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Physiological and morphological responses of Arabica coffee cultivars to soil compaction

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ABSTRACT: Compaction caused by mechanization affects soil quality and, consequently, the development of crops. This study aimed to evaluate the effect of different degrees of soil compaction on the physiology, morphology, and anatomy of different coffee cultivars in a controlled environment. The experiment was carried out in a greenhouse, with randomized block design in a 5 × 5 factorial arrangement, with five coffee cultivars (Arara, Catuaí Amarelo IAC 62, Catuaí Vermelho 144, MGS Paraíso 2 and Mundo Novo IAC 379-19) and five degrees of compaction (68, 74, 80, 86 and 92 %), with four repetitions, totaling 100 experimental units. The following variables were evaluated in the aboveground biomass: plant height, number of leaves, diameter of the orthotropic branch, fresh mass of leaves and stem, leaf area, gas exchange, and chlorophyll a and b index; in the roots: length, surface area, volume, diameter of fine and coarse roots, fresh and dry mass of roots, as well as anatomical characteristics. Results showed that soil with degrees of compaction above 80 % negatively affected the variables evaluated. Catuaí Vermelho 144 presented the worst performance regardless of the degree of compaction, while Arara and MGS Paraíso 2 showed the best performance under the evaluated compaction degrees. Anatomical structure of the roots was modified with soil compaction, and no differences were observed among cultivars.

Keywords: *Coffea arabica* L., plant development, soil resistance to penetration, coffee root system.

INTRODUCTION

Soil quality is understood as the capacity of the soil to perform its functions, preserving its biological, physical, and chemical properties, thus ensuring the health of plants and animals (Doran and Parkin, 1996). Mechanization may negatively affect soil quality (Deperon Júnior et al., 2016), especially when used under inadequate moisture conditions, which can lead to soil compaction. This compaction may occur throughout agricultural production, from soil preparation to crop care and harvest (Keller et al., 2017).

Compaction is characterized by adjusting soil particles and/or aggregates, boosted by applying tensions beyond soil mechanical resistance. Fine and medium-textured soils, such as clayey soils, are more susceptible to compaction than sandy-textured soils (Ampoorter et al., 2010; Cambi et al., 2015; Naghdi et al., 2020). The main factor that increases the soil's vulnerability to compaction is moisture, which interferes with the particles' cohesion (Ampoorter et al., 2012). In compacted soils, it is possible to observe the presence of deformation in the structure of the soil, macropore reduction, increased root penetration resistance, decreased soil hydraulic conductivity, increased oxygen deficit, and restrictions on root growth (Shah et al., 2017), culminating in productivity losses of the agricultural crops (Colombi and Keller, 2019).

Coffee crop development is affected by soil compaction mainly due to the increase of the water deficit, nutritional and oxygen deficiency (Pulido-Moncada et al., 2022) and changes in soil temperature, which directly interfere with net photosynthesis, stomatal conductance, and enzyme activity (Dias et al., 2021). Physiological, morphological and anatomical aspects of the plants are affected and can lead to a reduction in growth, root diameter, decrease in leaf area and induction of stomatal closure, aiming to reduce losses by transpiration (Morales et al., 2018; Potocka and Szymanowska-Pulka, 2018). Therefore, in compacted soils, the plant has its physiological functioning altered, which compromises the productive performance of the crop, mainly due to water deficit, nutritional deficiency, and oxygen deficiency (Liu et al., 2017).

Cultivars selection is an important factor when planning the implementation of the coffee crop, since there are cultivars with specific characteristics of resistance or tolerance to different biotic and abiotic factors (Guerra et al., 2021). In the state of Minas Gerais, cultivars such as Arara, MGS Paraíso 2, Catuaí Amarelo IAC 62, Catuaí Vermelho 144 and Mundo Novo IAC 379-19 are commonly adopted in coffee plantations due to their high vigor, high production potential and beverage quality (Fazuoli et al., 2008; Cruz et al., 2020). In addition, they have abundant and well-developed root systems (Carvalho et al., 2008; Botelho et al., 2010; Ronchi et al., 2015). Arara cultivar also has greater tolerance to drought conditions (Cruz et al., 2020).

Good growth and development of the plants depend on the interactions between soil properties and root system (Shaheb et al., 2021). Root system of the coffee tree is classified as pseudo-pivoting, with roots that are generally short and thick. It is highly plastic and varies according to genotype, plant age, cultivation density, climate and soil structure (Ronchi et al., 2015). It adapts its structure to optimize resource access and response to biotic and abiotic factors (Gallagher, 2013; Ronchi et al., 2015). Thus, cultivars with more vigorous root systems tend to show a higher efficiency in nutrient uptake, translocation, and utilization even under restrictive soil physical quality conditions.

This study starts from the hypothesis that compaction interferes with plant growth and development, which may become a limiting factor, even post-correction, either during cultivation or coffee plantation renovation. Soil compaction evaluation influences crop performance, and the identification of cultivars that better adapt to this condition contributes to minimizing the caused damages. From the soil physics point of view, there is a lack of information related to the behavior of cultivars of Arabic coffee in the face of soil structural limitations. Considering the implementation or renovation of the tillage, it is important to conduct studies like these, which help identify and indicate crops that are more adapted and responsive to compaction. This study aimed to evaluate if different degrees of soil compaction affect growth, physiology, morphology, and anatomy of Arabic coffee seedlings from five different cultivars in a controlled environment.

MATERIALS AND METHODS

The experiment was carried out in a greenhouse on the experimental area from the Department of Soils at the Universidade Federal de Viçosa, located in the municipality of Viçosa - MG (20° 45’ 30.55” S and 42° 52’ 12.31” W) at 658 m of altitude. The soil was collected in a depth of 0.20 to 0.40 m, and was classified as *Latossolo Vermelho-Amarelo Distrófico típico,* according to the Brazilian Soil Classification System (Santos et al., 2018), which corresponds to an Oxisol (Soil Survey Staff, 2014). The sampled soil was air-dried, homogenized, and sieved through a 2-mm mesh. Soil was corrected following the recommendations of Alvarez and Ribeiro (1999), in which 600 g of dolomitic limestone was applied, and fertilization followed the recommendations for experiments in the greenhouse, according to Novais et al. (1991).

Arabic coffee seedlings belonging to the Arara, Catuaí Amarelo IAC 62, Catuaí Vermelho 144, MGS Paraíso 2, and Mundo Novo IAC 379-19 cultivars, were planted with three pairs of leaves. Irrigation was carried out on alternate days, using as a control the difference in weight of the PVC column used to carry out the test, on an electronic scale, bringing the soil to field capacity, determined with the use of the methodology proposed by Teixeira et al. (2017). For this, on the first day, water was added to the set (soil+seedling+PVC) to complete the humidity at field capacity and weighed. In the following days, weighing was repeated to maintain the weight corresponding to the field capacity determined the day before. It is noteworthy that a screen was placed at the bottom of each column to prevent soil loss.

The experimental scheme used was a factorial scheme 5 × 5, corresponding to five cultivars and five compaction degrees (68, 74, 80, 86 and 92 %), arranged in a randomized block design, with four repetitions, with the experimental plot represented by one plant per PVC column. Different compaction levels were determined by the soil compaction degree (CD, %) using equation 1.

$$CD = (\text{Soil bulk density}/\text{maximum soil bulk density}) \times 100 \qquad \text{Eq. 1}$$

Maximum density was determined by the uniaxial compression test (Hakansson, 1990). Soil in the collection location presented a compaction degree of 74 %. From there, the treatments were defined: CD1 = 68 % (Ds = 0.94 Mg m^{-3}), CD2 = 74 % (Ds = 1.03 Mg m^{-3}), CD3 = 80 % (Ds = 1.11 Mg m^{-3}), CD4 = 86 % (Ds = 1.19 Mg m^{-3}) and CD5 = 92 % (Ds = 1.68 Mg m^{-3}). Subsequently, the volume of the PVC column was determined (V = 4,128.25 cm^3), and the soil mass corresponding to each degree of compaction was determined.

Experimental units were set up with soil at the optimum compaction moisture (0.32 g g^{-1}), placed on PVC columns and compacted with a hydraulic press of 15 t of capacity. For this, the amount of soil corresponding to each compaction degree was divided into five layers. Each layer was compacted once to achieve greater uniformity while maintaining the desired bulk density throughout the column. The volume of the coffee bag seedling (V = 409.98 cm^3) was discounted in each column, leaving a hole equivalent to the average volume of the coffee seedlings using a metal cylinder in the compaction process, ensuring the initial volume occupied by the root system and substrate of the seedlings used.

The relationship between compaction degree and soil resistance to penetration was determined using undeformed samples from soil columns at five degrees of compaction, with moisture balance after saturation, on a tension table at 3, 6, 10, 100 and 300 kPa. An electronic penetrometer, model MA-933, with penetration velocity of 0.02 mm s^{-1} was used, the evaluation needle was inserted in the geometric center of each sample, reaching a maximum depth of 4.3 cm. This procedure aimed to identify the relationship between the shape used to assemble the PVC columns and the soil penetration resistance, a simple measure to be evaluated in field conditions (Figure 1).

At 120 days after transplanting the seedlings, the plants were evaluated regarding the number of leaves, diameter of the orthotropic branch using a digital pachymeter and plant height using a graduated ruler. Subsequently, the plants were harvested and separated into aerial part and roots, and the mass of leaves and stem and leaf area were determined using a leaf area meter model LI-3100C (LI-COR, 1995).

Gas exchanges (internal carbon concentration, net photosynthesis, stomatal conductance and transpiration) were determined using an infra-red gas analyzer (IRGA) Li-6400XT (Infra-red Gas Analyzer) under the following conditions: environment temperature, light intensity of 1000 µmol, CO_2 concentration equal to 400 µmol s^{-1}, between 7 and 11 a.m., on the first pair of fully expanded leaves and in good phytosanitary condition, at 65 days after transplanting. The efficiency of carbon utilization was determined according to equation 2.

$$EiCi = A/Ci \qquad \text{Eq. 2}$$

in which: EiCi is efficiency of carbon and A is photosynthesisand Ci is internal carbon concentration.

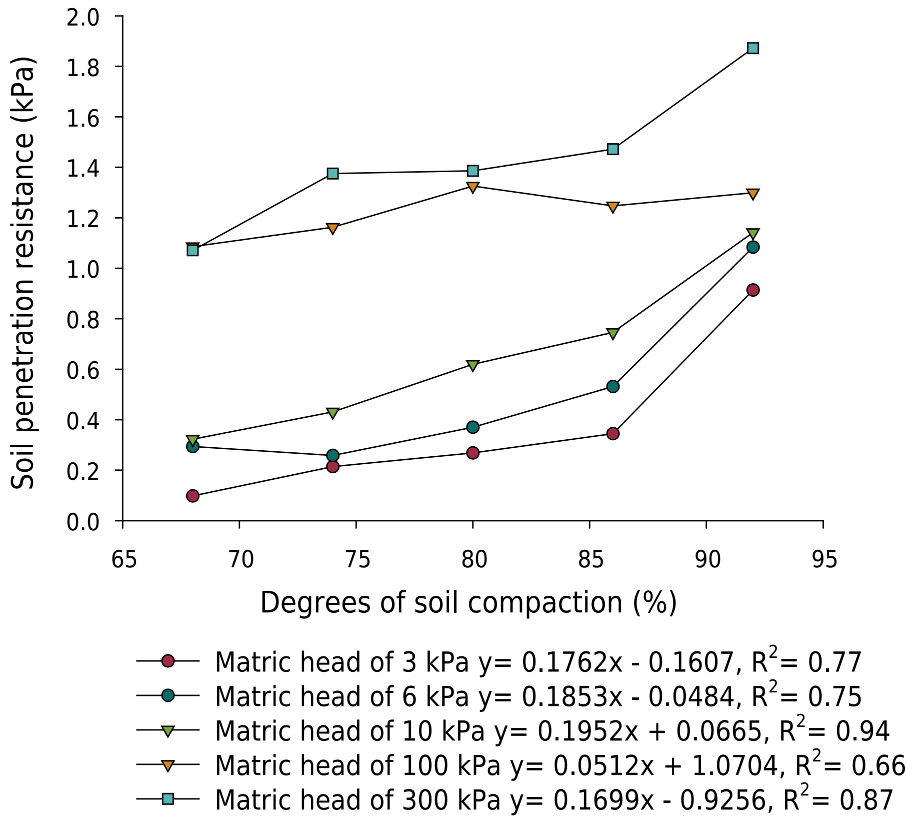

Figure 1. Relationship between degree of compaction and soil resistance to penetration at matrix tensions of 3, 6, 10, 100 and 300 kPa and their respective linear regression equations.

Chlorophyll *a* and *b* indices were also determined using the chlorophyll meter chlorophiLOG, model CFL 1030 (Falker, 2008) on the first pair of fully expanded leaves in good health.

Root samples, obtained by manual and visual selection, were destined for determining root morphology through digitization in an Epson professional scanner coupled to a computer with the aid of WinRHIZO PRO 2009 software. Samples were disposed of on the scanner's surface so that the roots do not overlap, and the images were acquired directly. The data obtained allowed us to obtain the total length, the average diameter of fine roots (<2 mm) and the coarse roots (2 to 5 mm), the total volume and the total surface area of the roots. In addition, the fresh and dry mass of the roots was determined.

Anatomical evaluations of the roots were performed with those roots arranged at the bottom of the soil column, main and lateral. The roots were separated, washed, and fixed in neutral buffered formalin (NBF) and stored under refrigeration for one week (Kraus and Arduin, 1997). After fixation, the samples were placed in an ethanol bath at 30 and 50 % for 24 h each and then stored in 70 % ethanol. Subsequently, the samples were submitted to dehydration, pre-infiltration, infiltration and polymerization. Dehydration was carried out via two-stage immersion in 85 and 95 % ethanol in a vacuum desiccator for two hours. During pre-infiltration, the samples were placed in a 1:1 (v/v) solution of pure historesin (Historesin, Leica), which was activated in 95 % ethyl alcohol for 12 h. After infiltration, the samples were held in histomolds using historesin plus hardening solution. After polymerization, the histomolds were placed in an oven at 30-40 °C for 48 h. The material was removed from the histomold and then sections with 5 µm thick were obtained on an automatic rotary microtome (Leica RM2265, Deerfield, IL, USA). Sections were stained with Toluidine blue at pH 4.4 (O'Brien and Mccully, 1981) and permanent slides were mounted on Permount synthetic resin (Fisher®, Germany). The photographic documentation was made in photomicroscope (Olympus AX 70, Tokyo, Japan) at the Laboratory of Plant Anatomy at the Universidade Federal de Viçosa (Federal University of Viçosa).

Obtained results were submitted to variance analysis at 5 % probability, unfolding the interaction cultivars × compaction degrees, regardless of whether it was significant or not by the F-test. The behavior of the cultivars in relation to the degrees of compaction was evaluated using regression. The choice of the models took into consideration the significance of the equation and the coefficients (R^2), as well as the possibility of biological explanation of behavior. Statistical analysis was performed with the aid of SISVAR software (Ferreira, 2008) and graphs were fitted in Sigma Plot 12.5 software.

RESULTS

Reduction in values was observed for plant growth parameters as the compaction degrees (CD) increased, fitting linear and quadratic polynomial models (Figure 2), with determination coefficients between 0.65 and 0.95. The cultivars Mundo Novo IAC 379-19, Catuaí Amarelo IAC 62 and MGS Paraíso 2 showed an increase followed by a decrease, especially for all variables evaluated number of leaves and leaf fresh mass and leaf arearespectively. Other cultivars did not present differentiation regarding the studied compaction degrees, that is, $\hat{Y} = \bar{Y}$.

As physiological responses (Figure 3), the occurrence of the decreasing linear model for all variables evaluated and quadratic polynomials for the photosynthesis variables was observed (Figure 3d), as well as the carbon assimilation efficiency (Figure 3e). Such behaviors were observed for the cultivars MGS Paraíso 2, in all the evaluated variables and Catuaí Vermelho 144, for the carbon internal concentration variables (Figure 3a) and carbon assimilation efficiency (Figure 3e). The cultivar MGS Paraíso 2 presented the highest photosynthesis values (11.33 µmol m^{-2} s^{-1} in 75 % de CD) and EiCi (0.036 mol m^{-2} s^{-1} in 79 % de CD).

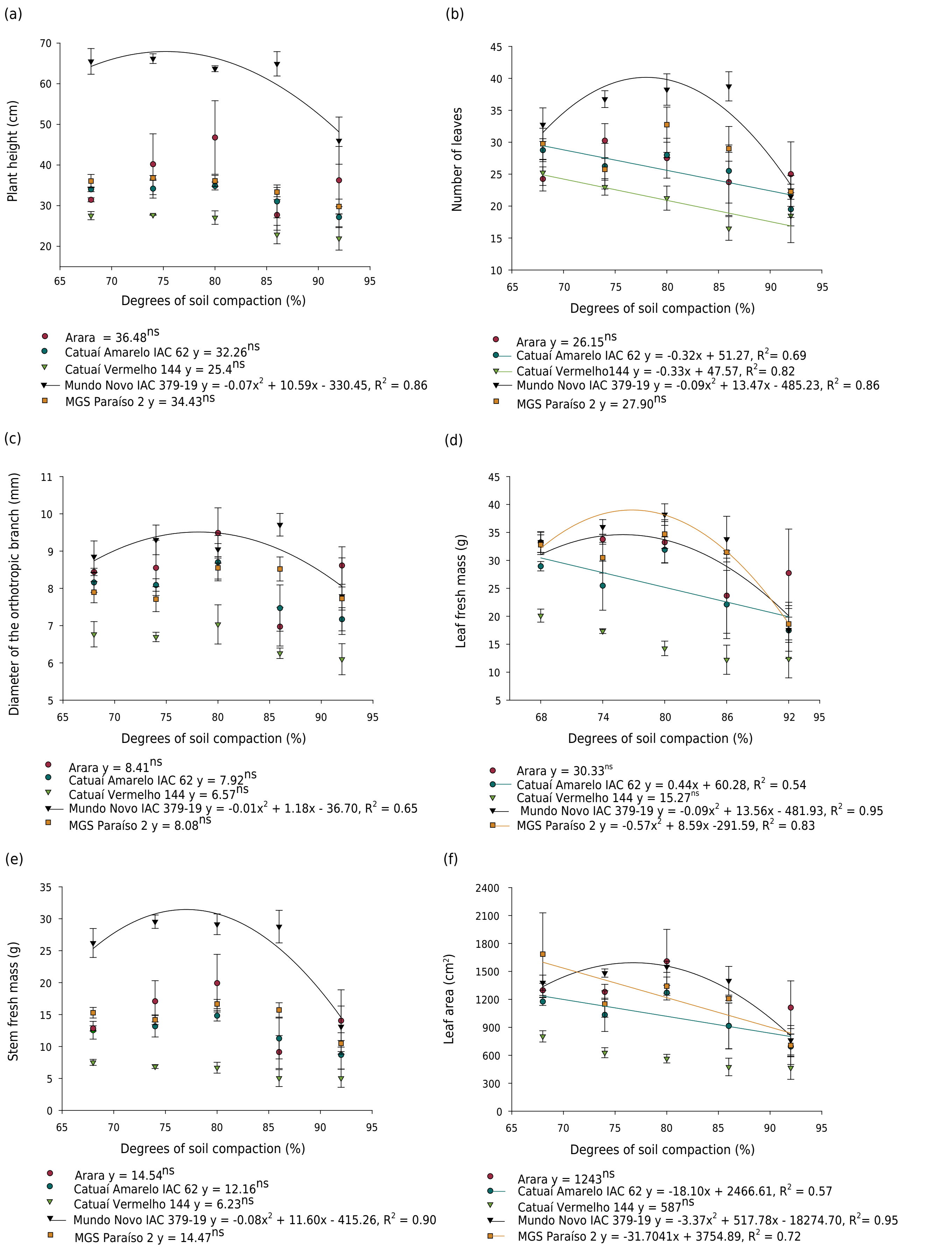

Figure 2. Plant height (a), number of leaves (b), diameter of the orthotropic branch (c), leaf fresh mass (d), stem fresh mass (e) and leaf area (f) from the cultivars Arara, Catuaí Amarelo IAC 62, Catuaí Vermelho 144, MGS Paraíso 2 and Mundo Novo IAC 379-19 in different compaction degrees. Ns: not significant.

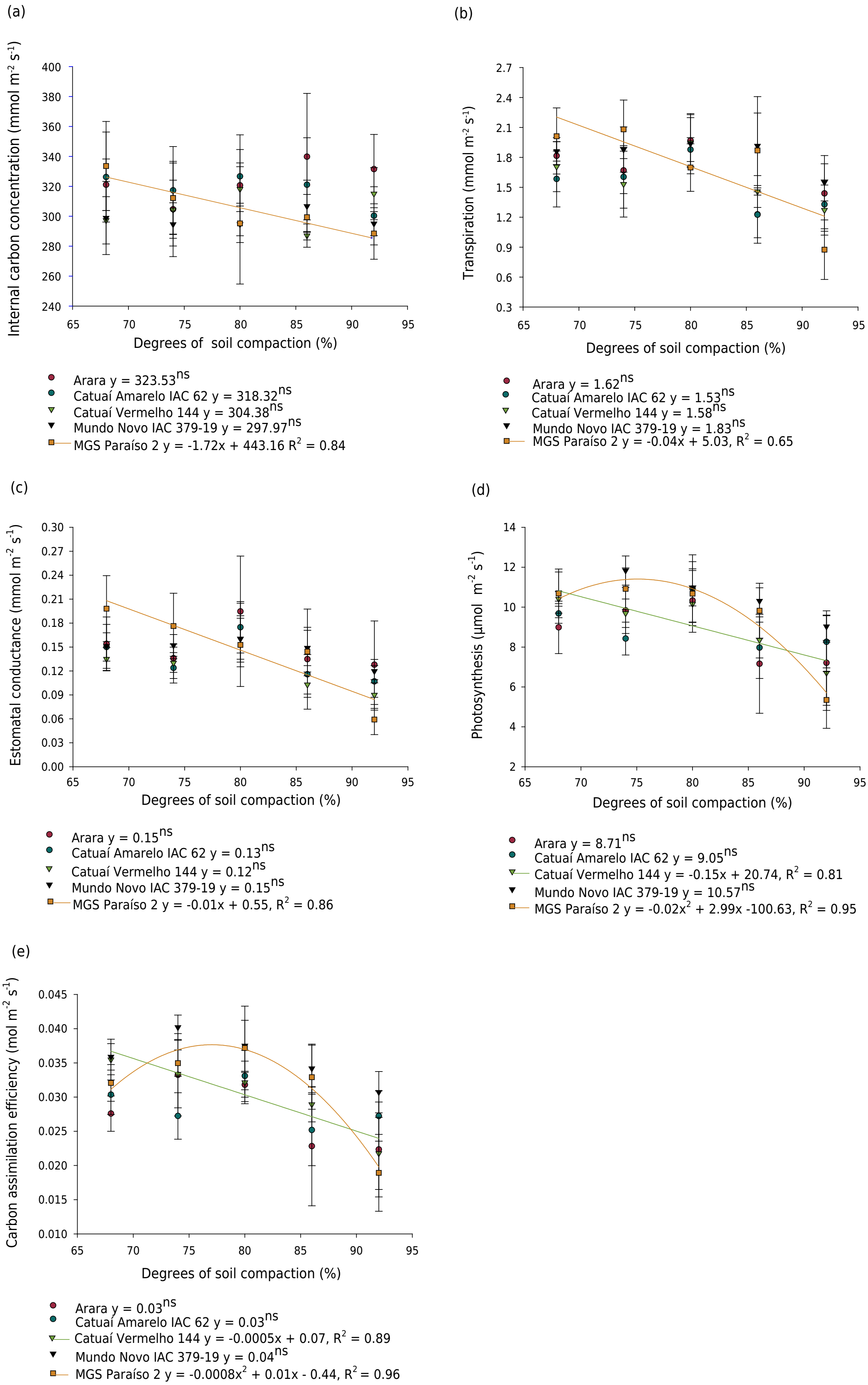

Figure 3. Internal carbon concentration (a), transpiration (b), stomatal conductance (c), photosynthesis (d) and carbon assimilation efficiency (e) from the cultivars Arara, Catuaí Amarelo IAC 62, Catuaí Vermelho 144, MGS Paraíso 2 and Mundo Novo IAC 379-19 in different compaction degrees. Ns: not significant.

Regarding the chlorophyll index *a* and *b*, only the cultivars Arara and Catuaí Amarelo IAC 62 presented influence from the different compaction degrees (Figure 4), where the first cultivar showed linear and quadratic polynomial reduction (Chlorophyll *a*) and linear (Chlorophyll *b*) for the second.

Results concerning root morphology, collected separately in the three column layers, will be presented by summing the results of the variables obtained for each layer. The reasons for this procedure are associated with the fact that a large part of the roots occurred in the surface layer, and it was found during root collection that when they penetrated the compacted soil, the proportions of roots in the remaining layers were reduced, especially at higher compaction degrees.

For the root morphological variables evaluated (root length, root surface area, root volume, diameter of fine and coarse roots, fresh and dry root mass), it was observed that the cultivars were significantly affected by compaction since the reduction of values was observed, either linear or quadratic polynomial (Figure 5). However, the cultivars MGS Paraíso 2 and Mundo Novo IAC 379-19 showed gains in these variables of up to 74 % in the degree of compaction.

For the root length (Figure 5a), the cultivars Catuaí Amarelo IAC 62, Catuaí Vermelho 144 and MGS Paraíso 2 showed quadratic behavior, and the maximum values were respectively: 2,969.45 cm obtained in the CD of 67 %; 3,430.5 cm in the CD of 70 %; and 4,065.78 cm when CD was 75 %.

Root surface area (Figure 5b), root volume (Figure 5c) and the fine root diameter (Figure 5d) presented quadratic behavior only for the cultivars Catuaí Amarelo IAC 62 and MGS Paraíso 2, whose maximum values were at 535.00 and 594.51 cm^2 (both for CD of 75 %), 6.50 and 5.48 cm^3 in CD of 74 and 75 % and of 909.23 and 1,088.87 mm in CD of 75 and 76 %, respectively. Alterations on the coarse root diameter variable were not observed (Figure 5e) either for the cultivar Catuaí Vermelho 144 or Arara. All the evaluated cultivars suffered a reduction in the root fresh mass as the compaction degree increased (Figure 5f). Only cultivar MGS Paraíso 2 was not significantly influenced by this variable (Figure 5g).

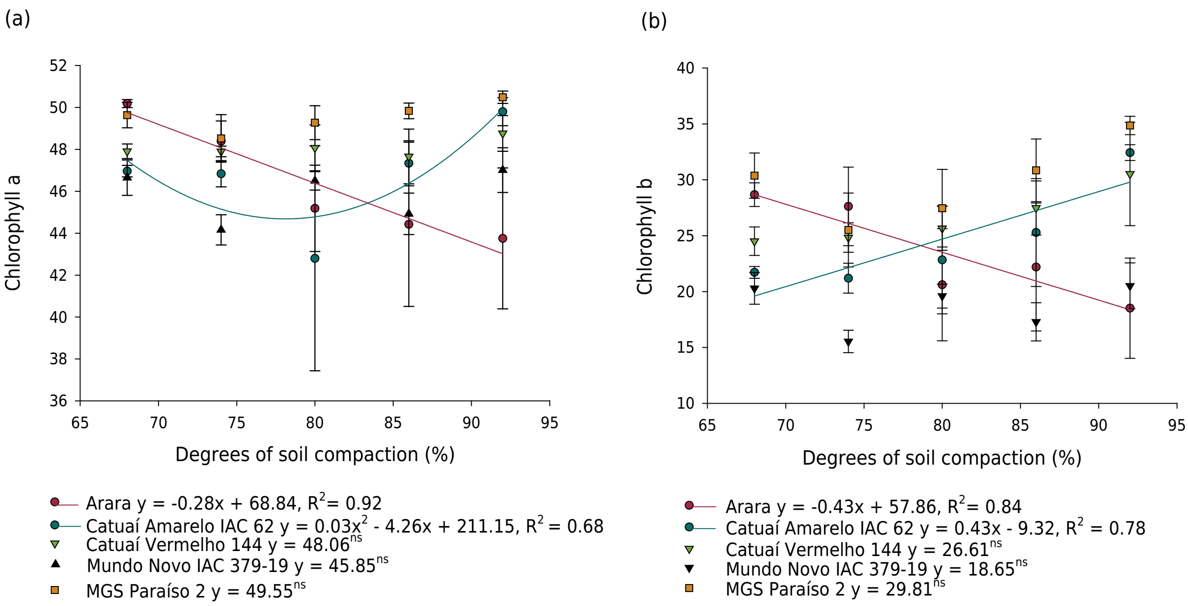

Figure 4. Chlorophyll indices a (a) and b (b) of the cultivars Arara, Catuaí Amarelo IAC 62, Catuaí Vermelho 144, MGS Paraíso 2, and Mundo Novo IAC 379-19 at different degrees of compaction. Ns: not significant.

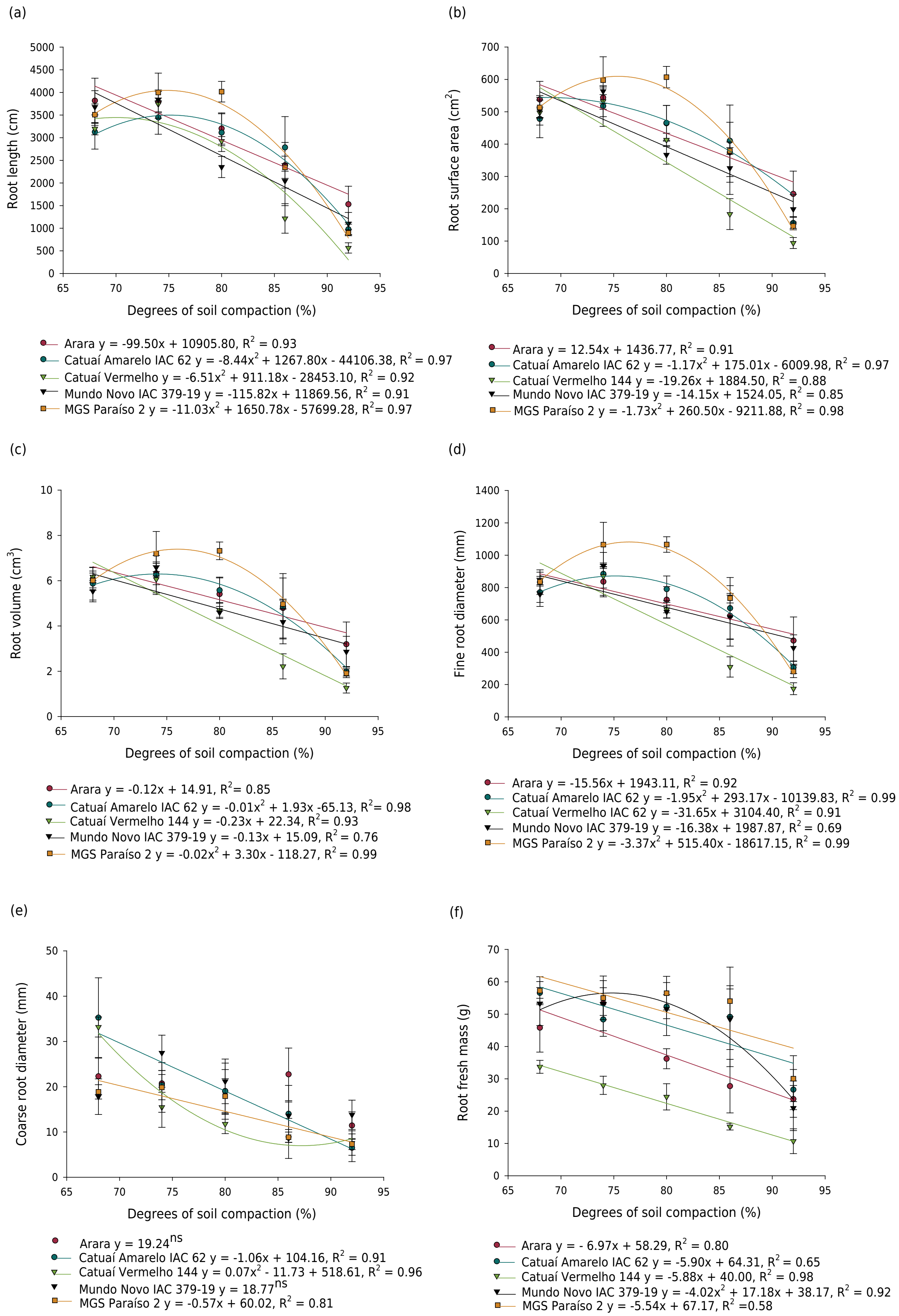

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Figure 5. Root length (a), root surface area (b), root volume (c), fine root diameter (d), coarse root diameter (e), root fresh mass (f) and root dry mass (g) from the cultivars Arara, Catuaí Amarelo IAC 62, Catuaí Vermelho 144, MGS Paraíso 2 and Mundo Novo IAC 379-19 in different compaction degrees. Ns: not significant.

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(g)

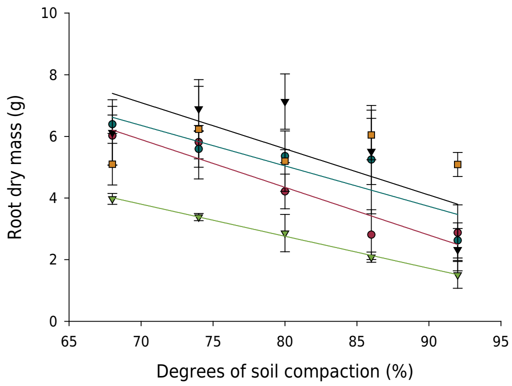

Figure 5. Root length (a), root surface area (b), root volume (c), fine root diameter (d), coarse root diameter (e), root fresh mass (f) and root dry mass (g) from the cultivars Arara, Catuaí Amarelo IAC 62, Catuaí Vermelho 144, MGS Paraíso 2 and Mundo Novo IAC 379-19 in different compaction degrees. Ns: not significant.

Approximately 120 slides were produced to evaluate the anatomy. After microscopic observation, we noticed that the damage was similar for all cultivars at different degrees of compaction, so it was decided to select and not present slides for all cultivars, thus avoiding a repetitive analysis. Anatomical evaluation of the roots indicated that the epidermis in the region of root elongation is formed by cells presenting thin walls and thin cuticle (Figure 6). In general, the epidermis in the region of elongation and branching showed few deformations in its structure. The main changes were observed in the apical region, when comparing the roots submitted to 80 % CD (Figure 6a) with those which were submitted to superior degrees, such as the CD of 86 % (Figure 6b). At the root apical region, the root cap was deformed with few cells, almost imperceptible; the protodermal cells presented a vacuolated aspect and more scaled.

At the root apical region, a set of meristemal cells covered by the root cap was observed, therefore the root apical meristem is subterminal. This region undergoes successive cell multiplications that result in the formation and development of root tissues, which can be observed by the presence of cells with conspicuous nuclei at different stages of the cell cycle (Figure 6).

Figure 6c illustrates the meristematic portion that was observed in roots that developed in soils with up to 80 % degree of compaction. It can be observed that the cells are in intense metabolic activity, as it is suggested by the evident presence of the voluminous nuclei. On the other hand, at higher degrees of compaction, there was an absence of dividing cells, few evident nuclei, and the apical meristematic portion of the root and root cap were practically absent, as illustrated in figure 6d. In the compaction degree of 92 % the cells from the fundamental meristem are voluminous, hyaline and the cytoplasm/nucleus ratio is smaller, and cells in division are not observed (Figures 6b and 6d).

In the transversal sections (Figures 6e and 6f), it was identified that the cortex did not undergo major changes due to compaction. Some changes, such as the presence of collapsed cells (no activity), may result from the onset of secondary development with tissue additions from cambium activity or damage caused during seedling transplantation. Compaction-associated damage was identified in compactions above 86 %. The region of the vascular cylinder was the most affected, with the portions corresponding to the pericycle and phloem being the most damaged (Figure 6f), mainly due to the typical presence of large cells with thin walls on this region.

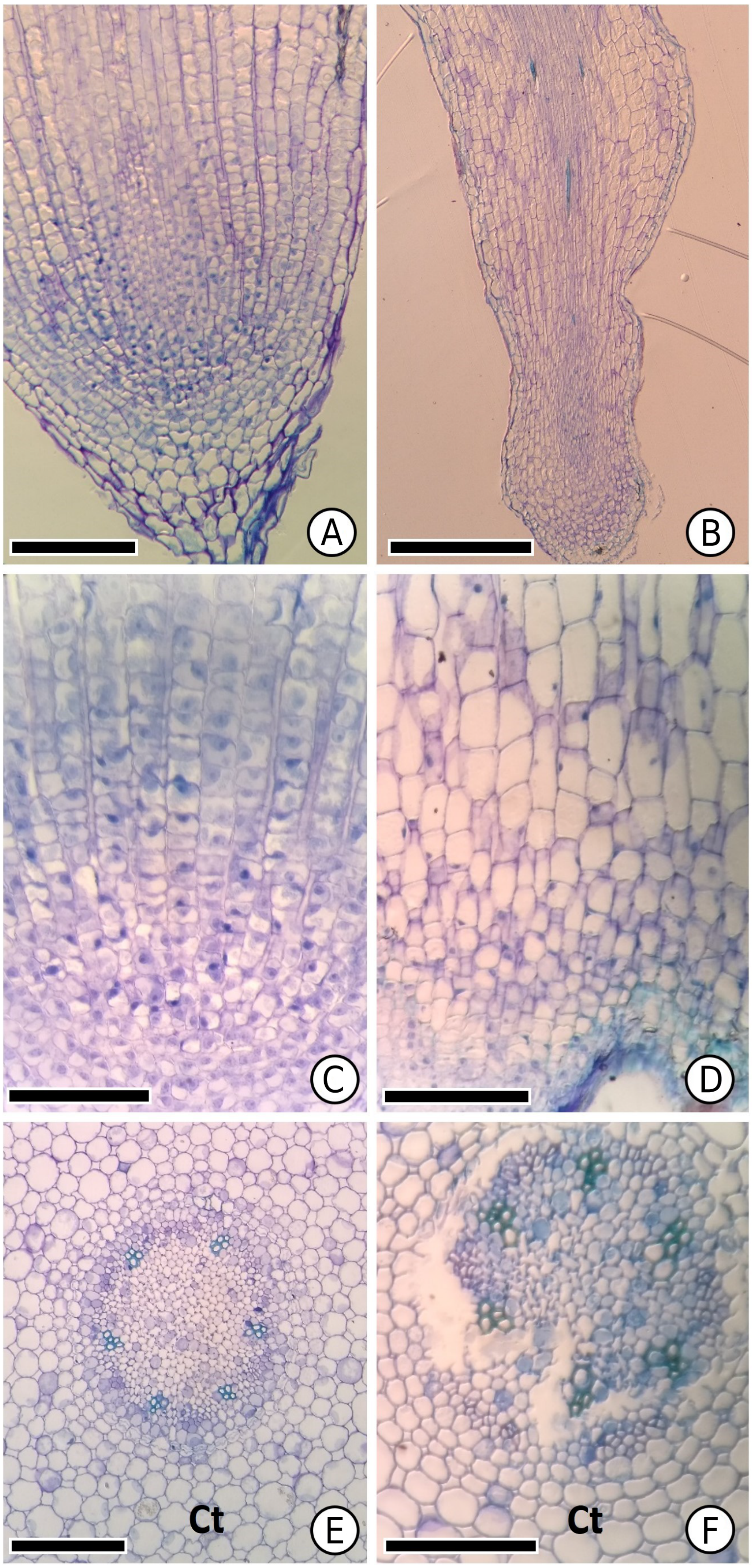

Figure 6. Longitudinal (a-d) and cross-sectional (e, f) sections of coffee roots in primary structure. (a) Main root apex of the Arara cultivar in the CD3 compaction degree (80 %); (b) Meristematic region of the lateral root of the Mundo Novo cultivar IAC 379-19, GC4 (86 %); (c) detail of the apical meristem, cultivar Mundo Novo IAC 379-19 in the CD3 (80 %); (d) detail of the apical meristem, cultivar Arara in the CD5 (92 %); (e) overview of the lateral root vascular cylinder of the cultivar MGS Paraíso 2, CD3 (80 %); and (f) overview of the vascular cylinder of a lateral root from Catuaí Vermelho 144 cultivar CD5 (92 %). Ct is cortex cells. Scale bar: a, b and e equal to 50 μm and c, d and f equal to 30 μm.

DISCUSSION

As the degree of soil compaction increases, there is a reduction in growth and physiological parameters, as well as morphological and anatomical changes in the roots of the plants. Furthermore, distinct responses of the cultivars evaluated were observed in relation to the degrees of compaction. Thus, the correct choice of cultivar and management when transplanting seedlings in field conditions with a degree of compaction similar to those studied is fundamental when one wants to increase production efficiency and sustainability.

Compaction affects plant development, especially in the seedling establishment phase due to impeded root growth caused by high penetration resistance and decreased water and oxygen availability (Bassett et al., 2005). Results obtained for the growth variables (Figure 2) in this study corroborate with the literature, which states that high compaction values negatively influence plant growth (Szatanik-Kloc et al., 2019; Wolf et al., 2019). Masaka and Khumbula (2007) evaluating the compaction effect in the coffee tree seedlings, noticed a lower biomass accumulation, lower height and growth of seedlings grown in compacted soils when compared to those grown without compaction. Shaheb et al. (2021) propose that the possible causes of reduced plant growth in compacted soils are increased bulk density and resistance to soil penetration, reduced porosity, and reduced soil hydraulic properties.

Furthermore, the maximum values obtained for the plant height variables, number of leaves, orthotropic branch diameter, leaf and stem fresh mass as well as leaf area were obtained at moderate compaction degrees, between 75 and 78 %. Generally, reductions in growth variables such as plant height, biomass, aerial part, density and root length are observed due to soil compaction (Bello-Bello et al., 2022; Costa and Coutinho, 2022), which is similar to what was observed in this study at compaction levels of 80, 86 and 92 %.

Leaf area is considered an excellent parameter to evaluate plant growth and physiology, since it reflects light interception, photosynthetic efficiency and transpiration (Cavallaro et al., 2020). Thus, any change caused by soil management can reflect gains or losses in photosynthetic leaf area. Cambi et al. (2017) point out that due to the reduced macroporosity caused by compaction, there can be reduced root and leaf growth, nutrient and water uptake. Cultivars Catuaí Amarelo IAC 62 and MGS Paraíso 2 presented a reduction in the leaf area (Figure 2f) as compaction degrees increased. Coffee plant presents high plasticity in the face of biotic and abiotic stresses by developing specific characteristics to adapt to these conditions (DaMatta, 2004). The smaller leaf area observed in these cultivars appears to have been a consequence of low water availability due to reduced soil macroporosity, culminating in a drop in leaf water potential and reduced leaf expansion and growth.

Different behavior among cultivars was already expected, since they come from different crossings, each aiming to develop varieties with resistance or biotic tolerance and abiotic stresses and high yield. Melo et al. (2006) evaluated vegetative and productive characteristics and found differences in plant height between Catuaí Vermelho 144, Catuaí Amarelo IAC 62 and Mundo Novo IAC 379-19 cultivars and also found a greater vegetative development of the last two when compared to Catuaí Vermelho 144. Different compaction degrees affected negatively the physiology and the plant development. This effect can be explained by the decrease in oxygen availability and water (Bassett et al., 2005), which affects the available water quantity for plant growth and transpiration. Oxygen deprivation due to soil compaction decreases root aerobic respiration, reducing root growth and photosynthesis and altering biomass production (Cambi et al., 2017).

Negative effect of compaction on gas exchange was also reported by Mariotti et al. (2020) through meta-analysis, where the authors attributed the significant decrease in gas exchange values to compaction, water limitation, and nutrient acquisition. Another point is the limitation in plant growth and consequent decrease in light energy absorption, reflecting in biomass gain losses. Although gas exchange decreased due to compaction, the values found are within the range of average values found by Silva et al. (2013) and Martins et al. (2014) for coffee plants.

Chlorophylls *a* and *b* are pigments in the leaves that are responsible for the absorption and conversion of light radiation to carry out photosynthesis. Chlorophyll fluorescence analysis is an important way to evaluate the effects of stresses on plant physiology, mainly by providing information on their photosynthetic state and in the evaluation of photoinhibition under adverse conditions that influence photosynthesis (Patil et al., 2019). As observed in the present study, Silva et al. (2020) also observed an increase in the chlorophyll *b* value when the soil density increased (1.7 g cm^{-3}).

Regarding chlorophyll *a*, a decrease was observed with the increase in the degree of compaction (Figure 4a). Cambi et al. (2017) also found a decrease in chlorophyll *a* fluorescence in plants grown in compacted soil, explained by a depression in photosynthetic efficiency and a decrease in the Calvin cycle. Cultivar MGS Paraíso 2 presented the highest index of chlorophyll *a*, suggesting a close relationship between its adaptability to various soil and climate conditions and chlorophyll a indices (Rodrigues et al., 2018).

However, moderate soil compaction can be beneficial to the plant as it brings the root closer to the soil, increasing the contact between them, which can favor the absorption of nutrients and consequently the growth of the plant (Mariotti et al., 2020). Increased root surface area increases the plant’s ability to access and absorb nutrients and water, which can culminate in greater biomass accumulation and plant growth. The cultivar MGS Paraíso 2 was efficient when compared to the other cultivars regarding the gain of the root surface area (Figure 5b) in the 68 to 80 % range.

Root diameter directly influences the biomechanical properties and penetration capacity of roots in compacted soils (Chimungu et al., 2015). Catuaí Vermelho 144 and Arara cultivars showed an increase in root diameter in response to the higher degree of soil compaction. The values found are within the range of average values observed by Ronchi et al. (2015).

The larger the root diameter, the greater its ability to penetrate compacted soil and withstand lower soil stresses and friction (Chen and Weil, 2010; Correa et al., 2019; Lynch et al., 2021).In addition, it is known that changes in root diameter are dependent on soil density (Popova et al., 2016). According to Pierce et al. (1983), clay-textured soils with a density ranging from 1.39 to 1.49 Mg m^{-3} suffer a reduction in root growth. However, Clark et al. (2003) point out that the increase in root diameter can be accompanied by a decrease in activity and growth in the apical meristem, as observed in the present study at a degree of compaction of 92 %.

High soil resistance to penetration reduces the length of the roots, leading to less soil exploration, resulting in less interception of water and nutrients, thus reducing the supply of these to the aerial part, which can directly compromise the total growth of the plant in compacted soils (Rich and Watt, 2013). The cultivars Catuaí Amarelo IAC 62, Catuaí Vermelho 144 and MGS Paraíso 2 showed greater root length. According to Duan et al. (2023), the greater root length obtained in compacted soils may be associated with the secretion of organic acids in the rhizosphere, which allows for greater rooting at depth. In this sense, root anatomy analysis is an excellent strategy for monitoring plant performance, making it possible to identify impediments to its development. Some anatomical features of the root, structure of the cortex, lining layers and vascular system are important, since they are directly related to crop physiology and growth (Wahl and Ryser, 2000).

Morphological and anatomical changes in the roots are expected in adverse conditions. Adaptive strategies that limit the root’s metabolic costs and maximize growth and resource capture efficiency are of paramount importance in compacted soil conditions with high penetration resistance (Colombi and Keller, 2019; Correa et al., 2019; Lynch, 2021). Colombi et al. (2017) also noticed that the increase in the soil bulk density affected the morphology and root growth in wheat, where there was a modification of tip geometry and root anatomy to counterbalance the increase of energy demand.

Part of the changes present in the cortex are related to the installation and activity of the cambium (Evert and Esau, 2013). This fact combined with the internal changes of the root, which occurred in the region of the vascular cylinder and in the apical portion, may help to understand the effects of soil compaction. According to Moraes et al. (2020), changes in these regions negatively affect the two main functions of the root, that is, absorption and support, once the disorganization of the vascular cylinder makes the connection between the cells and the vascular cambium differentiation process impossible.

Inactivation of the apical meristems of the primary root resulted in the development of numerous lateral roots, which had their growth limited by contact with the compacted soil. Therefore, it is likely that the increase in the emission of lateral roots is a strategy to compensate the compaction effects (Bertollo and Levie, 2019). Soil compaction reflects changes in root length and surface area and the number and density of lateral roots (Potocka and Szymanowska-Pułka, 2018). It is known that increased ethylene production by roots leads to the formation of lateral roots above the compacted soil layer, delayed root elongation or inhibition of root growth, due to ethylene's primary role in regulating root morphology and development (Okamoto et al., 2008; Vanhees et al., 2020; Lynch et al., 2021; Pandey et al., 2021; Zhang et al., 2023).

This can be observed in the response of MGS Paraíso 2 (Figure 6e) against different degrees of compaction, once the plants showed vigorous vegetative growth even at higher compaction levels. However, many lateral roots were formed, probably due to the inactivation of the apical meristem in both primary and lateral roots. This demonstrates that the effects on the anatomy and development of these root portions result in direct interference in the development of the cultivars. Therefore, cultivars with greater root system plasticity, through morphological and anatomical changes, can provide the coffee plant with greater efficiency in the absorption and use of resources and, consequently, greater plant growth and development (Zarebanadkouki et al., 2019; Andrade et al., 2022; Costa and Coutinho, 2022).

CONCLUSION

Compaction at high levels, from 80 % on, negatively affected the development of the coffee tree crop, reducing its growth and modifying its physiology, morphology and root anatomy. However, the interval between 75 and 78 % allowed for greater plant growth and development, as observed through the variables plant height, leaf area, number of leaves, orthotropic branch diameter, leaf and stem fresh mass.

Cultivars Arara and MGS Paraíso 2 presented better growth performance and other physiological parameters under high compaction levels, whereas the worst performance was observed for the cultivar Catuaí Vermelho 144. Anatomically, all coffee cultivars tested, Arara, Catuaí Amarelo IAC 62, Catuaí Vermelho 144, MGS Paraíso 2 and Mundo Novo IAC 379-19, had similar responses and presented structural rearrangement to better adapt to the different compaction degrees.

APPENDIX A. SUPPLEMENTARY DATA

Supplementary data to this article can be found online at https://www.rbcsjournal.org/wp-content/uploads/articles_xml/1806-9657-rbcs-47-e0230046/1806-9657-rbcs-47-e0230046-suppl01.pdf.

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REFERENCES

Alvarez V VH, Ribeiro AC. Calagem. In: Ribeiro AC, Guimarães PTG, Alvarez V VH, editors. Recomendações para o uso de corretivos e fertilizantes em Minas Gerais: 5ª aproximação. Viçosa, MG: Comissão de Fertilidade do Solo do Estado de Minas Gerais - CFSEMG; 1999. p. 43-60.

Ampoorter E, Schrijver A, van Nevel L, Hermy M, Verheyen K. Impact of mechanized harvesting on compaction of sandy and clayey forest soils: Results of a meta-analysis. Ann Forest Sci. 2012;69:533-42. https://doi.org/10.1007/s13595-012-0199-y

Ampoorter E, van Nevel L, De Vos B, Hermy M, Verheyen K. Assessing the effects of initial soil characteristics, machine mass and traffic intensity on forest soil compaction. Forest Ecol Manag. 2010;260:1664-76. https://doi.org/10.1016/j.foreco.2010.08.002.

Andrade LIF, Linhares PCA, Fonseca TM, Silva AA, Santos JP, Pereira MP, Silva VA, Marchiori PER. Photosynthetic efficiency and root plasticity promote drought tolerance in coffee genotypes. Acta Physiol Plant. 2022;44:109. https://doi.org/10.1007/s11738-022-03434-2

Bassett IE, Simcock RC, Mitchell ND. Consequences of soil compaction for seedling establishment: Implications for natural regeneration and restoration. Austral Ecol. 2005;30:827-33. https://doi.org/10.1111/j.1442-9993.2005.01525.x

Bello-Bello E, Lópes-Arredondo D, Rico-Chambrón TY, Herrera-Estrella L. Conquering compacted soils: Uncovering the molecular components of root soil penetration. Trends Plant Sci. 2022;27:814-27. https://doi.org/10.1016/j.tplants.2022.04.001

Bertollo AM, Levien R. Compactação do solo em Sistema de Plantio Direto na palha. Pesq Agrop Gaucha. 2019;25:208-18. https://orcid.org/0000-0002-4699-0738

Botelho CE, Rezende JC, Carvalho GR, Carvalho AM, Andrade VT, Barbosa CR. Adaptabilidade e estabilidade fenotípica de cultivares de café arábica em Minas Gerais. Pesq Agropec Bras. 2010;45:1404-11. https://doi.org/10.1590/S0100-204X2010001200010

Cambi M, Certini G, Neri F, Marchi E. The impact of heavy traffic on forest soils: A review. Forest Ecol Manag. 2015;384:124-38. https://doi.org/10.1016/j.foreco.2014.11.022

Cambi M, Hoshika Y, Mariotti B, Paoletti E, Picchio R, Venanzi R, Marchi E. Compaction by a forest machine affects soil quality and *Quercus robur* L. seedling performance in an experimental field. Forest Ecol Manag. 2017;384:406-14. https://doi.org/10.1016/j.foreco.2016.10.045

Carvalho CHS, Fazuoli LC, Carvalho GR, Guerreiro Filho O, Pereira AA, Almeida SR, Matiello JB, Bartholo GF, Sera T, Moura WM, Mendes ANG, Rezende JC, Fonseca AFA, Ferrão MAG, Ferrão RG, Nacif AP, Silvarolla MB, Braghini MT. Cultivares de café arábica de porte baixo. In: Carvalho CHS, editor. Cultivares de café: Origem, características e recomendações. Brasília, DF: Embrapa Café; 2008. p. 157-224.

Cavallaro RJ, Uber-Bucek E, Finzer JRD. Mathematical model for determining the coffee leaf area. ASRJETS. 2020;71:11-9.

Chen G, Weil RR. Penetration of cover crop roots through compacted soils. Plant Soil. 2010;331:31-43. https://doi.org/10.1007/s11104-009-0223-7

Chimungu JG, Loades KW, Lynch JP. Root anatomical phenes predict root penetration ability and biomechanical properties in maize (*Zea Mays*). J Exp Bot. 2015;66:3151-62. https://doi.org/10.1093/jxb/erv121

Clark LJ, Whalley WR, Barraclough PB. How do roots penetrate strong soil? Plant Soil. 2003;255:93-104. https://doi.org/10.1023/A:1026140122848

Colombi T, Keller T. Developing strategies to recover crop productivity after soil compaction-A plant eco-physiological perspective. Soil Till Res. 2019;191:156-61. https://doi.org/10.1016/j.still.2019.04.008

Colombi T, Kirchgessner N, Walter A, Keller T. Root tip shape governs root elongation rate under increased soil strength. Plant Physiol. 2017;174:2289-301. https://doi.org/10.1104/pp.17.00357

Correa J, Postma JA, Watt M, Wojciechowski T. Soil compaction and the architectural plasticity of root systems. J Exp Bot. 2019;70:6019-34. https://doi.org/10.1093/jxb/erz383

Costa MCG, Coutinho IAC. Root systems of agricultural crops and their response to physical and chemical subsoil constraints. In: Oliveira TS, Bell RW, editors. Subsoil constraints for crop production. Cham: Springer International Publishing; 2022. p. 225-61. https://doi.org/10.1007/978-3-031-00317-2_10

Cruz RS, Araújo FHV, França AC, Sardinha LT, Machado CMM. Physiological responses of *Coffea arabica* cultivars in association with arbuscular mycorrhizal fungi. Coffee Sci. 2020;15:151641. https://doi.org/10.25186/cs.v15i.1641

DaMatta FM. Ecophysiological constraints on the production of shaded and unshaded coffee: A review. Field Crop Res. 2004;86:99-114. https://doi.org/10.1016/j.fcr.2003.09.001

Deperon Júnior MA, Nagahama HdJ, Nelci O, Cortez JW, Souza EBd. Influência de implementos de preparo e de níveis de compactação sobre atributos físicos do solo e aspectos agronômicos da cultura do milho. Eng Agric. 2016;36:367-76. https://doi.org/10.1590/1809-4430-Eng.Agric.v36n2p367-376/2016

Dias SM, França AC, Silva RS, Carvalho RCR, Aguiar FR. Interaction soil compaction and soil moisture in physiological responses of freshly planted coffee. J Environ Anal Prog. 2021;6:370-8. https://doi.org/10.24221/jeap.6.4.2021.4532.370-378

Doran JW, Parkin TB. Quantitative indicators of soil quality: A minimum data set. In: Doran JW, Jones AJ, editors. Methods for assessing soil quality. Madison: SSSA Special Publications; 1996. p. 25-37. https://doi.org/10.2136/sssaspecpub49.c2

Duan X, Jin K, Mao Z, Liu L, He Y, Xia S, Hammond JP, White PJ, Xu F, Shi L. Compacted soil adaptability of *Brassica napus* driven by root mechanical traits. Soil Till Res. 2023;233:105785. https://doi.org/10.1016/j.still.2023.105785

Evert RF, Esau K. Anatomia das plantas de Esau - Meristemas, células e tecidos do corpo da planta: Sua estrutura, função e desenvolvimento. São Paulo: Editora Blucher; 2013.

Falker Automação Agrícola. Manual - Medidor eletrônico de teor clorofila (ClorofiLOG/CFL1030). Porto Alegre: Falker; 2008.

Fazuoli LC, Carvalho CHS, Carvalho GR, Guerreiro Filho O, Pereira AA, Bartholo GF, Moura WM, Silvarolla MB, Braghini MT. Cultivares de café arábica de porte alto. In: Carvalho CHS, editor. Cultivares de café: Origem, características e recomendações. Brasília, DF: Embrapa Café; 2008. p. 227-52.

Ferreira DF. SISVAR: Um programa para análises e ensino de estatística. Rev Symposium. 2008;6:36-41.

Ferreira Júnior LdG, Silva FM, Ferreira DD, Sales RS. Recomendação para colheita mecânica do café baseado no comportamento de vibração das hastes derriçadoras. Cienc Rural. 2016; 46:273-278. https://doi.org/10.1590/0103-8478cr20141679

Gallagher KL. Cellular patterning of the root meristem: Genes and signals. Plant Roots: The Hidden Half. 2013;3.1-26.

Guerra AF, Santos JF, Ferreira LT, Rocha OC. Cafés do Brasil: Pesquisa, sustentabilidade e inovação. In: Telhado SFP, Capdeville G, editors. Tecnologias poupa-terra. Brasília, DF: Embrapa; 2021. p. 63-75.

Hakansson I. A method for characterizing the state of compactness of the plough layer. Soil Till Res. 1990;16:105-20. https://doi.org/10.1016/0167-1987(90)90024-8

Keller T, Colombi T, Ruiz S, Manalili MP, Rek J, Stadelmann V, Wunderli H, Breitenstein D, Reiser R, Oberholzer H, Schymanski S, Romero-Ruiz A, Linde N, Weisskopf P, Walter A, Or D. Long-term soil structure observatory for monitoring post-compaction evolution of soil structure. Vadose Zone J. 2017;16:1-16. https://doi.org/10.2136/vzj2016.11.0118

Kraus JE, Arduin M. Manual básico de métodos em morfologia vegetal. Seropédica: Editora Universidade Rural; 1997.

LI-COR. LI-3100 Area Meter Service Manual Lincoln. Lincoln, NE: LI-COR Biosciences; 1995.

Liu Q, Liu B, Yanhui Z, Lin Z. Can biochar alleviate soil compaction stress on wheat growth and mitigate soil N_2O emissions? Soil Biol Biochem. 2017;104:8–17. https://doi.org/10.1016/j.soilbio.2016.10.006

Lynch JP, Mooney SJ, Strock CF, Schneider HM. Future roots for future soils. Plant Cell Env. 2021;45:620-36. https://doi.org/10.1111/pce.14213

Lynch JP. Harnessing root architecture to address global challenges. Plant J. 2021;109:415-31. https://doi.org/10.1111/tpj.15560

Maia PL, Nadaleti DS, Botelho C, Botelho D, Moreira P, Carvalho G. Agronomic performance of coffee in response to framework pruning in cycles of the “safra zero”. CS. 2020;15:1-7. https://doi.org/10.25186/.v15i.1629

Mariotti B, Hoshika Y, Cambi M, Marra E, Feng Z, Paoletti E, Marchi E. Vehicle-induced compaction of forest soil affects plant morphological and physiological attributes: A meta-analysis. Forest Ecol Manag. 2020;462:118004. https://doi.org/10.1016/j.foreco.2020.118004

Martins SCV, Galmes J, Cavatte PC, Pereira LF, Ventrella MC, DaMatta FM. Understanding the low photosynthetic rates of sun and shade coffee leaves: Bridging the gap on the relative roles of hydraulic, diffusive and biochemical constraints to photosynthesis. PLoS One. 2014;9:e95571. https://doi.org/10.1371/journal.pone.0095571

Masaka J, Khumbula N. The effect of soil compaction levels on germination and biometric characteristics of coffee (*Coffee arabica*) seedlings in the nursery. Intl J Agri Res. 2007;2:581-9. https://doi.org/10.3923/ijar.2007.581.589

Melo B, Marcuzzo KV, Teodoro REF. Desenvolvimento vegetativo e produção de linhagens de cafeeiro em Uberlândia-MG. Biosci J. 2006;22:21-5.

Moraes MT, Debiasi H, Franchini JC, Mastroberti AA, Levien R, Leitner D, Schnepf A. Soil compaction impacts soybean root growth in an Oxisol from subtropical Brazil. Soil Till Res. 2020;200:104611. https://doi.org/10.1016/j.still.2020.104611

Morales F, Pavlovič A, Abadía A, Abadía J. Photosynthesis in poor nutrient soils, in compacted soils, and under drought. In: Adams III WW, Terashima I, editors. The leaf: A platform for performing photosynthesis. Cham: Springer; 2018. p. 371-99.

Naghdi R, Solgi A, Labelle ER, Nikooy M. Combined effects of soil texture and machine operating trail gradient on changes in forest soil physical properties during ground-based skidding. Pedosphere. 2020;30:508-16. https://doi.org/10.1016/S1002-0160(17)60428-4

Novais RF, Neves JCL, Barros NF. Ensaio em ambiente controlado. In: Oliveira AL, Garrido WE, Araújo JD, Lourenço S, editors. Métodos de pesquisa em fertilidade do solo. Brasília-DF: Documentos Embrapa; 1991. p. 153-89.

O'Brien TP, Mccully ME. The study of plant structure principles and select methods. Melbourne: Termarcarphi Pty; 1981.

Okamoto T, Tsurumi S, Shibasaki K, Obana Y, Takaji H, Oono Y, Rahman A. Genetic dissection of hormonal responses in the roots of Arabidopsis grown under continuous mechanical impedance. Plant Physiol. 2008;146:1651-62. https://doi.org/10.1104/pp.107.115519

Pandey BK, Huang G, Bhosale R, Hartman S, Sturrock CJ, Jose L, Martin OC, Karady M, Voesenek LACJ, Ljung K, Lynch JP, Brown KM, Whalley WR, Mooney SJ, Zhang D, Bennett MJ. Plant roots sense soil compaction through restricted ethylene diffusion. Science. 2021;371:276-80. https://doi.org/10.1126/science.abf3013

Patil S, D'Souza GF, Umesh DK, Rudragouda C. Rootstock scion interaction effects on biochemical and gas exchange drought tolerant traits in arabica (*Coffea Arabica* L.) coffee. Plant Physiol Rep. 2019;24:316-27. https://doi.org/10.1007/s40502-019-00452-0

Pierce FJ, Larson WE, Dowdy RH, Graham WAP. Productivity of soils: Assessing long-term changes due to erosion. J Soil Water Conserv. 1983;38:39-44.

Popova L, van Dusschoten D, Nagel KA, Fiorani F, Mazzolai B. Plant root tortuosity: An indicator of root path formation in soil with different composition and density. Ann Bot-London. 2016;118:685-98. https://doi.org/10.1093/aob/mcw057

Potocka I, Szymanowska-Pulka J. Morphological responses of plant roots to mechanical stress. Ann Bot-London. 2018;122:711-23. https://doi.org/10.1093/aob/mcy010

Pulido-Moncada M, Petersen SO, Munkholm LJ. Soil compaction raises nitrous oxide emissions in managed agroecosystems. A review. Agron Sustain Dev. 2022;42:38. https://doi.org/10.1007/s13593-022-00773-9

Rich SM, Watt M. Soil conditions and cereal root system architecture: Review and considerations for linking Darwin and Weaver. J Exp Bot. 2013;64:1193-208. https://doi.org/10.1093/jxb/ert043

Rodrigues WN, Martins LD, Tomaz MA. Avanços sobre o desempenho de cultivares em diferentes condições de cultivo da cafeicultura capixaba. Alegre, ES: Caufes; 2018.

Ronchi CP, Souza Júnior JM, Ameida WL, Souza DS, Silva NO, Oliveira LB, Guerra AMNM, Ferreira PA. Root morphology of arabica coffee cultivars subjected to diferente spatial arrangements. Pesq Agropec Bras. 2015;50:187-95. https://doi.org/10.1590/S0100-204X2015000300001

Santos HG, Jacomine PKT, Anjos LHC, Oliveira VA, Lumbreras JF, Coelho MR, Almeida JA, Araújo Filho JC, Oliveira JB, Cunha TJF. Sistema brasileiro de classificação de solos. 5. ed. rev. ampl. Brasília, DF: Embrapa; 2018.

Shah AN, Tanveer M, Shahzad B, Yang G, Fahad S, Ali S, Bukhari MA, Tung SA, Hafeez A, Souliyanonh B. Soil compaction effects on soil health and cropproductivity: An overview. Environ Sci Pollut R. 2017;24:10056-67. https://doi.org/10.1007/s11356-017-8421-y

Shaheb MR, Venkatesh R, Shearer SA. A review on the effect of soil compaction and its management for sustainable crop production. J Biosyst Eng. 2021;46:417-39. https://doi.org/10.1007/s42853-021-00117-7

Silva FG, Assis Junior RN, Mesquita RO, Marques ES, Mota JCA. Gas exchanges and growth of maize as affected by aeration porosity and soil compaction. Rev Cienc Agron. 2020;51:e20196834. https://doi.org/10.5935/1806-6690.20200043

Silva PEM, Cavatte PC, Morais LE, Medina EF, DaMatta FM. The functional divergence of biomass partitioning, carbon gain and water use in *Coffea canephora* in response to the water supply: Implications for breeding aimed at improving drought tolerance. Environ Exp Bot. 2013;87:49-57. https://doi.org/10.1016/j.envexpbot.2012.09.005

Soil Survey Staff. Keys to soil taxonomy. 12th ed. Washington, DC: United States Department of Agriculture, Natural Resources Conservation Service; 2014.

Szatanik-Kloc A, Horn R, Lipiec J, Siczek A, Boguta P. Initial growth and root surface properties of dicotyledonous plants in structurally intact field soil and compacted headland soil. Soil Till Res. 2019;195:104387. https://doi.org/10.1016/j.still.2019.104387

Teixeira PC, Donagemma GK, Fontana A, Teixeira WG. Manual de métodos de análise de solo. 3. ed. rev e ampl. Brasília, DF: Embrapa; 2017.

Vanhees DJ, Loades KW, Bengough AG, Mooney SJ, Lynch JP. Root anatomical traits contribute to deeper rooting of maize under compacted field conditions. J Exp Bot. 2020;71:4243-57. https://doi.org/10.1093/jxb/eraa165

Volsi B, Telles TS, Caldarelli CE, Câmara MRG. The dynamics of coffee production in Brazil. PLoS One. 2019;14:1-15. https://doi.org/10.1371/journal.pone.0219742

Wahl S, Ryser P. Root tissue structure is linked to ecological strategies of grasses. New Phytol. 2000;148:459-71. https://doi.org/10.1046/j.1469-8137.2000.00775.x

Wolf EC, Rejmánková E, Cooper DJ. Wood chip soil amendments in restored wetlands affect plant growth by reducing compaction and increasing dissolved phenolics. Restor Ecol. 2019;27:1128-36. https://doi.org/10.1111/rec.12942

Zarebanadkouki M, Trtik P, Hayat F, Carminati A, Kaestner A. Root water uptake and its pathways across the root: quantification at the cellular scale. Sci Rep. 2019;9:12979. https://doi.org/10.1093/jxb/eraa165

Zhang F, Hou Y, Zed R, Mauchline TH, Shen J, Zhang F, Jin K. Root exudation of organic acid anions and recruitment of beneficial actinobacteria facilitate phosphorus uptake by maize in compacted silt loam soil. Soil Biol Biochem. 2023;184:109074. https://doi.org/10.1016/j.soilbio.2023.109074