Growth kinetics at early stages of sunflower (*Helianthus annuus* L.) under soil compaction.

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ABSTRACT

- Due to sunflower importance (*Helianthus annuus* L.) in the French context, the emergence of soil compaction in the French South West (main productive area) represents a determinant issue. Sunflower production takes place throughout complex interactions between genotype, crop management and environment. Sunflower rooting depth is strongly related to structural behavior and gravimetric water availability.
- The aim of this work was to study how soil compaction and its interactions with soil water content act on sunflower root and shoot growth and growth rate.
- A destructive experiment in controlled conditions was implemented in pot, with the aim of determining the consequences of soil compaction in interaction with water management on sunflower root and shoot system growth. Six treatments were tested which was the combination of 3 level of soil compaction (C1: 1.03 g.cm⁻³, C2: 1.19 g.cm⁻³, C3: 1.31 g.cm⁻³) and two level of soil water gravimetric content (H1: 21.7%, H2: 30.3%). Strong modifications on root exploration, architecture and growth were reported under low and high compactions depending on their water regime, at each stage sampled and among the time. This negatively acted on resources uptake and use efficiency. Modifications on the above ground part of the plant through plant water and nutrients uptake, plant growth indicators, biomass production and leaves growth kinetics were also observed.
- Those modifications were the direct and indirect consequences of soil structural changes and water regimes, and could have acted simultaneously or not.
- Soil compaction and water management have been studied in many crop under control conditions, but only few studies have been carried out in sunflower, only one dealing a kinetic aspects, and none involving fine root study. The alterations of below and above ground systems were quantified in order to propose an allometric model of root growth and exploration thought root length and root branching.

Key words: Sunflower, soil compaction, water management, root system, shoot growth, allometric model.
INTRODUCTION
From sowing to floral initiation, root system is the main plant resources sink, feeding the above ground system, which allows a suitable growth. Sunflower rooting depth is strongly related with the soil water availability, which constitutes with nutrient availabilities the main growth limiting factors (Merrien and Milan, 1992). Sunflower root system is characterized by a tap root and secondary order root, their growth depends on soil chemical (water and nutrient availability, anoxia) and physical constraints (mechanical constraint, temperature). Contrary to many crop, the sunflower root system is very efficient in water uptake, specifically from soil depth (the tap root can reach 2 m depth, (Connon and Saddras, 1992)). During the crop cycle, 95% of sunflower root system is contained in the first 40 cm of soil depth (Sadras et al., 1989), and the contact with the soil matrix is strongly linked with soil bulk density (Lipiec and Stepniewski, 1995).
The negative impact of soil compaction on root growth has been studied in many areas, for many crops (Bengough et al., 2006; Saddras et al., 2005). Only few studies has been reported on sunflower especially in controlled condition (Rosolem et al., 2002); and only one including a kinetic description (Andrade et al., 1993). Cropping sunflower under soil compaction, in field and in controlled conditions, results in a decrease of root length from 10% to more than 80% (Heidari Soltanabadi et al., 2008; Rosolem et al., 2002), of 40% of root growth and of 35% of root biomass (Petcu and Petcu, 2006), with an associate increase of root diameter in the top soil and in depth. Those modifications lead to an alteration of root system exploration, which have strong and negative influence on the above ground system functioning (Sadas et al., 2005). Thus, decreases of plant growth have been reported, -12% of plant height (Petcu and Petcu, 2006), -25% of leaf extension (LE) and -65% of leaf area surface (LAI, (Andrade et al., 1993)). Those events are associated with resulting decreases of yield up to 68% (Diaz-Zorita, 2004), oil content (Petcu and Petcu, 2006), and phenological delay all along the crop cycle (Sessiz et al., 2008). An experiment was implemented in controlled conditions with the aim of determining the consequences of soil compaction on sunflower root and shoot system growth. Since the soil compaction is strongly linked with the soil water content, the hypothesis tested was: soil compaction and its interactions with soil water content act negatively on sunflower root and shoot growth and growth rate.

MATERIAL AND METHOD
The trial was set up in controlled conditions on the experimental station of INRA (Auzeville Tolosane, Midi-Pyrénées, FRANCE, UMR AGIR 1248). Those treatments were the combination of i) three compaction levels, C1 low compaction, C2 medium compaction, and C3 high compaction; ii) and two water regimes, H1 hydric constraint (soil water gravimetric content, 0c, maintained between 70% of field capacity (Fc) and wilting point (Wp); and H2 no hydric constraints (soil water gravimetric content maintained over 50% of Fc). The design used was a complete randomization design, four plants replicated per soil treatment per date of sampled; in addition 2 plants replicated by soil treatment were implemented as control pots. The experiment was destructive. Four sample date were defined: B1, B4, B8, B10. Each sampled date was estimated using Maertens and Bosc sunflower root growth rate (1981). According to their observation stage B1 correspond to the maximum root system growth rate. The soil used was a Mollic Udifluvents soil sampled in 30 cm depth of a field of INRA experimental farm (Clay: 34.0 %, Silt: 36.3 %, Sand: 25.2 %, pH: 8.5, CaCO3: 0.4 %, SOM: 1.17, Fc: 35.32 % and Wp: 20.7%), air dried and shifted in a 5 mm grid before the experimentation. The soil compaction was realized in each pot (PVC tube), by adding pre-known soil weight and by pressing soil trench of 0.25 m height with a hydraulic pump. The compaction management was monitored by weighing pots after compaction process, and by calculating bulk density (BD) at the end of the experiment. For each treatment, soil gravimetric water content (0c) adjustment was carried out by soil trench at the same time as soil compaction. During the experimentation, the water management was monitored by i) weighting a sample of 12 randomized pots (2 per soil treatment) each two days; ii) and using probes on control pots dedicated to soil measurements. The 0c was adjusted by direct water addition. The temperature in the greenhouse was maintained at 25°C/20°C, the mean air moisture was 59%, and a 14/24h photoperiod was carried out for all the experiment. The cultivar used was MELODY (half late, Syngenta Seeds SAS). The sowing was done directly on April the 12, 2010. Leaf area surface (LAI) was determined using Casadebaig (et al., 2008). Leaf emergence rate traduced the rate of leaf appearance for (NEL, leaves > 4cm length). Shoot and root parts were sampled at four consecutive stages: A1; B1; B5; and B10. The root systems were obtained by a first cleaning on a 2 mm grid then the roots were put in three consecutive bath of water. Each root system was photographed; cleaned (GIMP 2.6), and analyzed (Winhizo® 2009a, Régent Instruments Canada). Data obtained were: root length (cm) and number of forks (root branching). The dry matter was obtained by organs at 65°C during 72h. Data were analyzed using analyze of variance with
RESULTS

Despite the homogenous irrigation protocol and because of soil structural modifications due to soil compaction and soil characteristics, the level of soil gravimetric water content was not homogenous inside the both levels H1 and H2. Thus, at the beginning of the experiment the soil treatments were: i) C1H1, BD : 1.02 g.cm⁻³, 0c: 17.2 %; ii) C1H2, BD : 1.04 g.cm⁻³, 0c: 24.8 %; iii) C2H1, BD : 1.18 g.cm⁻³, 0c: 25.5 %; iv) C2H2, BD : 1.21 g.cm⁻³, 0c: 30.8 %; v) C3H1, BD : 1.32 g.cm⁻³, 0c: 22.4 %; vi) C3H2, BD : 1.30 g.cm⁻³, 0c: 35.2 %. The drought stress situations were then composed of C1H1, C1H2 and C3H1. During the experiment, an increase of soil bulk density (BD) with soil depth was observed for each soil compaction modalities (P<0.001) for H1 and H2, however the ranking was conserved (C1<C2<C3).

Under low compaction the hydric constraint had a strong negative effect on root growth. Among all soil treatments, H1 presented the lowest values of root length (-44% at stage B10, 750 degrees.days⁻¹ base 4.8°C since the sowing, P<0.05), and number of forks (-53% at stage B10, P<0.05); while H2 presented the highest (P<0.05, figure 1). At stage B10, low compaction without hydric constraint (C1H2) presented a significant higher root length and number of forks than all the other treatments (P<0.001), while the lower root length and number of forks were observed under low compaction with hydric constraint (C1H1). Under medium compaction, the hydric constraint had a negative effect at the same stage (C2H1); while a positive effect of hydric constraint was reported under high compaction (C3H2).

Leaf indicators (LAI, LE, NEL) presented significant differences at each stages of measurements. At stage B10, the ranking observed was the same for LAI, LE and NEL (P<0.001). The highest LAI rate was reported under C2H2 (at stage B10, LAI: 1.2 m².m⁻², P<0.001, figure 1) while the lowest value was observed from stage B2 to B6 for C1H1 (at stage B6, LAI: 0.19 m².m⁻², P<0.001); then at stage B8 for C3H2 (LAI: 0.46 m².m⁻², LE: 0.10m².days⁻¹, 613 degrees.days⁻¹; P<0.001). The highest NEL was observed under C1H1 and C2H2 depending of the stage, while the lowest was observed C3H2t (P<0.001). The hydric constraint had a negative impact on LAI and NEL on C1 and C2 compaction (respectively at stage B10, -19% of LAI for both, -13% and -2% of NEL P<0.001), while a positive effect was observed under C3 (at stage B10, +8% of LAI, +6% of NEL P<0.001).

Root and leaves biomass rate presented the same ranking between soil treatments. The highest values were observed under C2 (at stage B10, leaves biomass: 15 g, root biomass: 5 g, P<0.001). The lowest values were observed under C3 with and without hydric constraint (P<0.001). The hydric constraint had a negative impact on leaves and root biomass under C1 and C2 compaction (at stage B10 under low compaction: -33% of leaves biomass and -39% of root biomass; under medium compaction: -29% of leaves biomass and -31% of root biomass comparing to H2, P<0.001). Under C3 compaction, it had a positive impact on leaves biomass (up to +69% at stage B5 comparing to H2), but not on root biomass where no differences were observed.

The existing relations between i) root length (TRL), ii) number of forks (TRB), and soil, climatic and shoot growth traits of all stages were computed in equation 1 and 2; by integrating TRL (equation 1) and TRB (equation 2) with 0c, BD, GDD, and LAI through a non multiple linear regressions model. The traits explained (TRL and TRB), and the explaining traits (0c, BD, GDD, and LAI), were chosen according to the literature (Montagu et al., 2001; Sadras et al., 1989). The correlation matrix showed that LAI had the major impact on TRL and TRB (R²: 0.94, and R²: 0.92, respectively), just before GDD (R²: 0.88, and R²: 0.87, respectively, correlation matrix not shown). The correlation matrix showed also strong correlation between LAI and GDD (R²:0.87), medium between 0c and BD (R²: 0.55), and lowest between 0c and LAI (R²:0.20).

\[ TRL = 2498.2 + BD (-2655.51 + 994.42 \cdot BD) + 0c (-16+0.55 \cdot 0c) + LAI (-3139.22 + 3199.22 \cdot LAI) + GDD (-4.76 + 1.13 \cdot GDD) \]
\[ R^2: 0.97, \text{RMSE: 286.45}. \]

\[ TRB = 12555.02 + BD (-16201.17 + 5736.75 \cdot BD) + 0c (76.46 – 0.58 \cdot 0c) + LAI (-17371.70 + 15988.65 \cdot LAI) + GDD (-16.92 + 0.05 \cdot GDD) \]
\[ R^2: 0.95, \text{RMSE: 1544.1}. \]
DISCUSSION

Plant root systems have to dispose of an important phenotypic plasticity in order to react to the heterogeneity of the situations faced. As observed in our experiment, important alterations of the root system have been observed under soil compaction: -13% of root length (Heidari Soltanabadi et al., 2008, in field conditions), -40% of root surface (Petcu and Petcu, 2006, in field conditions). In the present experiment, medium soil compaction presented the optimal situation for root architecture and growth rate, especially under good water conditions. Under low compaction without hydric constraint the root architectural and growth rate showed a strong acceleration from stage B8, traducing the ability of root system to grow easily under no mechanical soil constraint without lack of resources required. In parallel, under water limitation in low compaction the root system did not have ability to grow, traducing both the lack of contact with the soil matrix allowing the necessary water and nutrient feeding. Under low compaction (BD: 1 g.cm$^{-3}$), Goodman (Goodman and Ennos, 1999) observed an increase of root biomass, and branching. This has been observed in our experiment only in favorable water condition under C1 (mean of BD: 1.03 g.cm$^{-3}$). Root elongation is possible only if the root pressure is superior to the soil mechanical constraint pressure. Under high soil compaction, the root system growth and exploration was greater under water limitations than under no water constraint. The soil of the experiment is mainly composed of silt and clay which can induce anoxia conditions in depth under high compaction in saturated conditions and in limited area. Under drought conditions, the high compaction could also have favored the contact with the soil matrix (Lipiec et al., 2003), thus the water and nutrient absorption in a certain amount, maintaining a constant growth rate. Root branching is correlated with locally available resource (Bingham et al., 2010). This implied that high compaction as well as low compaction had negative impact on resource availability for plants. As observed, decreases of water (Lipiec et al., 2003) and nutrients (Kuht and Reintman, 2004) uptake under high compaction have been reported in field.

Plant growth and development depends on water and nutrients supplies and is limited by biotic and abiotic stress. Shoot architectural alterations of the plant have been reported in the literature under high compaction. The plant is shorter (reduction up to 5%, Sessiz et al., 2008), with a smaller stem base diameter (Bayhan et al., 2002), smallest leaf area surface (reductions up to 65%, Andrade et al., 1993) and leaf expansion (reductions up to 25%, Andrade et al., 1993). This has been confirmed in our experiment where the highest soil compaction offered the strongest growth rate alteration, especially under no water stress constraint. The leaf survival is an essential characteristic for yield component implementation (Merrien et al., 1981), an early decrease of LAI will lead to a quick decrease of photosynthesis, and thus final production (Merrien and Milan, 1992). For leaves biomass, LAI and NEL the favorable hydric conditions led to an increase under low and medium compaction, but not under high compaction. This is explained by the reduced amount of macropores existing in the high soil compaction treatment. Under soil compaction, the reduction of the macroporosity leads to a decrease of soil hydraulic conductivity and water storage, which lead to an increase of soil matric potential (Lipiec et al., 2003). Moreover, an artificial increase of soil water availability led to anoxia conditions, especially in depth. This was visually observed at the end of this experiment, and can explain the negative impact of soil water increase under high compaction. In the present experiment, the growth indicators rate decreased under soil compaction, and this decrease was even accentuate under no limitation of water resources. Under low compaction, an increase of shoot biomass up to 40% has also been observed (Goodman and Ennos, 1999), but was not confirmed by the present study. As observed in the present experiment, under compacted soil shoot growth is more impacted than root, certainly because of the hormonal negative message send in response to soil compaction (Passioura, 2002) and of photosynthesis decrease (25% are allocated to root growth and functions maintenance, Marschner, 2003).

It exists direct relations between root growth and photosynthesis rate, which is proportional to temperature and radiation intercepted (Aguirrezabal et al., 1994), and between leaves and root elongation (Young et al., 1997). In our experiment, this strong relation is traduced by equation 1 and 2. Relation between the above ground and the below ground part of the plant has already been develop for sunflower in field (Sadras et al., 1989) and controlled conditions (Montagu et al., 2001). The equation 1 and 2 took into account soil parameter in order to establish those relationships in a context of soil mechanical constraint and water scarcity, with the aim to being use under a complex crop model dedicated to sunflower. Those equations have been built from all the data considering the growing degree days, thus depend of useful temperature to growth process. However, those last relationships are genotype dependant (Guilioni et al., 2008), and should be adjust under another cultivar. From this experiment, the author considers those equations as a suitable expression of root exploration through shoot and climatic data, easily obtain by direct measurements. This constitutes a good first step further implementation on much global sunflower crop model.
Figure 1. Effects of soil compaction and water management on sunflower root and shoot growth rate. ANOVA with repeated measure, P values Homogenous group tab according to Student test: growing degrees days base 4.8 from the sowing; a, b, c, d : homogenous group. * Difference Probability at 0.1, ** Significant Probability at 0.05, *** Significant Probability at 0.01. Effectives: 96.
CONCLUSION
Under soil compaction a decrease of root and shoot growth was observed, this was accentuated by the increase of water availability. In the present case, a reduction of soil porosity resulting from soil compaction, led to a decrease of plant water availability which has acted in addition with the actual lack of water resources applied as soil treatment. In parallel, low compaction under hydric constraint had the same impact on root and shoots systems growth. The macroporosity present under low compaction did not allow the diffusion process from the soil to the root. From this experiment, equations have been built to express root growth exploration, through simple above ground measurement. The authors consider those as good step further implementation on sunflower crop model.

REFERENCES