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ABSTRACT

Soil compaction heterogeneity and water content are supposed to be decisive factors influencing plant growth. Our experiment focused on simulation of two soil moisture levels (0.16 and 0.19 g/g) plus two levels of clod proportion (30 and 60% volume) and their effects on root and leaf variables of maize (*Zea mays* L.). We studied number of primary and lateral roots as well as primary root length at the particular soil depths. Statistical tests showed that the decrease rate of the number of roots versus depth was significantly affected by the two studied factors ($P < 0.01$). Soil moisture and clod occurrence, interactively, affected leaf biomass ($P = 0.02$). Presence of clods modified root morphological features. Particularly, the diameter of primary roots in the clods was significantly higher than of those grown in fine soil ($P < 0.01$). For primary roots, which penetrated clods, branching density decreased considerably for the root segments located just after the clods ($P = 0.01$). Regarding their avoidance to clods and tortuosity, large differences were found between primary roots grown in the contrasting soil environments.

Keywords: clod proportion; root distribution; root morphology alteration; water content

Influence of the soil environment on plant root growth and development is crucial and has been studied by a number of authors (e.g. Lambers et al. 2007). One of the most important characteristics that determines root spreading within the soil profile is compaction (e.g. Bengough and Mullins 1990, Unger and Kaspar 1994). Soil compaction in agricultural fields, especially caused by the passages of vehicles, can cause important economic and ecological impacts (Soane and Van Ouwerkerk 1994). The repetitive passage of vehicles and tillage lead to the formation of soil clods with different bulk densities, sizes and various proportions of compacted soil zones in the ploughed soil layer. Mainly these soil variables are conditioned by the type of machinery and soil moisture during operation (Richard et al. 1999).

A comprehensive study of the issue was presented by Taylor and Brar (1991) who reported that soil compaction can change the morphology and functioning of plant root systems by a number of mechanisms, not only physical, but also biological and chemical. The studies principally considered only physical aspects of soil compaction as the most relevant factor influencing root growth. Compaction increases bulk density or strength of the soil, which is commonly referred to as its "mechanical impedance", and affects its conductivity, permeability and diffusivity to water and air (Greenland 1977). Ability of plant roots to grow inside the compacted zones is closely related to the mechanical impedance of the soil medium. In some cases, plant roots are able to penetrate compacted soil zones, the environment may however

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modify root traits. The early work by Voorhees et al. (1971) indicated alterations on morphological properties of barley roots grown inside small size aggregates with simulated density between 1.4 and 1.8 kg/l. Furthermore, later results showed reduction of root elongation or variation in diameter and branching density of roots due to high bulk density of soil (Kirby and Bengough 2002).

The soil medium in natural and tilled conditions is heterogeneous, including fine soil, clods, peds (i.e. naturally formed units of soil structure), biopores and horizons with diverse physical structures. As a consequence, mechanical impedance is not evenly distributed and its heterogeneity induces complex influence on root systems, plants, and on crop production. Mechanical impedance of the clods depends mainly on their bulk density and fluctuates with water content (Bennie 1991).

In a review, Unger and Kaspar (1994) concluded that soil compaction decreases crop yields in some years but not in other years. In the current study, we have tested the hypothesis that the aforementioned controversies might be originated from interactions between clod proportions, their distributions and various soil moisture levels.

The main objectives of this paper are therefore: (i) to characterize the influence of soil moisture and bulk density on clod penetration resistance, (ii) to analyze the effect of clod proportion and soil moisture on maize (*Zea mays* L.) at the root, root system, and plant level.

MATERIAL AND METHODS

Soil preparation

Soil preparation was aimed at achieving four different soil environments, combination of two levels of compacted clod proportion and two levels of moisture. The desired proportions of clods were 30% and 60% of the total soil volume, and the soil moistures 16% and 19% of the dry soil weight (i.e. 0.16 and 0.19 g/g). Fine soil was collected in the plough layer of an experimental field at the INRA Research Centre of Avignon, Southern France. The soil used in this experimentation was the topsoil of a Calcosol developed from alluvium with a silty clay loam texture. The soil was composed of 34.1% clay, 53.7% silt, 12.2% sand and chemical analysis gave pH 8.3, CEC 11 cmol/kg, organic N 0.2% and C/N ratio 7.8. During the last decade, the field has been continuously used for growing a variety of agricultural crops, especially pea, sunflower, maize and wheat. The fine soil from the field was prepared by sieving (up to 0.5 cm diameter). The permanent wilting point and the field capacity of fine soil were 0.145 and 0.245 g/g, respectively.

The clods were obtained from the same field, but they were prepared independently from fine soil. Compaction of the soil was obtained by four passes of backhoe loader in the field. The weight of the backhoe loader was 7200 kg. The blocks of compacted soil were collected with a spade and broken by a chisel. 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. The shape of the clods was rather irregular, from ellipsoidal to bean-like shape. Both clods and fine soil were separately wetted with a sprayer to the desired soil moistures: 0.16 g/g (dry treatment hereafter) and 0.19 g/g (wet treatment hereafter) as calculated on a weight basis.

The wetted fine soil and the clods were placed in the pots. The pots consisted of PVC tubes 63 cm long, 19.2 cm inner diameter, and were placed on plastic plates. The soil column in the pots was 60 cm high representing a volume of 17.5 litres. The pots were filled with fine soil and clods, two levels of 30% and 60% of clods proportion from total volume of soil were prepared (procedure on clod volume estimate is explained in "Soil measurements"). For the 30% level, usually 3 or 4 clods were placed in one layer (the thickness was circa 5 cm) and inter-spaces between the clods were filled up with fine soil. Before placing a subsequent layer of clods, approximately 1 cm thick fine soil bed was placed in the pot. To avoid any undesired voids in the soil medium, the pots were gently shaken when pouring the fine soil. For the 60% level, the same procedure was used but inserting a double amount of clods. The combinations of two soil moisture levels and two clod proportions made up four treatments with 7 replicates, which represented a set of 28 pots fully randomized. Hereafter, the codes D-30, D-60 are used for the dry treatments with the clod proportions 30% and 60%, and W-30 and W-60 for the wet treatments with the clod proportions 30% and 60%, respectively.

Growth conditions

The pots were placed in a growth chamber. Air temperature was adjusted to 25 ± 1°C, air moisture 60 ± 5%, photo-period 15 h by day, and light intensity 300 µmol/s. Pre-germinated seeds (3 days in wet peat) of maize variety PR35Y65 were sown in the soil at a depth of circa 4 cm. Water losses via evapotranspiration were compensated by manual irrigation of the soil surface twice a week. Exact quantities of water to be added were established by measuring the soil column weight loss and represented approximately 50 ml per day.

Plant measurements

Leaf number was recorded on all plants every three days. The plants were harvested on day 23 after sowing (i.e. day 26 after seed germination). This harvest was performed at this time because roots reached the bottom of the pots in the wet treatments. Leaves were dried (75°C for 48 h) to obtain biomass quantity. Numbers of primary roots on the plant bases and their originating phytomer rank were recorded. Pots were subsequently horizontally cut into six layers (sub-columns), each 10 cm long. From this point onwards, five soil cross sections at the depths of 10, 20, 30, 40 and 50 cm were considered for further analyses. On these, the numbers of primary and lateral roots were counted. Three soil monoliths of each treatment were used for root biomass studies. In this case, all roots were separated from the soil sub-columns by a gentle wash. The lengths of primary roots were measured with a ruler. All roots were dried at 75°C for 48 h and their dry weights were measured.

Other four soil monoliths of each treatment were used for inspecting the morphological features of roots. In each soil sub-column, two 3 cm-long sections of roots located in the fine soil (outside the clods) were separated and cleaned. Moreover, the root segments placed directly before the clods, inside the clods and directly after the clods were excavated and washed. The diameters and branching densities of all root groups (i.e. placed before, inside, after the clods and in the fine soil) were measured under an illuminated magnifying glass.

Soil measurements

Sixty clods were selected to measure the distribution of bulk density. They were dried at 60°C for 48 h and individually placed in a plastic cylinder with calibrated volume. The cylinder was then filled with homogeneous sand of known bulk density, distributing it equally all around the clods by shaking. The weight of clod, weight of sand and bulk density of sand served for calculating the volumes of the clods, which were then used to calculate their bulk density. A subset of thirty clods was selected for additional measurements of penetration resistance. First, they were wetted at the moistures of 0.16 and 0.19 g/g and the penetration resistance was then 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 of 2 cm inside the clods. Penetration resistance was also measured with the penetrometer on all clods in the cross-sections of soil sub-columns at soil depths of 10, 30 and 50 cm. In addition, soil samples of sub-columns were taken for the measurement of the water content using the gravimetric technique.

Statistical analysis

In order to study the root distribution, we used non-linear modelling with the procedure "nls" of the R statistical package (http://www.r-project.org). For fitting the models, the least squares criterion was used. Embedded models were compared using Fisher tests. Homogeneity of variance and Gaussian distribution of residuals were checked for each variable, including the numbers of roots. Data on leaf development were analysed by estimating a leaf emergence rate on each plant individually (slope of the linear regression number of leaves versus time), and making an ANOVA on the estimated values.

Two-way analysis of variance (ANOVA) was used in order to test the treatment effects, i.e. clod proportion and soil moisture on biomass of roots and foliages, root tortuosity and number of primary roots in the clods. One-way analysis of variance and Tukey-Kramer's HSD test for separation of the means were implemented for testing morphological traits between the primary roots at different position with regard to the closest clod. Results were considered significant when probability values of the test were lower than 0.05. All analyses were performed using the statistical software R (version 2.4.1; Ihaka and Gentleman 1996).

RESULTS AND DISCUSSION

Soil

Considerable differences between fine soil and clod bulk density were observed, reaching mean values of 1.15 kg/l and 1.71 kg/l, respectively. The

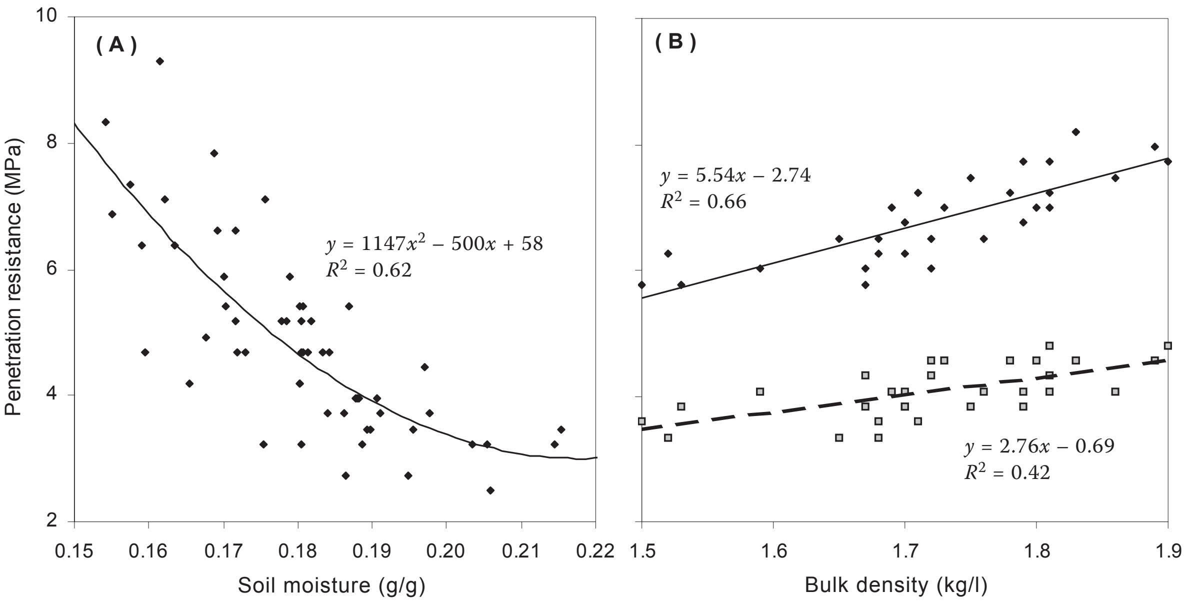

Figure 1. Relation between penetration resistance, soil moisture (A) and bulk density (B) for two moisture levels, i.e. 0.16 (diamonds and solid line) and 0.19 g/g (squares and dashed line)

soil moisture strongly influenced the penetration resistance of the clods (Figure 1A). Substantial changes of the penetration resistance were found, especially when soil moisture was lower than 0.19 g/g. The large variations of the penetration resistance around the regression curve can be explained, in part, by the relationship between the bulk density and the penetration resistance (Figure 1B). Penetration resistance increases with increasing bulk density. In this case, a significantly higher penetration resistance was measured for the soil moisture 0.16 than for that of 0.19 g/g. The slope of the fitting line was significantly steeper in the case of the soil moisture 0.16 g/g in comparison with the soil moisture 0.19 g/g.

Root distribution

Preliminary analyses were made by pooling the root parameters data, first by the soil moisture factor and then by the clod proportion factor. Consequently, separate comparisons of the root distribution parameters into two soil moisture levels and two clod proportion levels were done. Root distribution is presented graphically in Figure 2A–F. All variables showed a decreasing trend versus depth. Moreover, the effects of both treatments can be visually detected on the trend lines. From these curves, the moisture effect is particularly apparent, especially on the number of roots.

Further data analysis (two-way ANOVA with a linear model as a simplification; results not shown) indicated non-significant interactive effect of moisture and clods on root distribution. However, we noticed that distribution of roots over the soil profile was not perfectly linear (Figure 2A–F). Thus, in order to quantify and to test the significance of these treatment effects, exponential models of the following form were used:

$$Y = (a + a_C + a_M) \times \exp(-(\beta + \beta_C + \beta_M) \times D) \quad \text{(model 1)}$$

where: Y denotes the predicted variable (either the number of primary roots, or the number of secondary roots, or the length of primary roots), D denotes depth, a and β are fitted parameters representing the mean effects, a_C, β_C, a_M, β_M are the parameters representing the clod and moisture effects, respectively

The general model fits adequately to the data for the three variables, as shown in Table 1. Significance of the clod and moisture effects was tested by fitting several embedded models corresponding to the null hypotheses: $a_C = 0$, $\beta_C = 0$, $a_M = 0$, or $\beta_M = 0$. These hypotheses have been combined (e.g. $a_C = 0$ and $a_M = 0$).

From these comparisons, based on the Fisher tests, the best models were as follows:

$$Y = a \times \exp(-(\beta + \beta_C + \beta_M) \times D) \quad \text{(model 2)}$$

for the number of roots (both primary and secondary), and:

$$Y = (a + a_M) \times \exp(-(\beta + \beta_C + \beta_M) \times D) \quad \text{(model 3)}$$

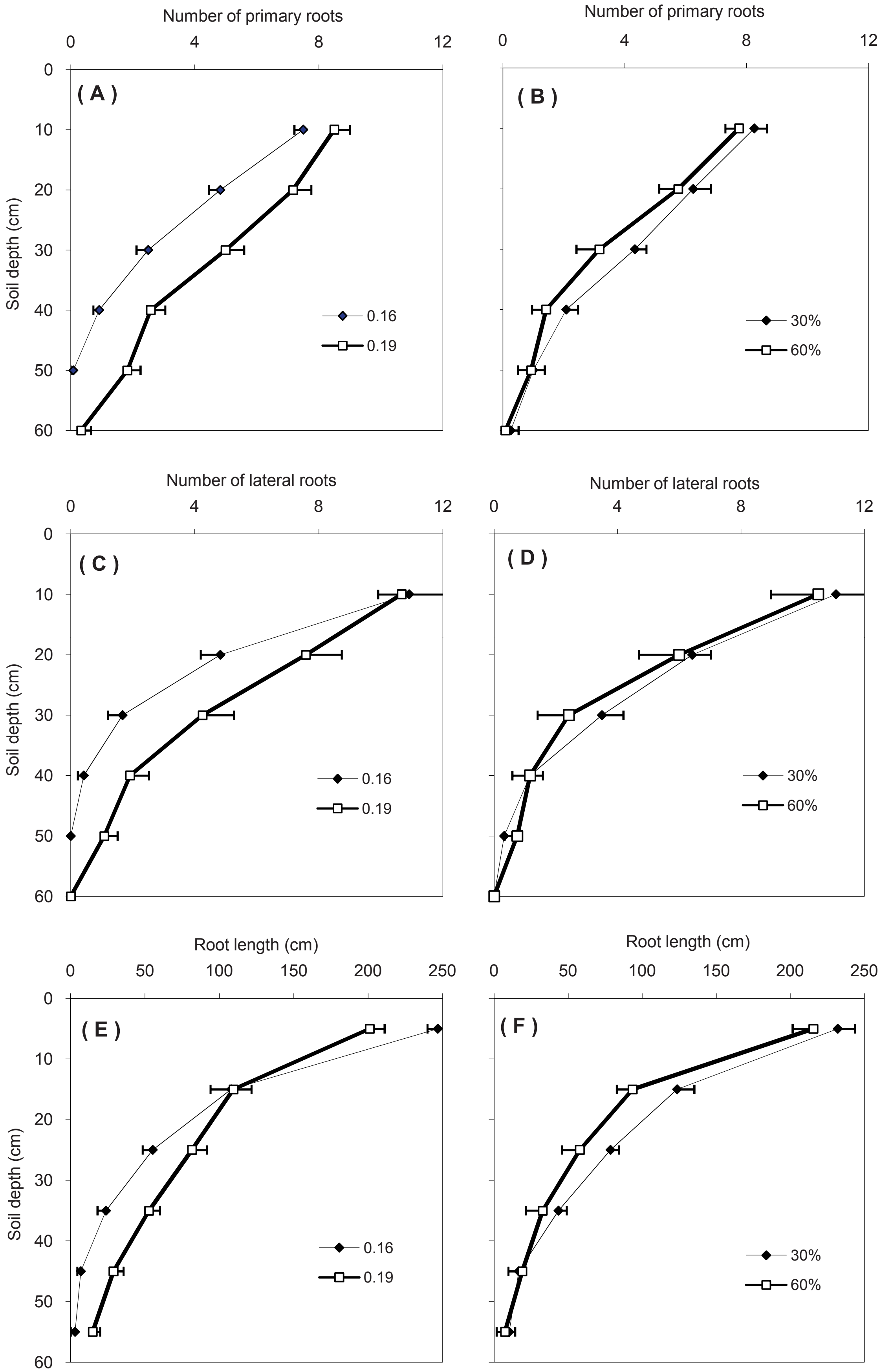

Figure 2. Comparison of number of primary roots (A and B), number of lateral roots (C and D) and primary root length (E and F) along the soil profile. Pooled means for two moisture levels (A, C, E) and two levels of clod proportion (B, D, F) together with standard errors are shown

Table 1. Comparison of embedded models (models 1–3) for number of primary and secondary roots, and primary root length plants along the soil profile using the Fisher tests. Analysis of variance results for number of primary roots (NPR), number of lateral roots (NLR), and primary root length (PRL) are shown

Equation of model	Residual degree of freedom	Residual sum of squares	*F*-value	*P*-value
NPR = a	119	1166	–	–
NPR = $(a + a_C + a_M) \times \exp(-(\beta + \beta_C + \beta_M) \times D)$	142	255	81.47	~0***
NPR = $a \times \exp(-(\beta + \beta_C + \beta_M) \times D)$	116	257	0.352	0.704
NLR = a	119	2755	–	–
NLR = $(a + a_C + a_M) \times \exp(-(\beta + \beta_C + \beta_M) \times D)$	114	951	43.24	~0***
NLR = $a \times \exp(-(\beta + \beta_C + \beta_M) \times D)$	116	981	1.822	0.166
PRL = a	71	424, 458	–	–
PRL = $(a + a_C + a_M) \times \exp(-(\beta + \beta_C + \beta_M) \times D)$	66	22, 500	235.82	~0***
PRL = $(a + a_M) \times \exp(-(\beta + \beta_C + \beta_M) \times D)$	67	22, 534	0.102	0.751

***$P \leq 0.001$; no symbol means non-significantly different

Table 2. Parameters of the retained models for number of primary roots (NPR; model 2), number of lateral roots (NLR; model 2), and primary root length (PRL; model 3) along the soil profile. For explanation of the parameters see the text

Parameter	Estimate	SE	*T*-value	*P*-value
NPR				
a_0	13.157	0.731	17.997	~0***
β	0.034	0.003	11.237	~0***
β_C	0.005	0.003	1.802	0.074
β_M	0.020	0.003	6.022	~0***
Residual standard error: 1.487 on 116 degrees of freedom				
NLR				
a_0	20.750	2.084	9.957	~0***
β	0.055	0.007	7.993	~0***
β_C	0.003	0.002	1.743	0.096
β_M	0.016	0.006	2.586	0.011*
Residual standard error: 2.909 on 116 degrees of freedom				
PRL				
a_0	323.4	19.090	16.939	~0***
a_1	216.9	40.020	5.420	~0***
β_0	0.045	0.003	13.788	~0***
β_C	0.008	0.003	3.232	0.002**
β_M	0.030	0.006	5.208	~0***
Residual standard error: 18.34 on 67 degrees of freedom				

***$P \leq 0.001$, **$P \leq 0.01$, *$P \leq 0.05$; no symbol means non-significantly different; SE – standard error

for the length of primary roots. The fitted parameters are shown in Table 2.

In addition, in order to confirm these results, another model was fitted, specifically:

$$Y = a_i \times \exp(-\beta_i \times D) \qquad \text{(model 4)}$$

on each individual *i*, for the variable number of primary roots and number of secondary roots. An analysis of variance with two factors (clod proportion and soil moisture) was performed on the estimated parameters a_i and β_i. This ANOVA confirmed that both factors have a significant effect on the decrease rate β_i but none have an effect on a_i (data not shown).

These tests showed that the decrease rate of the number of roots versus depth was significantly affected by both studied factors, i.e. clod proportion and soil moisture. The parameter values and residual sum of squares show that soil moisture had a stronger impact than clod proportion. Drought and clods decreased the rooting depth. Conversely, these two factors did not influence significantly the superficial number of roots.

Regarding primary root length, the results are rather similar, excepted that an effect of soil moisture on the superficial value of root length occurred. In addition to the previous effects, the drought tended to increase root length in the superficial layer.

The primary roots penetrated the clods most frequently in the top 10 cm of the soil (Table 3). Few primary roots grew through the clods at 10–20 cm depth, and no roots inside the clods were found in

Table 3. Number of primary roots in clods subjected to the treatments. Standard errors are shown between brackets

Soil depth (cm)	Treatment including soil moisture (g/g) and proportion of clods (%)			
	0.16 and 30	0.16 and 60	0.19 and 30	0.19 and 60
0–10	1.33 (0.33)	1.76 (0.33)	3.00 (0.58)	4.33 (0.33)
10–20	0	0.33 (0.33)	1.00 (0.58)	1.33 (0.33)

Table 4. Tortuosity of primary roots subjected to the treatments. Standard errors are shown between brackets

Soil depth (cm)	Treatment including soil moisture (g/g) and proportion of clods (%)			
	0.16 and 30	0.16 and 60	0.19 and 30	0.19 and 60
0–10	2.31 (0.02)	2.36 (1.14)	1.78 (0.02)	1.66 (0.07)
10–20	1.79 (0.16)	1.53 (0.23)	1.36 (0.12)	1.32 (0.01)

the depth of 20–60 cm. In both upper soil layers, the highest number of such primary roots was counted in the W-60 treatment and the lowest one in the D-30 treatment. Two-way ANOVA showed a significant effect of soil moisture on the number of roots inside the clods for both soil layers (P = 0.008 and P = 0.019 for 0–10 cm and 10–20 cm, respectively). No significant effects of clod proportion and, also, no interactive effects of water content and clods on the number of primary roots in the clods were found.

Morphological traits of roots

Tortuosity of the primary roots was calculated as an expression of the real root length in the 10 cm-thick soil layer divided by its thickness (Table 4). In soil layers 0–10 and 10–20 cm a significant effect of soil moisture (P = 0.026 and P = 0.042, respectively), but no effect of clods and no interactive effect of moisture and clods on root tortuosity were found.

In principal, the presence of the primary roots in the clods increased root diameter (Figure 3A). Primary root segments in the fine soil outside the clods (before and especially after clods) presented lower diameter values than those inside the clods. Significant differences (P = 0.008) were found between the primary root diameters inside the clods (1.01 mm) and those grown in the fine soil completely outside the clods (0.79 mm). The opposite situation was observed for the branching density of lateral roots (Figure 3B). The maximum value (7.21 cm^{-1}) was recorded for the primary roots grown in fine soil while the minimum value (5.18 cm^{-1}) in the roots penetrating the clods, particularly for the segments located just after the clods (significant differences were found between the aforementioned values; P = 0.010).

Leaves and the whole root system

After 26 days of growth, there were no significant effects of neither water content nor clods on below-ground (roots + hypocotyl) dry mass (Figure 4). On the other hand, more remarkable differences were found for leaf biomass. In this case, the significant alterations were not only due to soil moisture (P = 0.026) but also to interactive effect of moisture and clods (P = 0.018). The leaf biomass in W-60 in comparison with that of the D-60 was as much as twice larger. The root-shoot ratio tended to increase due to dry treatment (0.14 g/g) and decrease with wet treatment (0.10 g/g).

As for leaf kinetics, leaf emergence versus time is presented in Figure 5. The number of leaves increased linearly with time, showing that the leaf emergence rate was nearly constant over the studied period. This rate appeared to be slightly affected by soil moisture, but not by the proportion of clods. The results from ANOVA confirmed the significant effect of soil moisture (P = 0.040), and the non-significant effect of the proportion of clods. In addition, no interaction between these factors was detected.

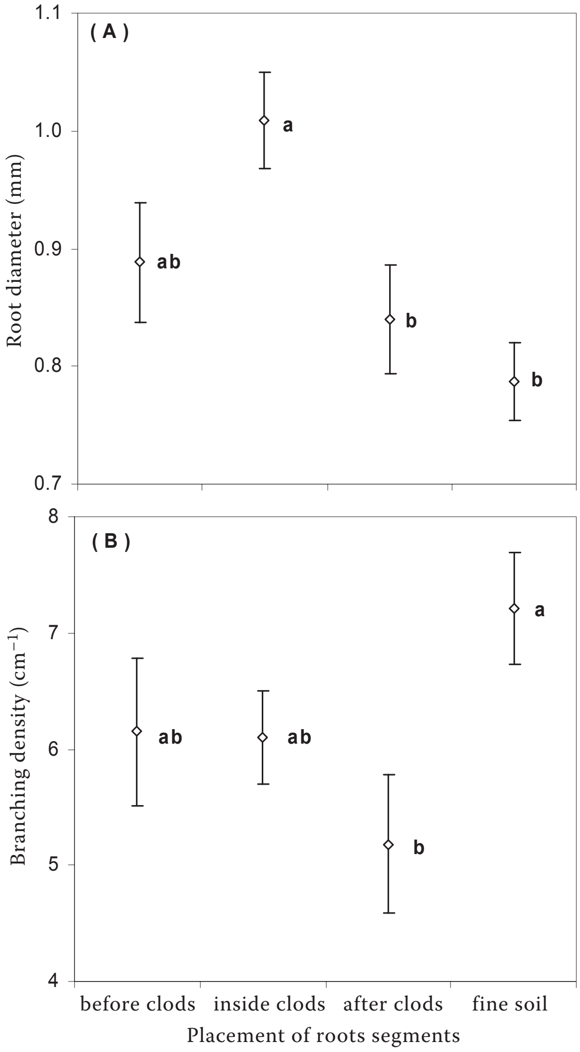

Figure 3. Diameter (A) and branching density (B) according to location of primary root segments: just before clods, inside clods, just after clods, and in fine soil. Error bars conform to standard errors; different letters denote significant differences ($P \leq 0.05$)

Root distribution dispute

Statistical analyses showed that both soil moisture and proportion of clods affected significantly the decrease rate on number of primary and lateral roots along the soil profile. Moisture influenced number of roots more clearly than proportion of clods. We found that higher soil moisture stimulated the primary root length at soil depth of 20–60 cm that coincides with trend in the number of roots in the soil layers. The opposite tendency was observed in the topsoil, which might be effect of a more straight vertical trajectory of primary roots in wet soil. These results are consistent with many works on a variety of agricultural crops which showed that soil compaction and/or dry soil retard the root development and delay its occurrence in deeper soil layers (e.g. Ehlers et al. 1982, Steen and Håkansson 1987). Sharp decrease of root elongation rate with increase of soil strength, particularly between 0.5 and 3.5 MPa, was shown for instance in maize, cotton, wheat, groundnut plants (Bennie 1991) and pine seedlings (Zou et al. 2001). It is likely that decreased depth of crop rooting and root extension due to clod occurrence can considerably limit the access to water and nutrient resources in the soil.

Some primary roots penetrated the clods in the top 10 cm of the soil and few also in the soil depth of 10–20 cm. No roots inside clods were found in the deeper soil depths. This is logically connected to the high root density in the topsoil and probably also to their limited possibility of avoiding the clods in the top layers, which were just near the originating phytomer. Results indicate that primary root avoidance of clods was specific in different soil environments. For instance, a number of primary roots in clods on the wet treatment as much as 2.4 times higher than that of the dry treatment was observed at soil depth of 0–10 cm despite the clod proportion. Approximately 1.4 times more roots were inside clods in the case of the high clod proportion in comparison with the low clod portion

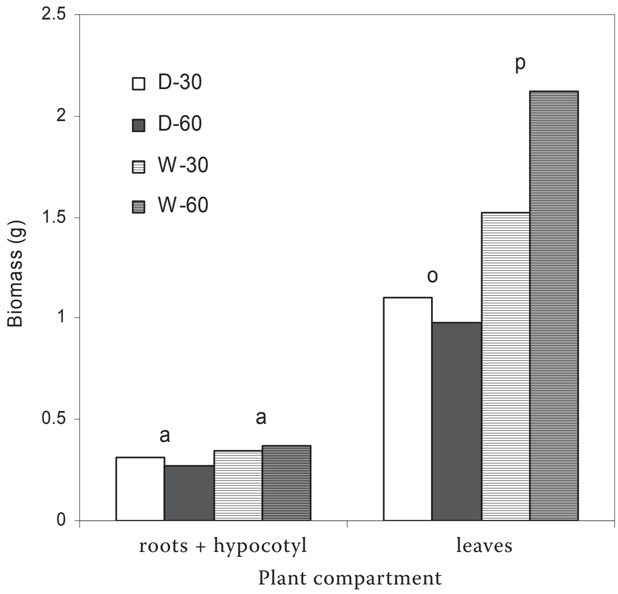

Figure 4. Biomass of plant compartments in the maize plants subjected to the particular treatments. The different letters indicate differences between the wet and dry treatment ($P \leq 0.05$). The letter "a" conforms to the below-ground biomass, "o" and "p" to the leaf biomass. See the text for explanation of the treatment codes

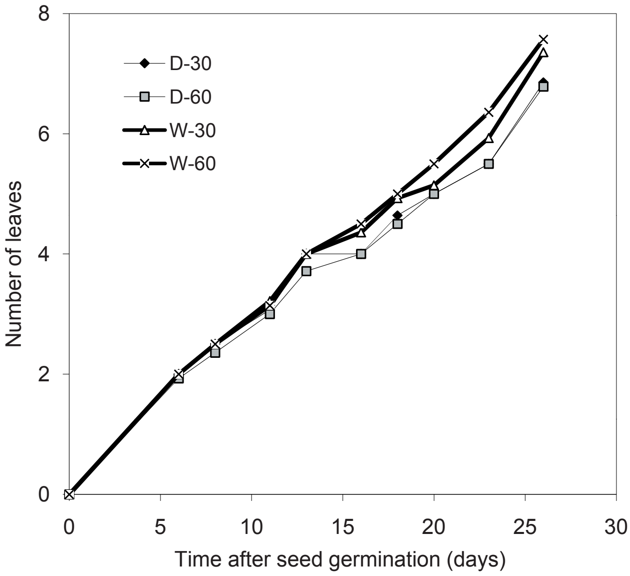

Figure 5. Development of the leaf number with regard to the treatments expressed in days after the seed germination. See the text for explanation of the treatment codes

level whatever the moisture level. Double proportion of clods in the soil should theoretically result in doubled number of primary roots penetrating the clods. However, we detected only 1.4, which suggests higher avoidance of roots to clods in the soil with the larger proportion of clods.

Root morphology dispute

Soil moisture influenced the tortuosity of primary roots in the topsoil. Roots in the dry treatment had longer trajectory than in the wet treatment while crossing the upper 10 cm-thick soil layer. This is logically linked to the fact that while some roots in the wet treatment penetrated the clods and got through them, the roots in the dry treatment had greater difficulty to penetrate the clods and, probably, their trajectories followed the surface of the clods.

In our experiment, the diameter of primary roots tended to increase due to the penetration of the clods. The segments of primary roots just after the clods showed significantly smaller diameter in comparison with the segments in the clods. Similarly, the roots grown outside clods (in the fine soil) manifested significantly smaller diameter in comparison to those in the clods. In fact, roots confronted with pores smaller than their own diameter could not decrease their size in order to penetrate into them and usually even increased in diameter (Wilson et al. 1977). This radial expansion may cause a reduction in mechanical impedance ("wedging" effect) and a consequent weakening of the soil in advance of the root tip (Hettiaratchi 1990). Radial expansion of the roots is a frequent phenomenon in case of contact between the root cap and an obstacle (Goss and Russell 1980). Bengough and Mullins (1990) explained the increase in diameter of the mechanically impeded roots by an increasing thickness of the cortex.

Results showed that the highest branching density was for the roots located in the fine soil away from the clods. The contact of primary roots with the clods lowered the branching density, especially in those root segments located just after the clods. The decrease of the branching density on the root segments just before the clods could probably be influenced by the stress on the root cap and the meristem (Bengough and Mullins 1990). The results of soil compaction on the branching density are inconsistent in the literature. For instance, Atwell (1988) found no effect of soil compaction on the lateral root density for lupins. More lateral roots per unit length of main axis were found for pea, wheat (Barley et al. 1965) and barley (Goss 1977) grown in the impeded treatment, as compared with the unimpeded. However, the total number of laterals decreased significantly for barley grown in the compressed soil. Thus, total lateral production decreased by mechanical impedance, even though the density on main root axes become higher (Goss 1977). Lowered length of both primary and lateral roots due to soil compaction can have serious physiological consequences, especially nutrient and water depletion in the zone around roots (Bengough 2003).

Plant level responses dispute

The parameters of above- and below-ground parts of maize have been recorded in order to evaluate the integrated impact of the treatments on the whole-plant development. Soil water content affected more leaf than root mass. For instance, root biomass was larger by ¼ but the leaf biomass by ¾ if comparing wet and dry treatment. This fact is consistent with the knowledge that shoots are more sensitive to growth inhibition by low water content than roots (e.g. Kang et al. 2000). An important finding is an interactive effect of soil moisture and clod proportion on leaf biomass. Thus, the largest amount of leaf biomass was recorded for maize in wet soil with higher clod proportion.

This might be a consequence of the combination of a good root-soil contact and water supply. The phenomenon is probably not related to situation in the primary roots only but also in lateral roots, which can find optimum conditions on the clod surface (possibly also inside them) with high water content. The lowest biomass of leaves was found in dry soil with the higher proportion of clods. Likely, positive or negative consequences of high portion of clods on plant growth depend on water quantity in soil. From an agronomic point of view, this means that the high impedance problem of clods can be alleviated, and thereby, crop production would be increased by the regulation of water regime in the soil with a proper irrigation system. A reduction in the number of leaves, their length and biomass in maize plants due to decreased water availability in the soil was shown previously in the literature (e.g. Pelleschi et al. 1997). However, information related to combined effect of soil moisture and clods on leaf biomass was missing for maize plants.

The work supposed a step forward in evaluating this influence and in testing ideas on how to integrate soil structure and water content in the modelling of the root system architecture and plant growth under field conditions.

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