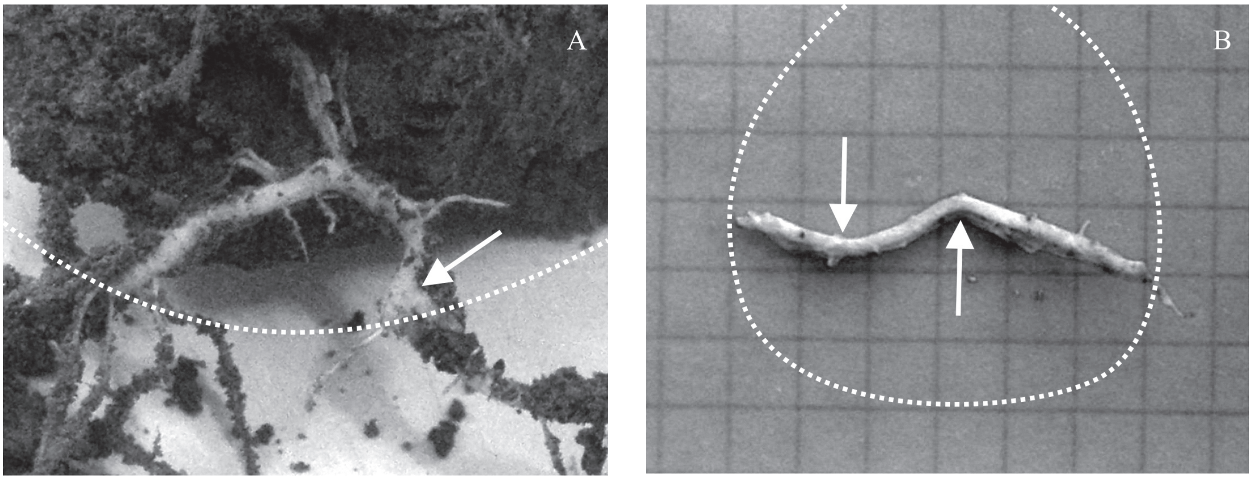

Figure 2. An example of root shallow-penetrating clod (A) and root deep-penetrating clod (B). In both photos, dashed curve indicates original clod edge, arrows show bends on the roots. Growth of the roots was from right to left

was 15, which is equal to the number of plants. It means that all roots were radicle seminal (roots, hereafter).

The visual observations showed two sorts of clod-penetrating roots: "shallow" and "deep" (Figure 2A and B). In principle, the shallow-penetrating roots did not enter the clods deeper than 1 cm. Usually they had one bend on the point of the first root-clod contact and then formed an arch-like segment inside the clod. Deep-penetrating roots, on the other hand, did not change considerably the general direction of their trajectory. However, the roots in the clods manifested curved short sections in form of several bends.

Table 1 shows the root probability of penetrating the clods (either shallow or deep), expressed as a ratio between penetrating roots and all clod-level reaching roots. The highest probabilities for shallow and, also, deep penetrations were found for the L-20 treatment. The lowest probabilities were recorded for the L-17 and H-17 treatments. Soil moisture was a significant factor for root deep-penetration into the clods ($P = 0.043$). The effect of bulk density, and the interactive effect of soil moisture and bulk density did not appear significant. Probability of roots to penetrate the clods deeply in certain treatments was linked to the estimated penetration resistance (Figure 3A).

The following root characteristics were compared: diameter of primary roots, branching density of laterals, and lateral root lengths, for root segments 4–6 cm before clods between shallow- and deep-penetrating roots as well as roots avoiding clods. The diameter of clod-avoiding roots (0.94 mm) was significantly higher than for shallow- (0.85 mm) and deep- (0.86 mm) penetrating roots ($P = 0.04$ in both cases). Branching density and lateral root length were not significantly different between root groups.

All root characteristics were analysed according to the specific placement of root segments in relation to the clods and two treatment factors (moisture and bulk density). While soil moisture was a significant factor for root diameter alterations ($P = 0.011$), bulk density was found to be non-significant (Table 2). Distance from a clod influenced the diameter significantly ($P < 0.001$) and there was also a significant interactive effect

Table 1. Root probability (%) for penetrating clods in particular treatments

Type of root-clod contact	Treatment			
	L-17	L-20	H-17	H-20
Shallow-penetrating	11.36 (2.66)	24.86 (3.08)	17.54 (3.74)	20.68 (6.35)
Deep-penetrating	20.20 (5.97)	34.15 (2.81)	10.85 (3.95)	28.25 (6.77)
All penetrating	31.56 (7.61)	59.01 (2.33)	28.39 (7.69)	48.93 (13.12)

See the text for explanation of the codes; standard errors are shown in brackets

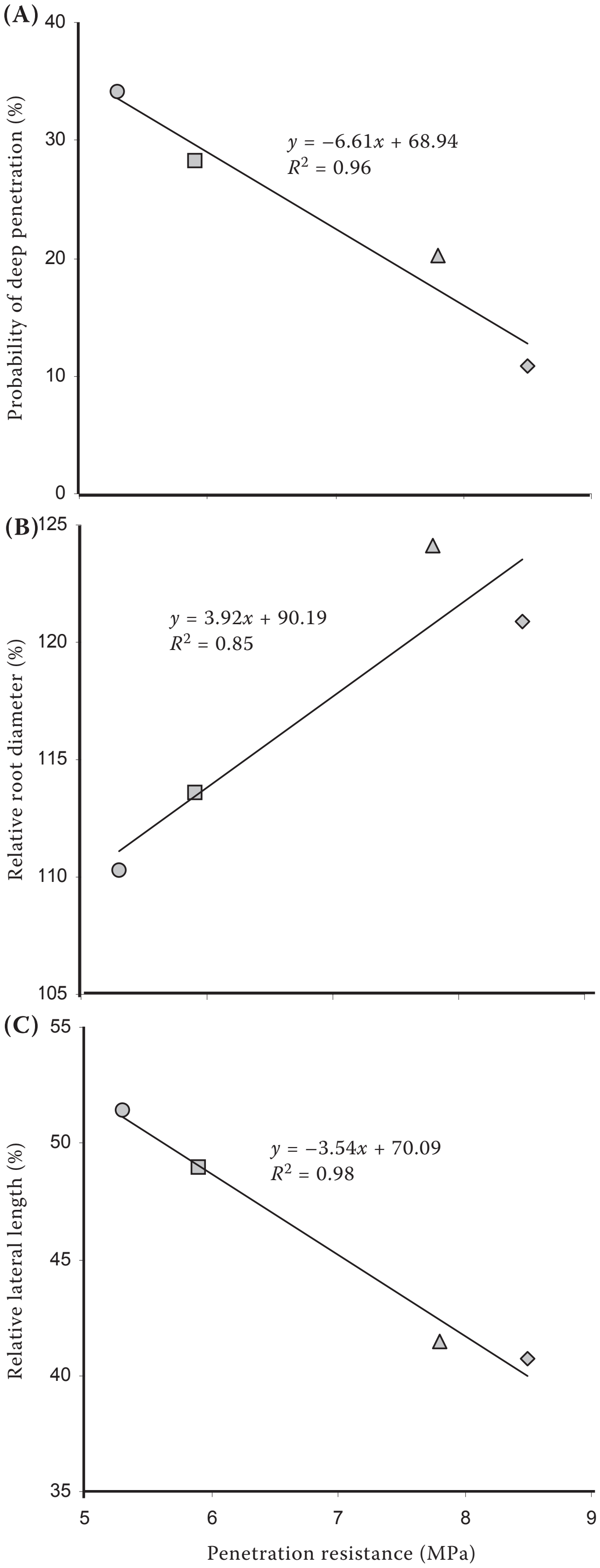

Figure 3. Penetration resistance in the clods versus probability of deep penetration by roots (A), relative root diameter (B), and relative lateral length (C). Circle, square, triangle and diamond indicate treatments L-20, H-20, L-17, and H-17, respectively (see the text for explanation of the codes)

of moisture and bulk density (P = 0.003). Larger effect of clods was found for deep-penetrating roots than for the shallow-penetrating roots (Figure 4). Maximum values of root diameters were found inside the clods. Especially dry treatment caused high peaks in deep-penetrating root diameters. Pooling all treatments together at the root segment 5 cm before the clods was considered as a reference. This showed that diameters of root segments contacting clods directly (clods entering and leaving spots, and the middle of clods) increased whereas root segments after the clods decreased significantly (Table 3).

For branching density, the Three-way ANOVA showed that both soil moisture and bulk density were non-significant (Table 2). Position of root segments influenced the branching density significantly ($P < 0.001$) and an interactive effect of moisture and bulk density (P = 0.019) was also observed. Larger effect of clods was found for deep-penetrating roots than for the shallow-penetrating roots (Figure 5). Maximum branching density was found inside the clods, especially in the H-17 treatment, where a peak in the case of deeply penetrating roots was observed. The branching density decreased significantly on root segments after the clods (Table 3).

Bulk density appeared to significantly alter the lateral root length (P = 0.021); soil moisture and interactions of soil moisture and bulk density were not significant (Table 2). Position of root segments also influenced the lateral root length significantly ($P < 0.001$). Furthermore, a larger effect of clods was found for deep-penetrating than for shallow-penetrating roots (Figure 6). Lateral length of root segments significantly decreased both inside and after the clods (Table 3).

Finally, we tested the relationship between root characteristics and penetration resistance of the

Table 2. Effect of soil moisture (M), bulk density (D), root position (P) and interactive effect of moisture and bulk density (M × D) on root characteristics tested by ANOVA

Root parameter	M	D	P	M × D
Diameter	5.90*	0.45	93.58***	11.33**
Branching density	0.30	2.33	115.42***	5.24*
Length of laterals	0.38	8.24*	108.34***	2.52

F-values are shown; no star – non-significant; *$P \leq 0.05$, **$P \leq 0.01$, ***$P \leq 0.001$

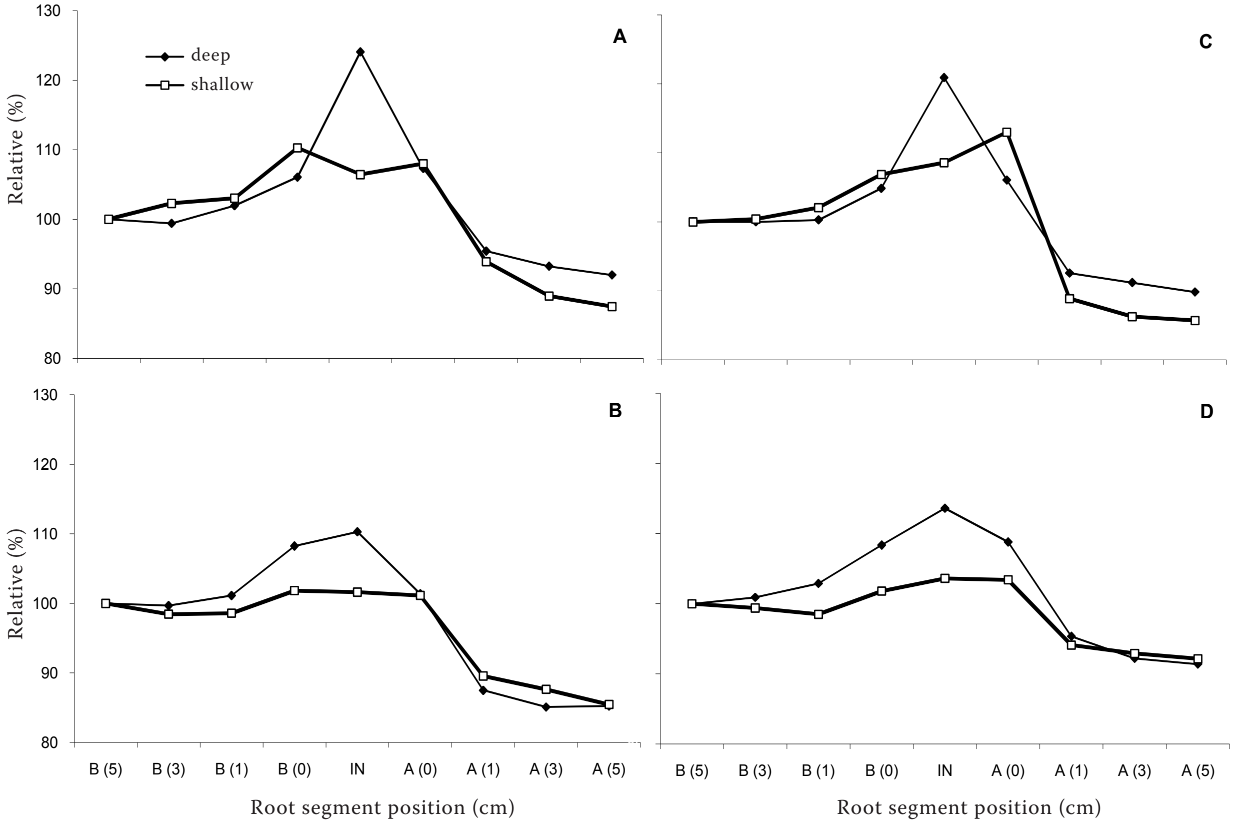

Figure 4. Relative root diameter on root segments at each specific position in the treatments L-17 (A), L-20 (B), H-17 (C), and H-20 (D) (see the text for explanation of the codes)

clods. While branching density did not clearly correlate with penetration resistance, relative root diameter and relative lateral length were sharply linked to penetration resistance (Figure 3B and C).

Table 3. Differences in root characteristics between 5-cm root segment (4–6 cm) before the clod (base equals 100) and other root segments assessed by *t*-test

Root segment	Relative diameter	Relative branching density	Relative length of laterals
B(3) or B(2–4)	99.90	96.15	104.29
B(1) or B(0–2)	102.69	104.56	127.82***
B(0)	107.90***	–	–
IN	113.53***	97.55	70.72***
A(0)	106.74***	–	–
A(1) or A(0–2)	88.76***	70.93***	70.41***
A(3) or A(2–4)	86.19***	68.80***	62.79***
A(5) or A(4–6)	85.85***	62.26***	56.16***

See the text for explanation of the codes; mean values and significance are shown; no star – non-significant; ***$P \leq 0.001$

Hence, relative root diameter increased with penetration resistance, whereas relative lateral length decreased.

For the roots penetrating deeply into clods, a number of bends was calculated (see also Figure 2B). The numbers of bends expressed for 1-cm-long root segment were: 3.71, 4.11, 4.70, and 5.81 for the treatments L-20, H-20, L-17, and H-17, respectively. Soil moisture is the significant factor ($P = 0.017$) influencing this root parameter, since drier compacted soil causes more bends per unit root length than the wetter one.

Soil compaction – root traits controversy

Our results showed that the effect of clod bulk density on mechanical impedance was more important in dry than in wet soil (see also Konôpka et al. 2008). Here, estimated penetration resistance during the processes of passing the clods by roots was between 5.3 and 8.5 MPa. Bengough and Mullins (1990, 1991) proved that penetrometer gives an empirical measure of the strength in the soil, but overestimate the penetration resistance experienced by roots between two and eight. Hence,

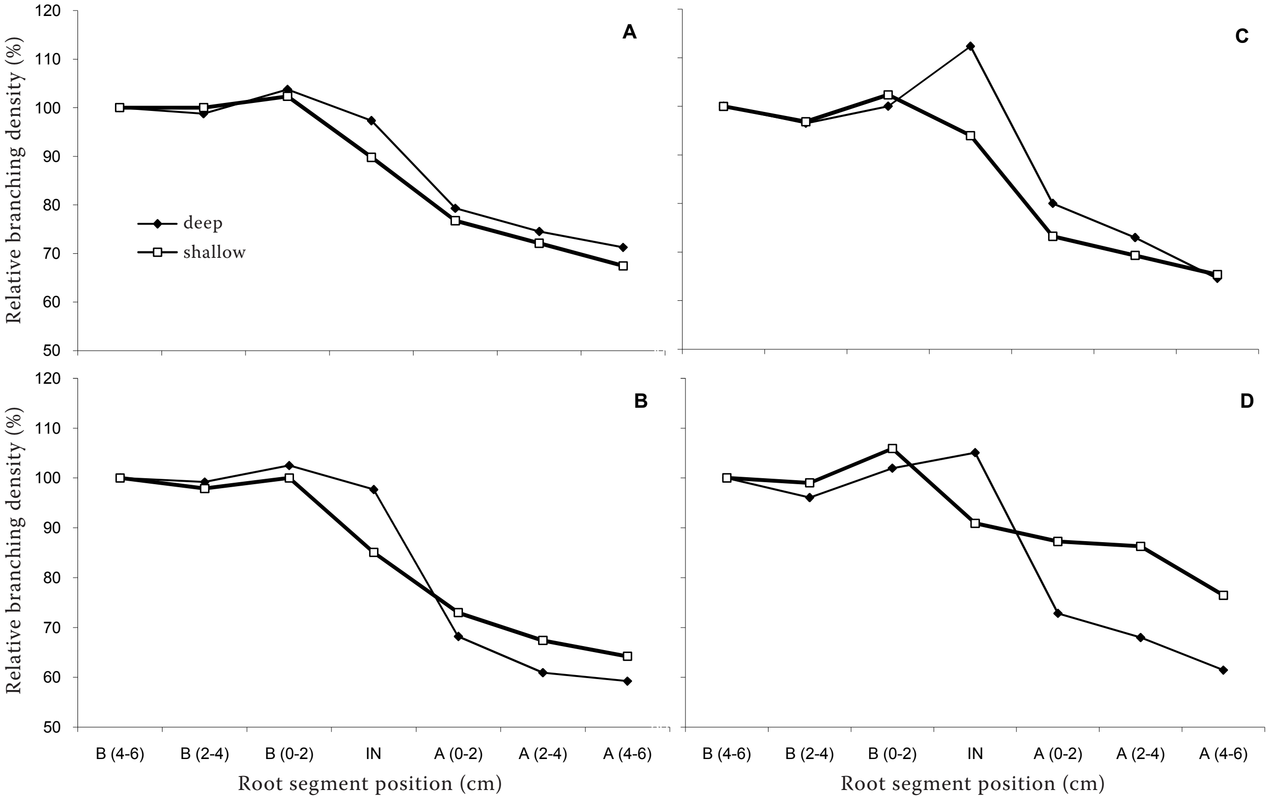

Figure 5. Relative branching density on root segments at each specific position in the treatments L-17 (A), L-20 (B), H-17 (C), and H-20 (D) (see the text for explanation of the codes)

when taking into account the extreme values of the above-mentioned overestimation, the resistance of clods to root growth could range between 0.7 and 4.3 MPa. In the case of the H-17 treatment, the resistance would be over 1.0 MPa even if we admit overestimation by 8 fold. This means that the estimated values of in-clod resistance to roots are close to the upper physiological limits given by some authors for a variety of crops (e.g. Pfeffer 1893, Misra et al. 1986).

Roots penetrating clods had smaller diameters at 5 cm before clods than those avoiding them. Thus, root diameter may be logically explained as a factor influencing ability of roots to enter into clods. Our finding could be supported by the fact that roots confronted with pores smaller than their own diameter cannot decrease their size in order to penetrate them and, usually, even increase in diameter (Wilson et al. 1977). Thus, probably, thinner roots are able to find more easily some pore of an adequate diameter than larger ones. Alternatively, roots with a thinner apex, even using the same force, can induce higher pressure on clod surface than those with a thicker apex.

In our experiment, several root morphological features were influenced by the soil strength constraint: curved main axis or arching root growth trajectory, modified diameter, branching density and length of laterals. In fact, these alterations occurred at different locations relative to the clods. Bennie (1991) explained the increase in the diameter of the mechanically impeded roots via stimulated thickness of the cortex. This is a result of the increase in the diameter of outer cells and possibly also in number of cells per root length unit (Bengough and Mullins 1990, Bengough 2003). Materechera et al. (1992) stated large differences between plant species in the extent to which root diameter vary in response to compaction. They suggested three mechanisms by which the root thickening may aid the penetration into strong soils. These are the resistance of thicker roots to bending and other root properties, the higher axial pressures exerted by thicker roots, and the stress relief at root tips caused by thickening.

Variations in branching density of maize roots due to root segment position relative to the clod were not high (see also Konôpka et al. 2008). One possible reason is that mechanical impedance and aeration could act in opposite directions, depending on soil moisture. Both positive (decreased impedance, better nutrient uptake) and negative (decreased aeration) effects of moisture on

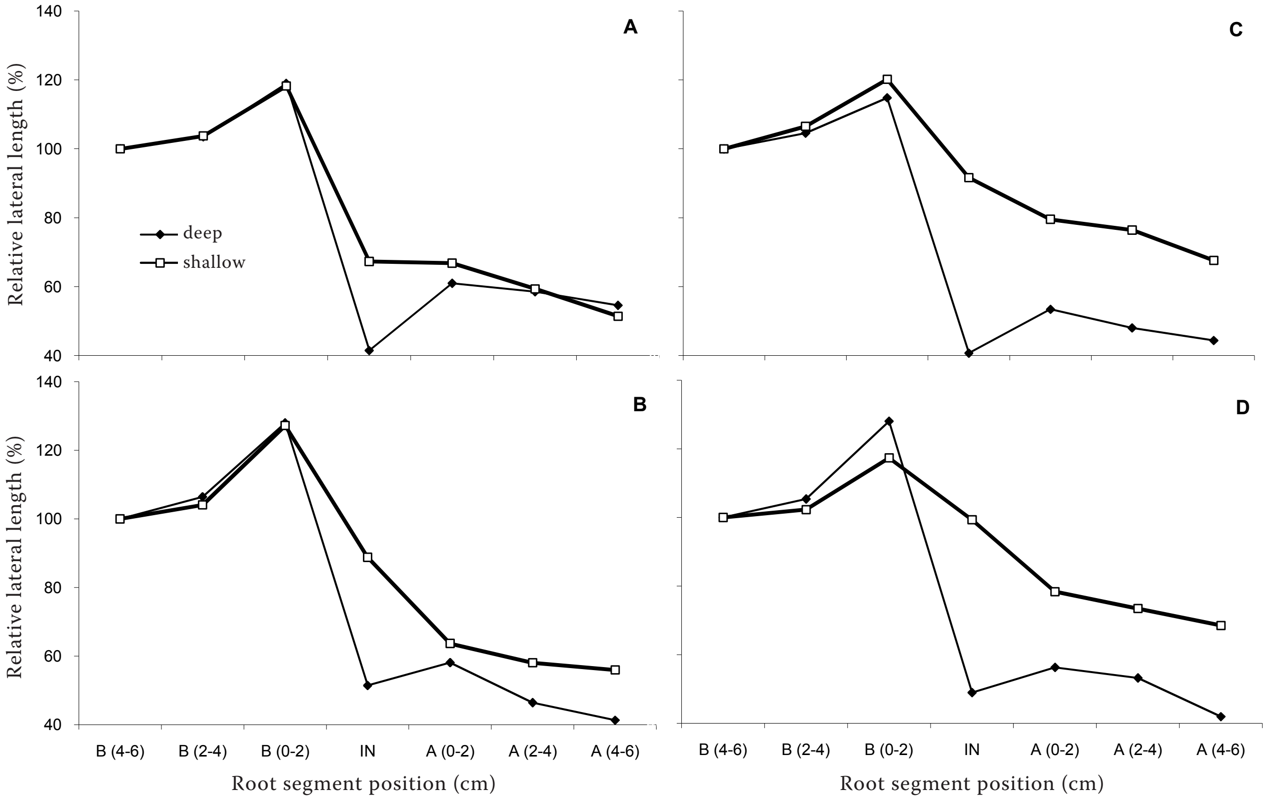

Figure 6. Relative length of laterals on root segments at each specific position in the treatments L-17 (A), L-20 (B), H-17 (C), and H-20 (D) (see the text for explanation of the codes)

lateral root formation can appear. Direction and magnitude of the moisture effect on inter-lateral distances depends on factors such as soil type, level of soil compaction, and distance from clod surface. In general, compacted soils contain less air-filled pores and have a lower level of aeration than fine soil, which may influence root growth and lateral root formation (Liang et al. 1996). The most evident increase of branching density was recorded inside the clods with the harshest conditions (the H-17 treatment). This root reaction has been reported by Barley et al. (1965) in pea and wheat, and by Goss (1977) in barley plants. The phenomenon can be caused by a decrease in final cell length and a consequent shortening of distances between lateral root-forming cells (Croser et al. 1999). Atwell (1988) also mentioned that compaction increases the lateral root number per unit length of the main axis by promoting new lateral root primordia.

As for the decrease in root lateral length inside compacted soil, it may be explained by the mechanical impedance which is parallel to findings on primary roots described by a variety of authors (e.g. Ehlers et al. 1982, Bennie 1991, Iijima et al. 2003). Goss (1977), for instance, showed that the length of lateral roots in barley was reduced by 50% in compacted soil with pores under 50 μm. This slowing of root elongation is associated both with a decrease in final cell length and a slower rate at which new cells are produced and added to the cell files that comprise the meristem (Croser et al. 1999). Moreover, we observed a rather sharp increase in the length of laterals on root segments located just before the clods, which could be explained as compensating growth. Atwell (1988) explained that the inhibition of growth on main axes leads to diminished assimilate demand in the terminal apex and to exploitation of a smaller soil volume by roots, unless lateral root formation provides some compensation.

An interesting and probably new finding is related to the characteristics of root segments located after the clods. Root diameter and branching density clearly decreased compared to the segments just before the clods. Only the relative lateral length tended to "recover" slightly in the case of deep-penetrating roots once these roots emerged on the other side of the clods. Since most previous works focused on responses of roots when penetrating a compacted surface or inside compacted zones, further studies should consider segments growing after compacted zones to confirm or refute our findings.

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Corresponding author:

Dr. Ing. Bohdan Konôpka, Národné lesnícke centrum, Lesnícky výskumný ústav, T. G. Masaryka 22, 960 92 Zvolen, Slovenská republika
phone: + 421 455 314 323, fax: + 421 455 321 883, e-mail: bohdan.konopka@nlcsk.org