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Left, right, up and downstage: leaves and lateral roots histological trait prospection for drought tolerance in commercial *Coffea arabica* cultivars

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Summary: The climate change and water deficit challenges plant producers all over the world, and have consequences to coffee production and quality. In this research we have approached anatomical traits from vegetative organs of 13 *Coffea arabica* genotypes, selected based on their contrasting behavior to water deficit. Leaf blade, petiole and primary root cross sections were evaluated, and the epidermal, fundamental, and vascular tissues descriptive anatomy, histometric and histochemistry examined. Despite all plants were in the same environment (CEPC/EPAMIG, Patrocínio, MG, Brazil), there were differences among the genotypes and groups of more tolerant and more susceptible accesses. Petiole cross section, vascular tissue and phloem and cambium; and percentage of stele, pericycle and phloem and cambium in primary roots exhibited differences among the contrasting genotypes, highlighting an inborn association of vascular tissue and other features with water deficit resistance. This association was observed in the mild to medium correlations among vascular tissue, epidermis, phloem and cambium in roots and petioles. Possible relation of qualitative traits such as the lignification of root epidermis, lipidic substances in outer cortical cell layers, and area/number of cell layers in the cortex are approached as possible traits in the seek for water deficit tolerance in *C. arabica*.

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Key words: water deficit tolerance, applied plant anatomy, histometry, histochemistry, plant breeding, coffee commercial cultivars

Introduction

Coffea arabica is originated from Ethiopia and has become one of the most cultivated and appreciated drinks throughout the world. Supposedly, it is one of the first coffee species to be cultivated. Coffee is the second most consumed drink in the world, a preference attributed to its aroma, body and flavor resulting from the fruits (Ferraz, 2013). Coffee farming plays a fundamental role in the global economy, being one of the most internationally traded commodities. Brazil and Colombia have consistently been the highest-producing countries and largest exporters since 2016, responsible for 40% and 20% of the world's arabica coffee production, hence, the 1st and 2nd largest producers, respectively (Panhuysen and De Vries, 2023; IOC, 2023). On the other hand, the European Union (EU), United States, and Japan have been the largest importers over this period (Bermudez et al., 2022). According to forecasts, coffee production in the 2023 harvest is estimated at 54.94 million bags, 7.9% above the previous cycle (CONAB, 2023).

The coffee plants were introduced in Brazil around the 18th century and is part of its historical context with consistent economic relevance for more than 2 centuries. Currently, 4

states, Minas Gerais, as the largest producer, followed by São Paulo, Espírito Santo and Bahia, concentrate 85% of Brazilian production, a large part of which is cultivated in a rainfed system. Coffee farming demands careful management and cultural treatments, being an important generator of direct and indirect jobs at all stages of its production, from cultivation and processing to commercialization (Moreira et al., 2004). In Brazil, coffee farming is responsible for 585,000 jobs, considering the countryside, industry, and coffee trade in the country (SNA, 2022).

The 2023 report by the Intergovernmental Panel on Climate Change (IPCC, 2023) reports an increase in global temperature by 1.1 °C in recent decades, with expected increases of 1.5 °C to 3.0 °C by 2050, if there are no mitigation measures for net CO_2 emissions. This could make some areas unsuitable for the cultivation of Arabica coffee due to harmful changes in the anatomy and, consequently, in the physiology of the plant.

The aspects that guarantee coffee acceptance (Ferraz, 2013) can be severely affected by drought. Responses to water deficit in coffee plants involve a complex network of physiological and morphological responses (Silva et al., 2019). Araújo et al. (2011) mentioned that the lack of water can compromise initial growth and, consequently, production by leading to loss of plant biomass. Water deficit can cause drastic changes in plant metabolism, reducing leaf water potential and relative water content in the leaf (Galmés et al., 2007). Water stress causes damage to cellular structures, which is reflected in reduced plant growth and development, leaf fall, decreased photosynthesis and, consequently, reduced fruit productivity and quality (Campos et al., 2021). The lack of water can, therefore, lead to a reduction in coffee productivity and quality, in addition to interfering with production costs (Seigui Kobayashi et al., 2008). The implementation of water reduction scenarios (IPCC, 2023) and exposure to periods of prolonged water deficit require that coffee irrigation be carried out with rational management (Souza, 2009). The identification of cultivars that can cope with water deficit stress can contribute the quality and production of coffee plants under such conditions. Accordingly, it is extremely important to have criteria available to estimate the water stress tolerance of coffee plants, linked to the productive potential of each variety.

Several environmental factors can influence leaf anatomy and, among them, the availability of water, which directly interferes with leaf development (Fahn & Cutler, 1992). The leaf anatomy of the coffee plant demonstrates plasticity for factors such as radiation conditions, through changes in the thickness of the palisade and spongy parenchyma, in the stomatal dimensions, among others (Ramiro et al., 2004; Pinheiro et al., 2005; Nascimento et al. 2006). Recently, anatomical characteristics of leaves and petioles showed low but significant correlations with coffee drinking quality, surprisingly, on a scale similar to the effect of altitude (Pérez-Molina et al., 2021). Studies carried out to evaluate leaf anatomy in response to water stress supported the use of anatomical variables to evaluate the potential resistance of the coffee plants. Contrarily, Grisi et al. (2008), observed that the leaf anatomy of Catuaí coffee remained constant at different levels of water stress. These contrasting responses among coffee cultivars highlight the existence of a genotype vs environment interaction should be considered.

The petiole is an important structure for supporting, and transporting water and nutrients, the leaf and has specific anatomical features. Accordingly, the petiole anatomy traits allow it being analyzed and associated with water deficit tolerance (Kulkarni et al., 2006; Laajimi et al., 2011; Dayer et al., 2017; Condé et al., 2020). Petiole anatomy can be useful and important given that it had exhibited low but significant correlations with coffee drink quality (Pérez-Molina et al., 2021). Furthermore, water stress may lead to a decrease in cell wall thickness and petiole diameter, which can affect the mechanical resistance of the plant vegetative organs such as leaves (Silva et al., 2008).

Based on the assumption that water deficit is one of the determinants of coffee productivity, the present work aims to describe and analyze anatomical and histometrical data of primary lateral roots, leaves and petioles of 13 commercial cultivars and breeding lines of *C. arabica*. The development of more tolerant and productive cultivars in conditions of water deficit is an alternative to overcome stress conditions. This report focused on the characterization and possible use of anatomical traits aiming a better understanding of tolerance, and the selection of coffee cultivars for sustainable production in water scarcity conditions.

Materials and methods

Sample collection and processing

The sampled plants were conducted as part of the germplasm bank and experimental field of the Campo Experimental de Patrocínio (CEPC-EPAMIG) (***Figure 1A***), located in Patrocínio, MG, Koppen climate, precipitation and average annual temperature, coordinates. The management of plants is carried out in accordance with the practices adopted in the experimental field (Guimaraes et al., 1999). The Active Germplasm Bank of Minas Gerais was implemented in 2005, in the Campo Experimental de Patrocínio – CEPC, of the Agricultural Research Company of Minas Gerais (EPAMIG) is at the Cerrado Mineiro Region, where a vast *Coffea* germplasm, currently consisting of 1,596 accessions, mainly by the groups of most commercial cultivars. Originally, this germplasm bank aimed to support the sensory characterization of these accessions, to grant access to these accessions, and foster the identification of the most promising cultivars (Nadaleti, 2020).

The CEPC experimental area is an experimental farm of the Agricultural Research Company of Minas Gerais (EPAMIG), located in the municipality of Patrocínio – MG, latitude 18º59'26" S and longitude 48º58'9.5" W, and altitude of approximately 1,000 meters. Fertility and classification information of the soil is dystrophic red-yellow Latosol type, the germplasm bank area has a flat topography with a slight slope. Soil and leaf sample mineral analysis is available at ***Supplementary Tables 1-2***. The climate of the municipality of Patrocínio is classified as humid subtropical, with dry winter and hot summer (Cwa), according to Köppen (EMBRAPA, 2004).

A literature search and consultation with coffee breeders were carried out to find a reference for the behavior of Arabica coffee genotypes in relation to water deficit. Based on the information collected and commercial genotypes available at CEPC-EPAMIG, 13 genotypes were selected (***Table 1***) and chosen as a reference for tolerance or susceptibility to water deficit in *C. arabica*. These comprise commercial cultivars and

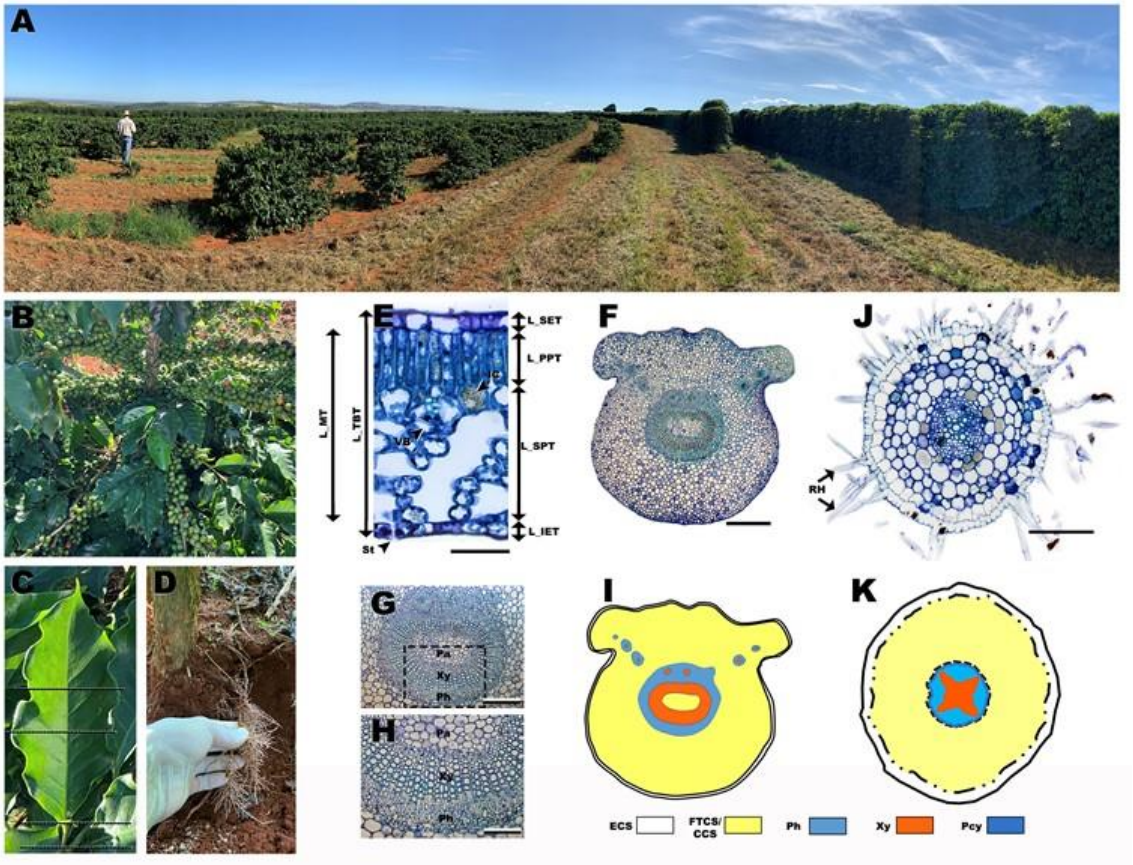

Figure 1. View of the Patrocínio/EPAMIG Experimental Field and illustrations of the sampled plant material. A - General view of the Patrocínio/EPAMIG Experimental Field; B – coffee plant in production with plagiotropic branches with fruits and leaves; C – regions of the middle third of the leaves and petioles sampled; D – Lateral roots sampled; E – cross-section of the leaf blade, schematic descriptive of the histometric variables evaluated; F – transverse section of the region of the middle third of the petiole; G – detail of the vascular tissue region in the petiole; H – greater increase in the vascular tissue region of the petiole; I – representative scheme of the histological regions evaluated on the petiole; J – histological section of a root in primary growth and; K – representative scheme of the histological regions evaluated in the primary roots. L_MT – total leaf mesophyll thickness; L_TBT – total leaf blade thickness; St – stomata; L_SET – leaf superior epidermis face thickness; L_PPT – palisade parenchyma thickness; L_SPT – spongy parenchyma thickness; L_IET – leaf inferior epidermis face thickness; ECS – epidermis cross section (petiole and root); FTCS – petiole fundamental tissue cross section area; CCS – root cortex cross section area; Ph – phloem; Xy – xylem; Pa – parenchyma; Pcy – pericycle; RH – root hair. Bars, E – 50 µm; F – 500 µm; G - 200 µm; H - 100 µm and J – 200 µm.

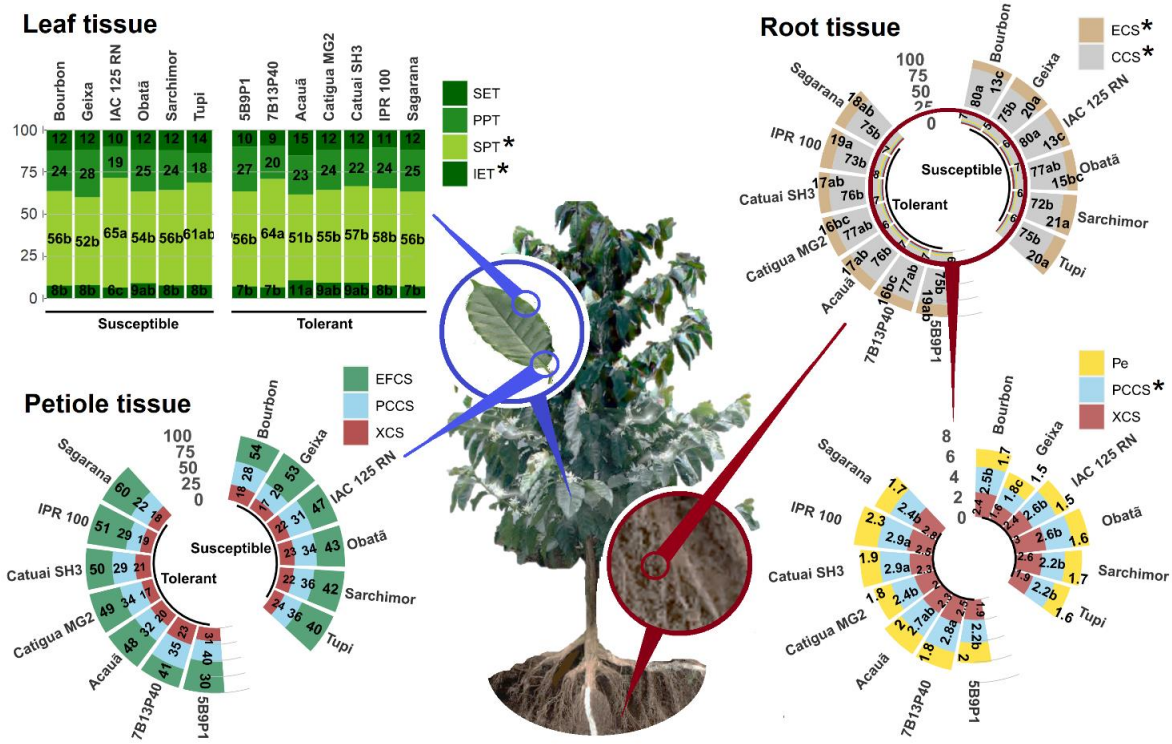

Figure 2. Percentage of leaf, petiole, and root tissues among contrasting (more tolerant and more susceptible) commercial *C. arabica* cultivars. Equal letters indicate no statistically significant difference between sampling cultivars ($P > 0.05$, *LSD*'s test). Means; *: $P < 0.05$, *LSD*'s test. See meaning of abbreviations in Table 2.

Table 1. Source, phenotype information, and reference on the alleged water deficit resistance among coffee genotypes evaluated

Genotypes coffee	EPAMIG/ Sudeste[1]	Matiello, (2017)[2]	Aguiar et al (2014)[3]	Consórcio Pesquisa Café/EMBRAPA[4]	SBI Café Souza *et al.* (2017) SBPC[5]	Cornélio *et al.* [6]	Phenotype (final reference)
Acauã	Tolerant	Tolerant		Tolerant			*Tolerant*
Catuaí SH3	Tolerant						*Tolerant*
IPR100	Tolerant						*Tolerant*
Catiguá MG2	Tolerant				Susceptible	Tolerant moderate	
Sagarana 19	Tolerant						
5B9P1	Tolerant						
7B13P14	Tolerant						
IAC125RN	Susceptible		Susceptible				*Susceptible*
Tupi	Susceptible		Susceptible				*Susceptible*
Obatã	Susceptible		Susceptible				*Susceptible*
Geixa	Susceptible						
Sarchimor	Susceptible						
Bourbon	Susceptible						

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Table 2. List of abbreviations of the histological parameters of leaf, petiole, and root

Organ	Tissue	Abbreviature	Unit
Leaves	*Total leaf blade thickness*	*L_TBT*	µm
	Total leaf mesophyll thickness	*L_MT*	µm
	Leaf superior epidermis thickness	*L_SET*	µm
	Palisade parenchyma thickness	*L_PPT*	µm
	Spongy parenchyma thickness	*L_SPT*	µm
	Leaf inferior epidermis thickness	*L_IET*	µm
	Specific leaf area	*SLA*	$cm^2\ g^{-1}$
	Percentage of superior epidermis	*pL_SET*	%
	Percentage of palisade parenchyma	*pL_PPT*	%
	Percentage of spongy parenchyma	*pL_SPT*	%
	Percentage of inferior epidermis	*pL_IET*	%
	Petiole total cross section area	*P_TCS*	$µm^2$
	Petiole vascular tissue cross section area	*P_VTCS*	$µm^2$
	Petiole epidermis and fundamental tissue cross section area	*P_EFCS*	$µm^2$
Petiole	*Petiole phloem and procambium cross section area*	*P_PCCS*	$µm^2$
	Petiole xylem cross section area	*P_XCS*	$µm^2$
	Petiole number of vessel elements per area	*P_NVA*	VE $µm^{-2}$
	Petiole average of vessel element per diameter	*P_AVED*	VE $µm^{-2}$
	Percentage of vascular tissue cross section area	*pP_VTCS*	%
	Percentage of epidermis and fundamental tissue cross section area	*pP_EFCS*	%
	Percentage of phloem and procambium cross section area	*pP_PCCS*	%
	Percentage of xylem cross section area	*pP_XCS*	%
Root	*Total cross section area*	*R_TCS*	$µm^2$
	Stele cross section area	*R_SCS*	$µm^2$
	Epidermis cross section area	*R_ECS*	$µm^2$
	Cortex cross section area	*R_CCS*	$µm^2$
	Pericycle	*R_Pe*	$µm^2$
	Phloem and procambium cross section area	*R_PCCS*	$µm^2$
	Xylem cross section area	*R_XCS*	$µm^2$
	Number of protoxylem poles	*R_NPX*	unitless
	Number of cell layers in the cortex	*R_NCC*	unitless
	Percentage of stele cross section area	*pR_SCS*	%
	Percentage of epidermis cross section area	*pR_ECS*	%
	Percentage of cortex cross section area	*pR_CCS*	%
	Percentage of pericycle	*pR_Pe*	%
	Percentage of phloem and procambium cross section area	*pR_PCCS*	%
	Percentage of xylem cross section area	*pR_XCS*	%
	Percentage of pericycle	*pR_Pe*	%
	Percentage of phloem and procambium cross section area	*pR_PCCS*	%
	Percentage of xylem cross section area	*pR_XCS*	%

Table 3. Comparison of histological parameters of leaf, petiole, and root tissue between susceptible and tolerant drought cultivars

Organ	Tissue (abbreviature, unit)	Susceptible	Tolerant	*t*-student or Wilcoxon (ǂ)	*P*
Leaves	*Total leaf blade thickness (L_TBT, µm)*	208±6.9	213.3±8.5	180ǂ	n.s.
	Total leaf mesophyll thickness (L_MT, µm)	172.1±7	176.4±8.4	186ǂ	n.s.
	Leaf superior epidermis thickness (L_SET, µm)	23.4±0.5	24.7±0.5	131ǂ	n.s.
	Palisade parenchyma thickness (L_PPT, µm)	48.6±2	48.4±2.3	0,1	n.s.
	Spongy parenchyma thickness (L_SPT, µm)	119.9±6.1	124.3±7.4	184ǂ	n.s.
	Leaf inferior epidermis thickness (L_IET, µm)	16.8±0.5	16.3±0.5	0,8	n.s.
	Specific leaf area (SLA, $cm^2\ g^{-1}$)	144±4.8	135.9±6.4	229ǂ	n.s.
	Percentage of superior epidermis (pL_SET, %)	11.5±0.5	11.9±0.5	161ǂ	n.s.
	Percentage of palisade parenchyma (pL_PPT, %)	23.5±0.9	22.9±1	191ǂ	n.s.
	Percentage of spongy parenchyma (pL_SPT, %)	56.8±1.2	57.4±1.3	181ǂ	n.s.
	Percentage of inferior epidermis (pL_IET, %)	8.3±0.4	7.8±0.3	1,0	n.s.
Petiole	***Petiole total cross section area (P_TCS, µm²)***	**56812.2±3100**	**66092.4±2178.4**	**113ǂ**	*
	Petiole vascular tissue cross section area (P_VTCS, µm²)	**30269.6±2446.2**	**35301.1±2012.1**	**117ǂ**	*
	Petiole epidermis and fundamental tissue cross section area (P_EFCS, µm²)	26542.6±1885	30791.2±1938.5	-1,6	n.s.
	Petiole phloem and procambium cross section area (P_PCCS, µm²)	**18011.4±1415.5**	**21472±1128.6**	**113ǂ**	*
	Petiole xylem cross section area (P_XCS, µm²)	12258.2±1163.3	13829.1±952.3	123ǂ	n.s.
	Petiole number of vessel elements per area (P_NVA, VE μm^{-2})	34195.3±5797	34787.9±6279.9	194ǂ	n.s.
	Petiole average of vessel element per diameter (P_AVED, VE μm^{-2})	6.3±0.2	6.4±0.2	-0,2	n.s.
	Percentage of vascular tissue cross section area (pP_VTCS, %)	53±2.6	53.5±2.5	186ǂ	n.s.
	Percentage of epidermis and fundamental tissue cross section area (pP_EFCS, %)	47±2.6	46.5±2.5	192ǂ	n.s.
	Percentage of phloem and procambium cross section area (pP_PCCS, %)	31.6±1.6	32.5±1.4	190ǂ	n.s.
	Percentage of xylem cross section area (pP_XCS, %)	21.4±1.3	20.9±1.2	183ǂ	n.s.
Root	*Total cross section area (R_TCS, µm²)*	464201±251260.6	278552.3±38719.2	1178ǂ	n.s.
	Stele cross section area (R_SCS, µm²)	32035.8±16914.8	17873.8±2596.9	1313ǂ	n.s.
	Epidermis cross section area (R_ECS, µm²)	47833.8±16730.3	36602.7±3078.3	1198ǂ	n.s.
	Cortex cross section area (R_CCS, µm²)	384331.4±217666.7	224075.8±33439.7	1154ǂ	n.s.
	Pericycle (R_Pe, µm²)	9523.4±5701.5	4244±532.9	1328ǂ	n.s.
	Phloem and procambium cross section area (R_PCCS, µm²)	11727.6±5956.8	6854.5±1046.9	1317ǂ	n.s.
	Xylem cross section area (R_XCS, µm²)	10784.8±5275.0	6777.8±1062.5	1249ǂ	n.s.
	Number of protoxylem poles (R_NPX, unitless)	4.6±0.2	4.8±0.2	1239.5ǂ	n.s.
	Number of cell layers in the cortex (R_NCC, unitless)	8.1±0.5	8.4±0.4	1171.5ǂ	n.s.
	Percentage of stele cross section area (pR_SCS, %)	**6.8±0.2**	**6.1±0.2**	**1642ǂ**	*
	Percentage of epidermis cross section area (pR_ECS, %)	17.3±0.7	16.8±0.7	1368ǂ	n.s.
	Percentage of cortex cross section area (pR_CCS, %)	75.9±0.6	77.1±0.7	1124ǂ	n.s.
	Percentage of pericycle (pR_Pe, %)	**1.9±0.1**	**1.6±0.1**	**1778ǂ**	**
	Percentage of phloem and procambium cross section area (pR_PCCS, %)	**2.6±0.1**	**2.3±0.1**	**1605ǂ**	*
	Percentage of xylem cross section area (pR_XCS, %)	2.4±0.1	2.3±0.1	1335ǂ	n.s.

Mean ± standard error; n.s.: not significant, $P>0.05$; *: $P<0.05$; **: $P<0.01$.

breeding lines which have been identified as contrasting genotypes, based on practical experience and the available bibliographical references.

Leaves, petioles, stems, and primary roots were collected randomly from three plants per cultivar (***Figures 1B, 1C and 1D***). The criterion adopted was the collection of expanded leaves located between the 3rd and 4th node of branches in the middle third of the plants. The middle third of the leaves and petioles were subsampled for sample processing purposes (***Figure 1C***). Root sampling was limited to primary lateral roots in the tree crown projection (***Figure 1D***). The primary stems were collected and processed (data not shown), but removed from the analyses due to recurring problems in embedding the samples.

The material collected in the field was fixed in FAA_{50} (formalin, acetic acid, 50% ethanol; 5: 5: 90 v/v) for 48 h, and was later taken to the Laboratory of the Department of Plant Biology - UFV. In the laboratory, after the fixation period, the samples were washed three times in 70% ethanol, transferring and keeping the samples in this solution until processing. Samples were dehydrated in an ethanolic series until 95% or 100% ethanol. This procedure was carried out under semi-vacuum to facilitate the penetration of the solution and removal of air from within the samples. Then, the samples were transferred to a (1: 1) ethanol: methacrylate resin solution, kept in this solution for 7 days and subsequently transferred for another 7 days in a pure resin solution. During this process, the vials with the samples were kept in a refrigerator.

The resin plus hardener was used to block the samples that were oriented in the transverse plane in the histomolds, previously filled with historesin. The procedure was performed according to the manufacturer's recommendations (Leica, Germany). The histomolds with the samples were kept in an oven at 37 ºC for 1 week and then mounted on wooden blocks.

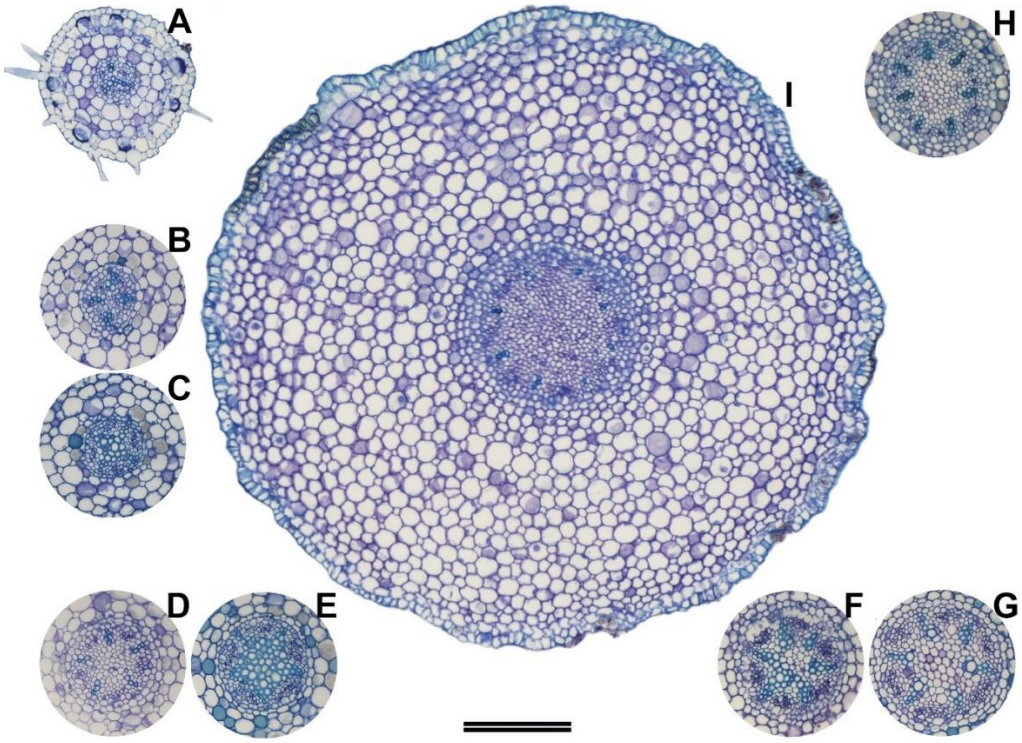


Figure 3. Cross sections of primary lateral roots of commercial coffee cultivars. Cross sections and details of the center cylinder. A – triach root, genotype 7B13P40 (differentiated metaxylem). Note the smaller amount of size and number of cortex cells; B - (undifferentiated metaxylem) and C (differentiated metaxylem) – tetrarch root, genotype 7B13P40; D (undifferentiated metaxylem) and E (differentiated metaxylem) – pentarch root, genotype 7B13P40; F (differentiating metaxylem) and G (undifferentiated metaxylem) – hexarch root, Bourbon variety; H – undifferentiated metaxylem heptarch root, genotype 7B13P40, and; I – entire cross section of a octarch primary root with a undifferentiated metaxylem, Bourbon variety. Note the difference in size and number of parenchyma cortex cells. Bar iquals to 200 µm in all sections.

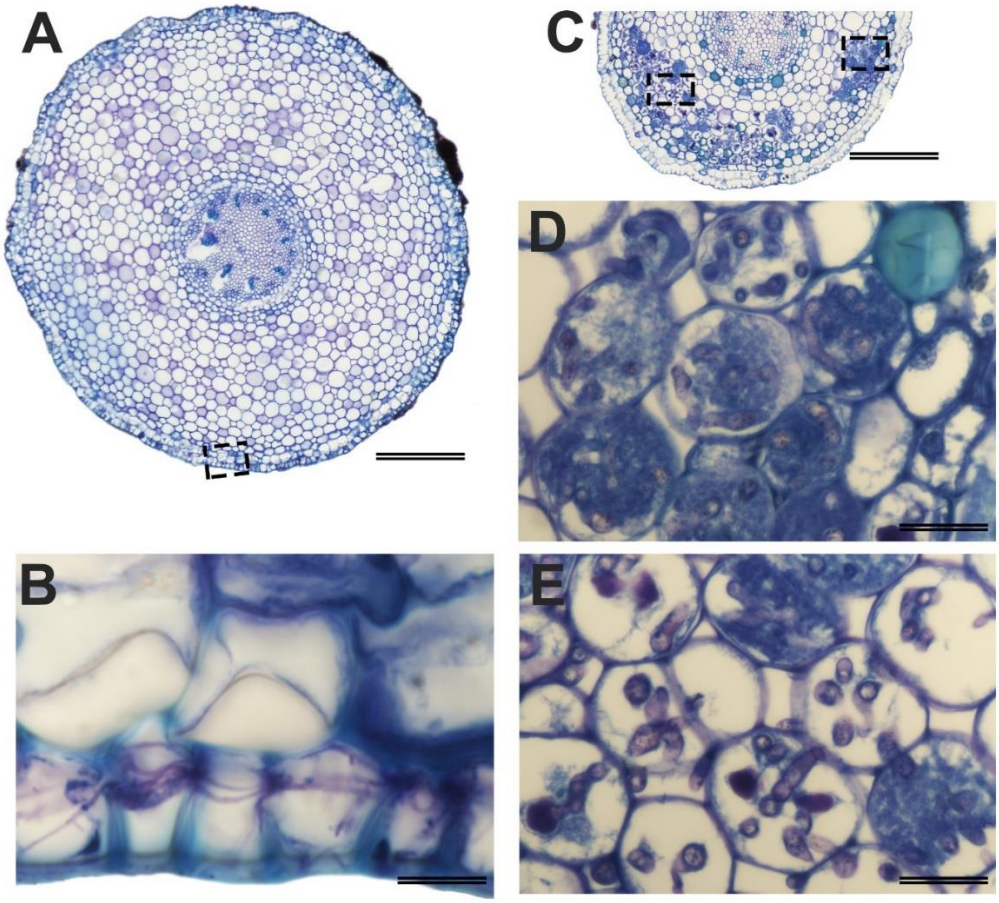


Figure 4. Cross sections of coffee roots with symbiotic interactions. A – cross section of a primary root; B – detail of hyphae associated with epidermal cells; C - – cross section of a primary root with visible endophytic hyphae; D and E, details of hyphae inside cortical parenchyma cells. A and C, bars = 100 µ; B, D, and E, bars = 10 µm. A and B, genotype Bourbon; C, D, and E; Genotype 7B13P40.

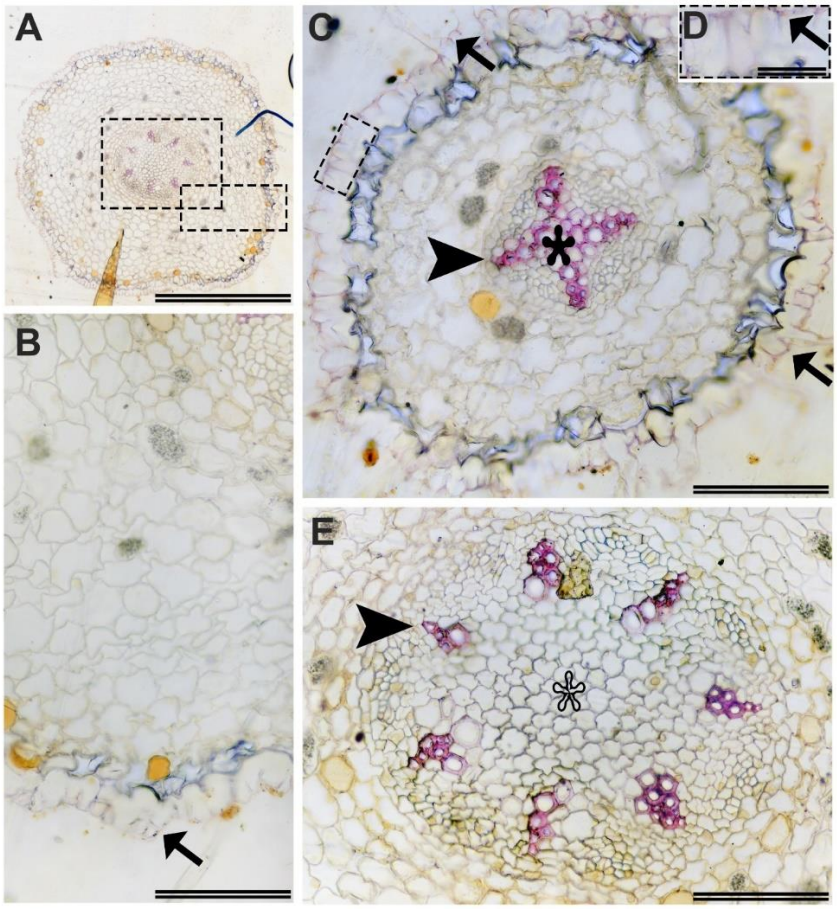


Figure 5. Histochemical tests on *C. arabica L.* root (cross sections), 7b13p40 genotype. A – Root treated with phloroglucinol; B – detail of the cortex and epidermis; C – detail of the central cylinder, note the presence of lignin and suberin stained with phloroglucinol; D – transverse section of the root, observe the layer below the epidermis stained due to contamination with another dye (Sudan); E – detail cut on the periphery of the root. Arrows - epidermal cells details; arrowheads – protoxylem cells; asterisk (full) – differentiated metaxylem, and; asterisk (contour) undifferentiated metaxylem). Arrow – epidermis cell layer. Bars A = 500 µm; B, C and E = 100 µm; D = 50 µm.

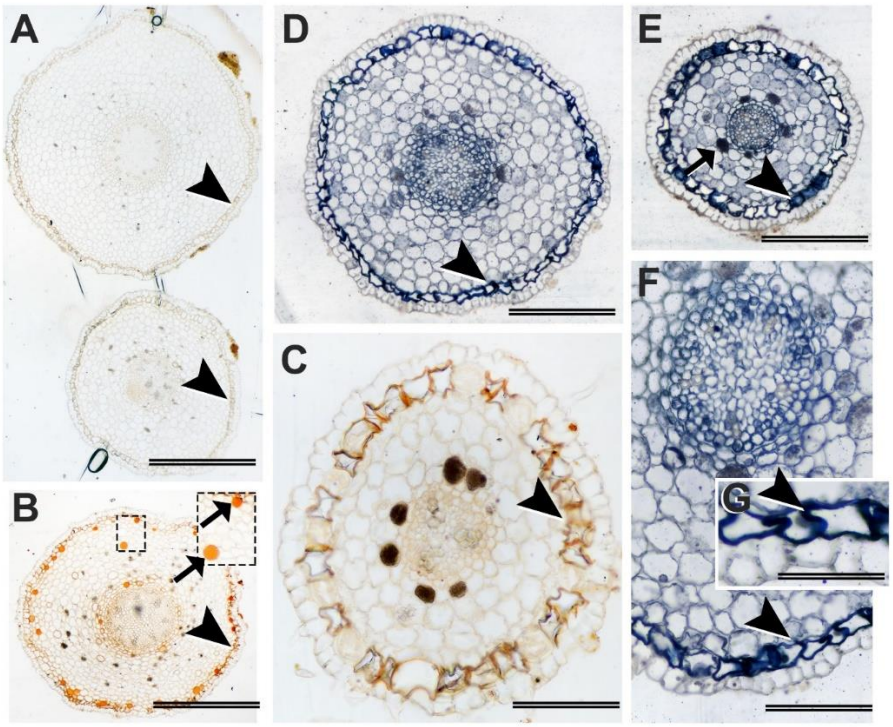


Figure 6. Histochemical tests on *C. arabica* L. root (cross sections), Bourbon genotype. A – Control; B – root treated with Sudan III, detail of lipid marking in yellow; C – detail of the epidermis, note the presence of lipids stained with Sudan in yellow; D – transverse section of the root, stained with Toluidine and Sudan Black; E – transverse section of the root, stained with Toluidine Blue and Sudan Black, detail for the presence of lipids; F - G – detail of the periphery of the root with exoderm and the presence of lipids. Bars A, B, C, D and E= 500 µm; Figure = Figures F = 100 µm; detail G = 50 µm.

Transverse sections 8 µm thick were obtained on an automatic rotary microtome (RM 2155, Leica Microsystems Inc., USA) with disposable glass or steel knives. The sections were placed in a container containing hot water, adhered to histological slides, stained with 0.05% Toluidine Blue, pH 6.5 and mounted with synthetic resin (Permount, Fisher Scientific, USA).

Images of selected sections were obtained with a digital camera (AxioCam HRc, Zeiss, Germany) and a microcomputer with an image capture program (Axio Vision, Zeiss, Germany) (***Figures 1E – 1I***), coupled to a light microscope (AX -70 TRF, Olympus Optical, Japan). Three representative images of each sample were obtained for descriptive anatomy and histometry. The photos were analyzed using Image Pro Plus image analysis software (MediaCybernetics), measuring three fields for each image of the leaf blade, or three images of cross sections of roots and petioles.

The histometric analysis was based on estimates of the thickness of the leaf blade, mesophyll, upper surface epidermis, palisade parenchyma, lacune parenchyma and lower surface epidermis (***Figure 1E***), for the leaf blade; proportion of epidermal, fundamental and vascular tissues (xylem and phloem), to the petiole (***Figures 1F – 1I***) and; proportion of epidermal, fundamental and vascular tissue (xylem and phloem) to primary roots (***Figures 1J and 1K; Table 2***).

Histochemical tests

Two histochemical tests were conducted with included samples using phloroglucinol, to evaluate the presence of lignin (Jensen, 1962) and Sudan III (Johansen, 1940) and Sudan Black (Lison, 1960), to identify lipids in the root samples. A treatment without reagents or staining was set up in water and used as a test blank or control.

Specific leaf area (SLA)

The specific leaf area was estimated from standardized leaf discs that were oven-dried at 60ºC, until reaching a constant weight, and SLA calculated as the ratio of leaf discs area and dry mass ratio (cm^2 g^{-1}). The list of the histological variables, and their respective units and abbreviations, is depicted in ***Table 2***.

Data analysis

All histological parameters of leaf, petiole, and root tissues from the 13 coffee cultivars/genotypes were evaluated by one-way analysis of variance (Fisher's ANOVA) or Kruskal-Wallis's test, *a priori* checking the statistical assumptions (*i.e.* normality of residuals by Shapiro-Wilk's test (Shapiro & Wilk, 1965), and homogeneity of variances by Bartlett's test (Barlett, 1937). The detection of the difference between means was by the least significant difference test (*LSD*, $P<0.05$). Spearman correlations were performed between all pairs of histological leaf, petiole, and root tissue percentage parameters of all cultivars combined. All statistical analyses were performed in R programming language, version 4.2.3 (R Core Team, 2021).

Results

C. arabica genotypes were chosen based on available empirical information on their responses of growth and production under water deficit stress (***Table 1***). These same plants were used as seed source for other experiments (not shown). In the absence acknowledged *C. arabica* water deficit resistant cultivars, leaf blade, petiole, and lateral primary root histometry (***Figures 1-2; Tables 2-3***) were evaluated comparing the alleged more tolerant and more susceptible cultivars according to the available data (***Table 1***) in the seek for inborn features that could be associated with the tolerance phenotype. Area and thickness measurements, and the proportion, of the respective tissues or regions were evaluated (***Tables 2-3***). In addition, anatomical and histochemical descriptive analysis of primary roots were performed (***Figures 3-6***). Despite primary stems were processed, the infiltration and inclusion of samples were not successful, hampering any further anatomical analysis and, for that reason, it will not be presented or discussed in this report.

There are leaf blade traits that differed among the evaluated coffee genotypes (***Figure 2***) but not when the tolerant and susceptible accesses were contrasted (***Table 3***). The other way around was observed for some petiole traits (***Figure 2 and Table 3***). The statistical test was able to capture differences of some root traits among the evaluated cultivars and between tolerant and susceptible groups (***Figure 2 and Table 3***). The spongy parenchyma and inferior face epidermis thickness in the leaf blade; the phloem and cambium cross section proportion; and cortex and epidermis cross section area in primary roots displayed significant differences, implying that epidermal, vascular and fundamental tissues may constitute a contrast among coffee plants (***Figure 2***). On the same hand, petiole cross section, vascular tissue and phloem and cambium cross section area, in petioles, and; percentage of stele, pericycle, and phloem and cambium in roots, also exhibited significant differences (***Table 3***), as the tolerant and susceptible cultivars were compared. This indicates that vascular tissue traits seem to have a significant contribution to water deficit tolerance in coffee.

There are significant correlations among leaf, petiole and root proportions of tissues and regions in the evaluated vegetative organs (***Table 4***). Medium to highly significant correlations were observed among each set evaluated such as the percentage of leaf (pL_PPT, pL_SPT, and pL_SET), of petiole (pP_VTCS, pP_EFCS, and pP_XCS), and root (pR_SCS, pR_ECS, pR_CCS, pR_Pe, and pR_PCCS) tissue percentages. There were also medium and significant correlation among petiole and root (pR_ECS and pP_VTCS, pP_EFCS, pP_PCCS) and leaf and root traits (pL_SET and pR_SCS, pR_Pe), but none between leaf and petiole traits.

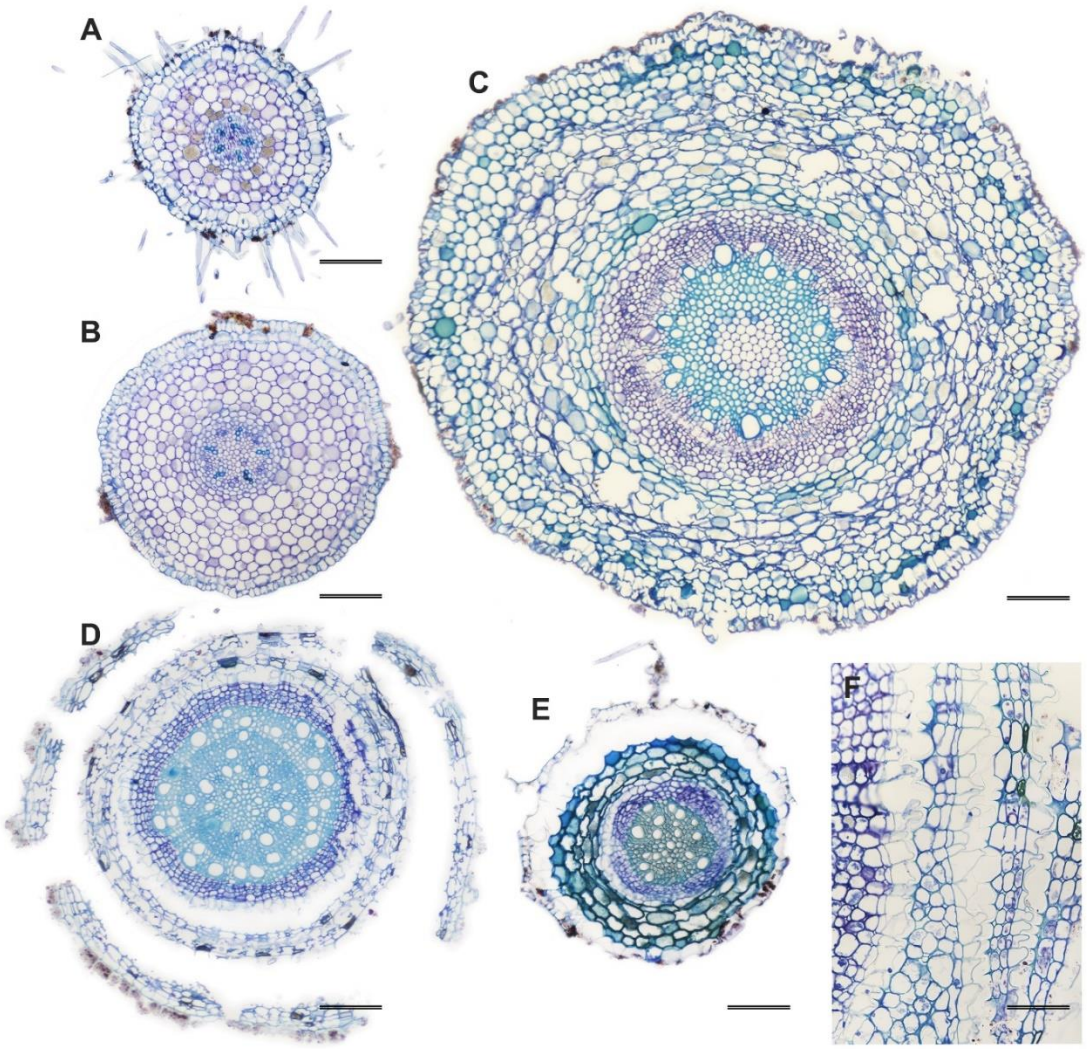
The connection of vascular tissue, phloem in particular, and epidermal tissues between roots and petioles (***Table 2***) highlight the importance of vascular tissue and photosynthates transport in the coffee cultivars refereed as more resistant to water deficit. It seems that there is a link of the amount of phloem tissue and cambium, and epidermal tissues between petioles and roots, what may be attributed to their origin, respectively. Nevertheless, similarly to the associations between stele cross section and pericycle in roots with the thickness of the upper epidermal face in leaves still, further and thoughtful scrutiny is needed.

The descriptive anatomical and histochemical study of primary roots bring to the spotlight interesting features of coffee plants root development that opens new venues in the seek for water deficit tolerance in *C. arabica*. Epidermis is simple and present variable number of root hairs, as well as these hairs can be absent despite primary roots (***Figures 1J, 3A, 3I, 4a, and Suppl Fig. 1A, and Suppl. Fig 1B***). Cortex ranged

Table 4. Spearman correlations matrix between all pairs of histological leaf, petiole, and root tissue percentage parameters of all cultivars combined. See meaning of abbreviations in Table 2.

Histological parameters		Leaf				Petiole				Root				
		pL_SET	*pL_PPT*	*pL_SPT*	*pL_IET*	*pP_VTCS*	*pP_EFCS*	*pP_PCCS*	*pP_XCS*	*pR_SCS*	*pR_ECS*	*pR_CCS*	*pR_Pe*	*pR_PCCS*
Leaf	*pL_PPT*	0.10												
	pL_SPT	**-0.66*** **	**-0.79*** **											
	pL_IET	**0.72*** **	-0.02	**-0.54*** **										
Petiole	*pP_VTCS*	-0.21	-0.21	0.29	-0.19									
	pP_EFCS	0.21	0.21	-0.29	0.19	**-1.00*** **								
	pP_PCCS	-0.22	-0.21	0.30	-0.20	**0.93*** **	**-0.93*** **							
	pP_XCS	-0.16	-0.17	0.23	-0.15	**0.91*** **	**-0.91*** **	**0.69*** **						
Root	*pR_SCS*	**-0.34***	0.02	0.19	-0.25	0.27	-0.27	0.27	0.21					
	pR_ECS	0.23	0.17	-0.19	-0.13	**-0.34***	**0.34***	**-0.42** **	-0.18	**-0.30** **				
	pR_CCS	-0.11	-0.18	0.12	0.22	0.25	-0.25	0.33*	0.11	-0.02	**-0.95*** **			
	pR_Pe	**-0.34***	0.04	0.15	-0.20	0.04	-0.04	0.05	0.02	**0.52*** **	0.04	**-0.22***		
	pR_PCCS	-0.28	-0.16	0.26	-0.10	**0.34***	**-0.34***	**0.34***	0.28	**0.90*** **	**-0.38*** **	0.10	**0.37*** **	
	pR_XCS	-0.25	0.13	0.08	-0.28	0.22	-0.22	0.22	0.17	**0.89*** **	**-0.28** **	0.00	0.17	**0.72*** **

*: $P<0.05$; **: $P<0.05$; ***: $P<0.01$.



Supplementary Figure 1. Differentiating roots from primary to secondary growth in commercial *C. arabica* cultivars. A – Differentiating pentarch primary root with root hairs; B – Differentiating pentarch primary root cross section without root hairs; C – secondary growth root with sustained cortical tissue; D – secondary growth root with a rhytidome and outter cortex layers being discarted; E – secondary growht root with reduced phloem tissue and similar diameter of primary growth roots, and; F – detail of the rhytidome and the elimiation of cortical/phloem cells. A, B, C, D, and E, barrs = 100 µm; F, barr = 50 µm.

from averages of 4 to 17 cell layers and the number of protoxylem poles in primary lateral roots from 3 to 8 (***Figure 3***), although neither differed statistically among the coffee genotypes (***Figure 2; Table 3***). Frequently mycorrhizal associations were observed at the epidermis (***Figures 4A and 4B***) and at cortical parenchyma (***Figures 4C, 4D, and 4E***) of coffee primary roots. It was not clear if there is a link between cortex cross section area, number of cell layers or of idioblasts harboring calcium oxalate (CaOx) crystals (data not shown) and the occurrence of these symbiotic associations.

It is worth to note that the tolerant genotypes had fewer poles than the susceptible cultivars, despite this difference was not significant. This reasoning and information are mentioned because, beyond the number of protoxylem poles, the amount and diameter of differentiated tracheary elements (TE) was not evaluated, and less differentiated metaxylem were observed in the roots with increased number of protoxylem poles (***Figure 3***). It is a common sense that smaller TE will transport less sap, the same applies to roots with smaller number of differentiated TE. Accordingly, although there is a statistically similar number of protoxylem poles among the coffee cultivars, the size and total number of TE differentiated can contribute to xylem sap transport among more tolerant or more susceptible genotypes. The number of protoxylem could be related to the number of cortex cell layers as well as the root cross section area (***Figures 1A and 1I***). As a footnote for sampling, any future study on root must also evaluate the anatomical structure as secondary growth roots of similar size of primary roots are observed (***Supp. Figure 1***).

Histochemical approach of coffee primary roots of different cultivars was useful to raise doubt of its epidermal cell wall constitution. There was a weak reaction for the presence of lignin in the epidermis (***Figures 5A, 5B, 5C, and 5D***), what may hinder water absorption if generalized or increased. It was also possible to observe less differentiated metaxylem in primary roots with greater number of protoxylem poles (***Figures 5C and 5E***). The xylem cell differentiation regarding vessel elements cell wall deposition and lignification are features associated with its assumed role in sap transportation. The outer cortex parenchyma cell layer was slightly thickened compared to inner cortex cells (***Figure 6***), independently from the cortex area. In the cortex there were also cells with lipid bodies (***Figure 6B***) and CaOx crystals (***Figures 5B and 5C***). The slightly thickened lipid containing cell walls may (***Figures 6D, 6E, and 6F***) or may not (***Figure 6C***) be continuous. The presence of lipids in outer cortex cell walls of coffee primary roots is a feature that may also hinder water absorption.

Discussion

The leaf is one of the most plastic organs considering the responses to environmental factors (Castro et al., 2009). Anatomical variations in leaves can provide plants with the ability to overcome unfavorable conditions for growth and survival. The leaf anatomy of different coffee tree genotypes exhibits variation in the thickness of the cuticle, blade, palisade and spongy parenchyma, stomatal dimensions, among other characteristics (Ramiro et al., 2004; Pinheiro et al., 2005; Nascimento et al., 2006; Batista et al., 2010; Nikolopoulos et al., 2024). The plasticity of leaf characteristics is based on their anatomical structure, therefore, they can support the phenotypic plasticity information, as well as the tolerance or susceptibility traits of coffee cultivars submitted to water deficit.

The histometric data of the leaf blade did not differed between water deficit tolerant and susceptible coffee genotypes, although there are differences in the thickness of the inferior epidermis face and spongy parenchyma. This raises the hypothesis that the genotypes tested in the present report may have a higher similarity among them (Carvalho, 2007) and water deficit resistance traits should be searched in other compatible *Coffea* genotypes. A wider sampling and the study of the environmental x genotype interaction should be evaluated as Santos et al. (2022) reported high genetic variability and heritability greater than 70% for leaf anatomical traits of 23 *C. arabica* varieties in Brazilian Savanna. Additionally, Perez-Molina et al. (2021) could successfully correlate leaf traits with coffee drink quality based on around 360 sampling points and despite uncontrolled differences on the management of the crops, and altitude and azimuthal orientation references.

Bone et al. (1985) mentioned that epidermal cells could function as lenses to direct light into the chlorenchyma cells. This was also evidenced in other reports (Martin et al., 1989; Brodersen & Vogelmann, 2010). There are negative correlations ranging from 54 to 66% of the thickness of the spongy parenchyma with the inferior epidermal face, and between adaxial epidermis and spongy parenchyma thickness. Whatever stimuli that would increase spongy parenchyma might had a negative effect on the thickness of the adaxial epidermal tissue, hence, covering up its assumed function of light funneling to chlorenchyma cells.

Queiroz-Voltan et al. (2014) reported that coffee plants more tolerant to drought stress exhibited thicker palisade parenchyma and vasculature in leaves blade and petioles. The palisade parenchyma is closely linked to photosynthesis and, greater development of this tissue may allow greater fixation of CO_2 with the opening of the stomata in a short space of time (Castro et al., 2009). Melo et al. (2014) observed a decrease in adaxial epidermis thickness and an increase in stomata density in coffee plants conducted under water deficit stress. There was a significant difference of the spongy mesophyll among the tested cultivars but no leaf blade trait was enough to differentiate the tolerant and susceptible genotypes. The differences in the spongy parenchyma thickness among Catuai and Siriema leaves were observed due the irrigated treatment, and palisade parenchyma thickness decreased in the non-irrigated 'Catuaí' (Grisi et al., 2008). The hypothesis of a reduced variability in, at least some of, the *C. arabica* leaf traits is corroborated as palisade parenchyma were similar, whereas the spongy parenchyma differed among 23 coffee varieties (Santos et al., 2022).

The anatomical structure can reflect environment adaptations conferring plants favorable traits under water stress such as xerophytes (Fahn & Cutler, 1992). Increased leaf blade thickness, typical of sun leaves, are characteristics that aim to minimize leaf heating and can provide less water loss to the environment (Nascimento et al., 2006). *C. arabica* was originally adapted for a lower light incidence (Araújo et al 2008; Carvalho, 2007), and, despite the significant difference for IEP, traits such as leaf relative (azimuthal) position, inclination (Nikolopoulos et al., 2024) and position in the treetop (Araújo et al., 2008) might played a role in the water deficit stress outcomes. Plant tissue responses to water stress depend on the physiological properties of cellular components and anatomical characteristics, which regulate the transmission of water stress to cells.

The petiole must be an efficient structure when it comes to transporting nutrients and water, as it joints the leaf to the stem, and that, due its position, it can contribute to improve light capture in addition to carrying water and nutrients from and off the leaf (Faisal et al., 2010). Schultz (2003) observed that the water conduction capacity of the grapevines stems and especially in the petioles is related to the stomatal behavior of different cultivars under water stress. Thus, the structure of the petiole is linked to the plant's hydraulic conductance, which is why its anatomical characteristics can interfere with resistance to water deficit (Dayer et al., 2017).

Curiously, the coffee petiole traits were similar among the 13 genotypes tested, but significant differences and correlations were observed between the stablished tolerant and susceptible groups. These accounted for the total petiole cross section area, vascular tissue, and phloem and cambium tissues. This is a trend to be followed as the plants were conducted under the same climate conditions, and despite the group tolerant/susceptible groups were gathered based on empirical observations. Picoli et al. (2021) argued that the prospection of water deficit traits should be conducted under water drought conditions at the risk, of otherwise, favor plants that would respond to optimized environmental conditions. This applies to all anatomical features approached here, as they should be considered inborn, as the coffee plants evaluated were not conducted under stress. Further, the anatomical differences observed may be amplified as water deficits is acknowledged as a driver for histological responses to water deficit in coffee plants (Grisi et al., 2008; Castro et al., 2009; Melo et al., 2014).

Condé et al. (2020a; 2020b) reported high accuracy and heritability of petiole vascular tissue traits, whereas Queiroz-Voltan et al. (2014) observed a positive effect of vascular tissue traits associated with water deficit resistance in coffee. Seemingly, the vasculature differentiation is a candidate trait that will cope with water deficit resistance as a differentiated and adapted vessel elements and sieve tube elements should sustain sap transport under stress conditions. On the other hand, the strong and significant correlations of fundamental tissue percentage and phloem and xylem implies a trait that will decrease the proportion of vascular tissues if environmental signals favor the first.

Under water stress, the conduction of photosynthates through the phloem is affected to such an extent that some tissues present a reduction in carbon reserves, which can, in extreme conditions, lead to the death of the plants (Sala et al., 2010). This maintenance can allow a greater flow of carbohydrates from the aerial part to the roots, as well as the translocation of nutrients necessary for plant development and fruit production (Pereira et al., 2008). This is corroborated by negative correlations between petiole vascular/phloem tissue with root epidermis, and fundamental tissue in petiole with phloem in roots. There is a small, although significative, negative correlation between xylem and phloem. Even though exchange activity in the cambium is modulated by genetic and hormonal factors and one or another vascular tissue prevails (Furuta et al., 2014; Simmons & Bergmmann, 2016), this correlation may reflect a balance and reallocation of water and nutrients in the phloem that should occur according to environmental stimuli.

Nutritional and mineral availability can be a game changer in this context. Melo et al. (2014) reported reduced nitrate reductase activity in coffee plants conducted under water deficit stress. Further, only coffee plants treated with high nitrogen application exhibited increased cell wall rigidity and some ability for osmotic adjustment under water drought (DaMatta et al., 2002). These reports imply a loop that coffee plants may go through under water deficit. There will be less nutrients (*e.g*. nitrogen) available, due reduced enzymatic machinery for nutrient assimilation, and a debilitated anatomical structure to deal with lower water potential, that in turn will hold back nutrient absorption/assimilation, therefore, maintaining a cyclic response decreasing the plant ability to deal with water deficit. Despite in the same environment, there were differences in soil and leaf samples mineral composition (***Supp. Table 1-2***), but were not discussed as there was not a systematic control of the mineral nutrition of the sampled plants that would allow further evaluation, so being attributed to random factors.

The root system, its morphology, development and anatomy have a potential impact on understanding water restriction in coffee plantations. We observed reports that aspects of anatomy can be useful for understanding the capacity for tolerance to water stress found in different *Coffea* species (Dias et al., 2005; Grisi et al., 2008). Roots play a fundamental role in the processes of obtaining water and nutrients and for fixing the plant in the soil, in addition to serving as a storage organ, where the photo assimilates produced in the aerial part are accumulated, and can be redistributed to the aerial part and thus cover expenses with flowering and fruiting (Zonta et al., 2018). Knowing the relationship between the aerial part and its roots and how this impacts the processes related to water absorption is essential for the good performance of coffee plants subjected to water scarcity. From a functional point of view, roots with reduced diameters (thin) or absorption roots are those that present intense metabolic activity, with the main physiological role being the absorption of water and nutrients, while roots with larger diameters (thick) are those responsible for the structural support of trees and for conducting the solutions absorbed between the rhizosphere and the aerial part (Magalhães, 2021).

Pinheiro et al. (2005) and Silva (2010) emphasized that the larger root system presented in *C. canephora* is an advantage in relation to *C. arabica* trees under water deficit. Santos & Mazzafera (2012) concluded that the *C. canephora* cultivar 'Apoatã IAC-3600', and grafted plants Mundo Novo IAC-464/Apoatã IAC-3600 better withstood the water stress when compared to cultivars of *C. arabica* 'Catuaí IAC-81', and 'Mundo Novo IAC-464' without grafting. When evaluating the behavior of the root system of Siriema coffee submitted to water deficiency, Paglis et al. (2009) observed that plants invested in dry matter in the root by changing the strength of the drain, with the advancement of the root system contributing to the plant was capable of absorbing water from the deeper layers of the soil. This is an important strategy for surviving long periods of water scarcity. Although acknowledged that the root system morphology has an important role on water deficit resistance, anatomical approach should also be considered as secondary roots, with a differentiated periderm and phenolized cortex cells, may have similar diameter as primary coffee roots. This similarity may impact the assumptions and responses taken based only on morphological traits.

Under drought, root water absorption capacity plays a fundamental role in regulating the transpiration rate and in the development of various adaptive strategies (Salsinha et al., 2021). In some species, the thickness of the cortex varies as a result of a decrease in water potential, which, in turn, leads to a contraction of cortical cells caused by a decrease in cell volume (Huang, 1998). Chimungu et al. (2014) confirmed that reduced

number of cortical cell layers reduced the metabolic costs in soil exploration in tolerant maize varieties. Despite non-significant, there is a considerable range of cortical cell layers (4-17) that, if conducted under water deficit (Picoli et al., 2021) could allow the evaluated coffee genotypes in the present report express and differentiate their roots in dissimilar pattern among tolerant and susceptible genotypes. The significant correlation between the cortex cell layers with protoxylem numbers, and the qualitative information of differences in the outer cell wall thickness and composition corroborates to possible roles of cortical cells in water deficit tolerance in coffee plants.

Cuneo et al. (2016) reported mechanical failure of fine root cortical cells, identified as the primary driver the hydraulic conductivity reduction, where these roots would function as fuses preserving hydraulic integrity of plant vascular tissues in the beginning of water deficit. Accordingly, despite the CCS and NCC did not differed significantly, a meticulous evaluation of root anatomical structure may cope with water deficit resistance in coffee. On the other hand, Melo et al. (2014) considered that the increase in cortex thickness in coffee plants under water deficit as a way of increasing root hydraulic retention or water availability. The lack of a significant difference among the 13 genotypes tested may imply in a reduced variability or lack of root cortex traits contributing to the tolerance phenotype. Under this standpoint, the sightly thicker cell walls with lipid deposition in the outer cortex cell layer (***Figure 6***) may drive a hydraulic protective trait or slow down water absorption. On the other hand, the root cortical aerenchyma seems to improve plant growth, soil exploration, and water acquisition in maize (Chimungu et al., 2015), what seems not to be the case in coffee plants (data not shown). Nevertheless, it is a hypothesis to be double checked.

Accordingly, Cuneo et al. (2020) reported the formation of lacunae, which is interpreted as associated with an aerenchyma, in water deficit-resistant grapevine fine roots under milder drought stress. A drought-susceptible grapevine genotype had suberin deposited in fine roots early developmental stages, what might had hampered the formation of the cortical lacunae in the roots of this latter genotype conducted under mild water deficit. It is interesting to date that increased aerenchyma were associated with decreased mycorrhizal colonization whereas root rots were positively correlated with the number of cortical cell files and inversely correlated with cortical cell size (Galindo-Castañeda et al., 2019).

In eudicots, the number of xylem poles varies widely between different species or between roots of the same plant (Esau, 2000; Fahn, 1982). The number of protoxylem poles may be correlated with root vigor and diameter (Mauseth, 1988). Sometimes, in roots at advanced stages of development and greater robustness, an increase in the number of xylem poles is observed. According to Dickison (2000), this variation is influenced by the level of hormones present in the root apex. There is a range of 3-8 protoxylem poles that were similar among the 13 coffee cultivars. Nevertheless, the sample coffee plants were not conducted under controlled water deficit stress, and is possible to observe that larger number of protoxylem poles implied in less differentiated metaxylem cells, what implies in less differentiated tracheary elements. It is reasonable to argue that there are indirect consequences of the protoxylem differentiation that will impact the amount of differentiated vessel elements that will be effectively conducting xylem sap.

The proportion of roots with different protoxylem poles was not be accessed, despite a range of 3-8 poles and a non-significant difference between the tolerant and susceptible coffee genotypes. Sampling of roots might be biased, as at least 9 samples were processed initially but there were roots with secondary growth, with similar diameter compared to the roots exhibiting primary growth. Roots with secondary growth were not considered, although at least 3 primary roots were sampled for each plant. Li et al (2022) reported that root length, diameter, stele, and hydraulic conductivity were significant and positively related to the number of protoxylem poles, independently the three species evaluated. Notably, higher (≥ 4 or 5) protoxylem poles, thicker stele and wider vessel elements are expected (Bagniewska-Zadworna et al., 2014), what may be increased with mycorrhizae colonization (Zadworny & Eissenstat, 2011; Moreira et al., 2018). Ecto and endomycorrhizae were observed in primary roots of the evaluated coffee genotypes. Absorption was highlighted in, despite decreased contribution to sap transportation in roots with smaller number of protoxylem poles (Zadworny & Eissenstat, 2011; Bagniewska-Zadworna et al., 2014). Contrarily these results, in coffee primary roots metaxylem was more differentiated in roots with protoxylem poles ≥5 or 6. Additional functional features associated with the number of protoxylem poles (groups), such as root lifespan and branching, are raised (Li et al., 2022), and should and could be further investigated in the coffee case of study.

Despite the evaluated coffee genotypes exhibited similar SLA, anatomical and physiological changes can occur due to water deficiency. Analyzing these changes together with the objective of obtaining differential tolerance to drought can generate discrimination between the plants studied (Grisi et al., 2008; Batista et al., 2010; Matos, 2016). This information can contribute to optimize the launch time of new coffee cultivars in the genetic improvement program (Batista et al., 2010; Matos, 2016). Some coffee trees may exhibit a level of drought tolerance due to the stability of several physiological parameters that remain relatively constant within a specific range of water deficit. However, there are variations in behavior between cultivars belonging to the two economically important species, *C. arabica* L. and *C. canephora*, in which some demonstrate high tolerance to drought, while others are more sensitive (Melo, 2008). The access and incorporation of *C racemosa*, *C liberica*, *C canephora* (Carvalho et al., 2017), and *C stenophylla* and *C. affinis* (Davis et al., 2020) must increase the genetic and phenotypic variability and benefit the seek for water deficit resistance for *C. arabica*.

Concomitant with the introgression of water drought resistant genes that might be available for coffee, the study of the underground of root traits may also benefit coffee plant production under water deficit stress (Comas et al., 2013). Moreira et al. (2018) observed an increase in growth, leaf area, and 21% more root mass and increased growth and tolerant to moderate water deficits in *Coffea* plants inoculated with mycorrhizae. The authors mentioned a colonization efficiency of 39% of plants derived from artificially inoculated seedlings., there were observed ecto and endomycorrhiza in the 13 *C. arabica* genotypes, despite the frequency of colonization was not quantified under natural conditions at the CEPC-EPAMIG. The evaluation, identification and selection of these mycorrhizae may benefit water and mineral absorption, alleviating water deficit stress and reducing essential mineral input.

Supplementary Table 1. Mineral analysis from leaf tissues of the sampled coffee plants/genotypes.

	dag Kg^{-1}						mg Kg^{-1}				
Sample	**N**	**P**	**K**	**Ca**	**Mg**	**S**	**Cu**	**Fe**	**Zn**	**Mn**	**B**
5B9P1 - PL1	2.75	0.11	1.65	1.46	0.44	0.21	27.53	107.89	16.38	51.77	51.58
5B9P1 - PL2	3.56	0.13	2.12	1.06	0.30	0.21	23.80	110.85	13.24	95.10	53.38
5B9P1 - PL3	3.48	0.13	1.96	1.50	0.41	0.23	34.78	112.44	16.96	111.59	65.11
7B13P40 - P1	3.52	0.12	2.01	0.98	0.28	0.20	32.08	88.15	18.33	70.88	49.75
7B13P40 - P2	2.94	0.13	2.17	1.06	0.31	0.20	25.62	97.62	12.12	86.46	51.67
7B13P40 - P3	3.09	0.13	2.18	0.99	0.27	0.21	35.30	74.21	20.02	82.32	53.29
ACAUÃ - PL1	2.40	0.12	2.04	1.67	0.48	0.24	73.20	93.60	37.39	81.10	67.34
ACAUÃ - PL2	2.41	0.11	1.71	1.68	0.45	0.21	63.69	117.47	38.86	96.48	73.32
ACAUÃ - PL3	2.91	0.12	2.22	1.64	0.40	0.30	61.60	86.70	27.87	123.21	77.20
BOURBON - PL1	3.79	0.12	2.44	0.97	0.27	0.21	28.00	78.51	14.95	110.11	51.13
BOURBON - PL2	3.17	0.12	2.23	0.91	0.26	0.20	31.79	59.60	16.71	82.93	43.86
BOURBON - PL3	3.25	0.12	2.29	0.86	0.24	0.18	31.69	61.30	18.11	74.80	37.50
CATIGUA MG2 - PL1	3.25	0.13	1.67	1.31	0.28	0.22	33.84	85.93	16.72	90.79	64.22
CATIGUA MG2 - PL2	3.45	0.14	2.07	1.27	0.27	0.22	33.91	96.76	17.25	187.67	70.40
CATIGUA MG2 - PL3	na	na	na	na	na	na	na	na	na	na	na
CATUAI SH3 - PL1	2.72	0.11	2.55	1.11	0.34	0.20	46.12	117.39	19.89	99.83	51.75
CATUAI SH3 - PL2	3.25	0.11	2.35	1.43	0.39	0.23	41.39	94.14	18.83	126.56	60.44
CATUAI SH3 - PL1	1.55	0.11	2.25	1.30	0.37	0.21	93.14	95.81	32.47	82.43	57.12
GEISHA - PL1	1.86	0.12	2.47	0.98	0.24	0.22	63.36	177.52	18.20	98.94	61.25
GEISHA - PL2	3.56	0.12	2.53	1.19	0.27	0.21	57.35	131.80	20.89	114.95	62.78
GEISHA - PL3	3.48	0.12	2.16	0.92	0.24	0.19	63.72	82.03	19.05	113.28	45.09
IAC 125 RN - PL1	3.32	0.12	1.93	1.07	0.28	0.20	22.86	82.26	8.70	46.80	43.75
IAC 125 RN - PL2	2.78	0.09	1.75	0.77	0.20	0.16	12.74	77.23	13.40	63.29	43.22
IAC 125 RN - PL3	3.40	0.13	1.53	0.67	0.20	0.18	33.32	92.89	13.82	44.07	36.39
IPR 100 - PL1	3.25	0.13	2.82	1.26	0.40	0.25	71.22	99.40	29.75	102.02	59.63
IPR 100 - PL2	2.13	0.11	2.36	1.35	0.39	0.21	36.23	75.86	15.77	85.00	51.89
IPR 100 - PL3	2.94	0.13	2.18	1.50	0.48	0.23	52.66	85.81	23.50	93.31	56.94
OBATA - PL1	3.40	0.13	2.44	1.27	0.37	0.21	47.76	111.20	23.23	124.94	62.02
OBATA - PL2	3.32	0.14	2.80	1.26	0.40	0.23	39.64	109.12	21.41	110.94	59.47
OBATA - PL3	2.63	0.15	3.12	1.50	0.40	0.26	75.66	128.66	38.22	82.90	62.66
SAGARANA 19 - PL1	3.32	0.14	2.10	1.01	0.40	0.22	43.35	96.03	23.06	58.22	74.13
SAGARANA 19 - PL2	3.01	0.13	1.89	1.06	0.44	0.21	35.28	99.66	15.89	63.23	64.74
SAGARANA 19 - PL3	3.09	0.15	2.13	1.08	0.43	0.21	36.77	87.86	17.49	67.68	67.30
SARCHIMOR 8840 - PL1	3.25	0.13	2.24	1.23	0.20	0.20	25.56	87.65	13.36	75.54	54.00
SARCHIMOR 8840 - PL2	3.17	0.11	1.87	1.18	0.21	0.17	26.61	72.71	15.34	117.49	58.75
SARCHIMOR 8840 - PL3	3.00	0.11	2.20	1.45	0.25	0.19	30.49	112.22	16.19	119.85	71.57
TUPI - PL1	2.94	0.14	1.95	1.39	0.41	0.21	33.74	146.14	15.73	72.86	73.82
TUPI - PL2	3.39	0.15	2.26	1.15	0.39	0.24	65.28	109.03	23.31	75.72	69.69
TUPI - PL3	2.86	0.10	1.90	1.17	0.38	0.19	45.88	155.10	23.01	60.37	77.28

na – not available

Supplementary Table 2. Mineral analysis from soil samples from planted areas with the sampled coffee genotypes.

		mg dm^{-3}	mg dm^{-3}	$cmol_c$ dm^{-3}	$cmol_c$ dm^{-3}	$cmol_c$ dm^{-3}	$cmol_c$ dm^{-3}	$cmol_c$ dm^{-3}	$cmol_c$ dm^{-3}	%	%	dag kg^{-1}	mg L^{-1}	mg dm^{-3}	mg dm^{-3}	mg dm^{-3}	mg dm^{-3}	mg dm^{-3}	mg dm^{-3}
Sample	**pH H_2O**	**P**	**K**	**Ca^{2+}**	**Mg^{2+}**	**Al^{3+}**	**SB**	**t**	**T**	**V**	**m**	**MO**	**P-Rem**	**S**	**B**	**Cu**	**Mn**	**Fe**	**Zn**
GEI SHA	5.43	9.80	82.00	2.51	0.93	0.00	3.65	3.65	8.95	40.80	0.00	4.52	13.00	35.00	0.35	3.87	19.50	34.80	3.21
CATUCAI SH3	4.79	17.80	88.00	1.74	0.61	0.20	2.58	2.78	9.48	27.20	7.20	3.72	10.90	109.40	0.53	6.05	7.50	23.60	4.12
SHARCHIMOR 8840	5.42	26.90	94.00	2.70	0.63	0.00	3.57	3.57	9.87	36.20	0.00	4.39	11.90	21.20	0.35	3.04	15.10	25.50	6.00
IPR 100	4.40	40.70	74.00	0.73	0.17	0.59	1.09	1.68	8.69	12.50	35.10	4.12	8.10	31.40	0.49	2.83	4.30	23.70	1.68
SAGARANA 19	5.76	4.50	116.00	2.63	0.96	0.00	3.89	3.89	7.79	49.90	0.00	4.39	11.90	3.60	0.23	4.77	23.20	18.00	4.19
CATIGUA MG2	5.34	3.60	112.00	2.67	0.47	0.00	3.43	3.43	8.93	38.40	0.00	3.86	10.70	17.20	0.39	4.07	17.10	17.60	4.60
TUPI	4.54	2.90	68.00	0.55	0.19	1.07	0.91	1.98	6.51	14.00	54.00	2.79	13.10	35.90	0.42	3.75	2.20	20.30	1.32
BOURBON	5.34	3.40	78.00	2.34	0.48	0.00	3.02	3.02	8.22	36.70	0.00	3.99	9.10	13.40	0.31	3.87	22.30	17.30	4.42
ACAUÃ	4.69	156.50	162.00	1.21	0.39	0.59	2.02	2.61	8.12	24.90	22.60	3.19	19.10	61.70	0.69	4.43	7.40	24.40	3.56
OBATA	4.72	31.90	247.00	1.62	0.61	0.49	2.86	3.35	8.66	33.00	14.60	3.86	18.40	51.10	1.40	6.12	7.00	21.80	3.73
7BL13 P40	6.07	2.70	112.00	2.83	0.83	0.00	3.95	3.95	7.05	56.00	0.00	3.33	11.10	6.30	0.25	5.75	28.10	17.50	6.15
IAC 125 RN	6.41	15.30	92.00	3.62	1.03	0.00	4.89	4.89	8.39	58.30	0.00	4.52	11.90	12.00	0.25	2.33	20.30	23.40	5.72
5B5P1	6.43	5.00	136.00	2.44	1.24	0.00	4.03	4.03	6.93	58.20	0.00	3.46	9.80	7.50	0.19	3.01	11.20	15.70	3.26

Supplementary Table 3. Histological parameters of leaf, petiole and root tissue of 13 coffee genotypes.

Organ	Tissue (abbreviature, unit)	Susceptible-drought					
		Bourbon	**Geixa**	**IAC 125 RN**	**Obatã**	**Sarchimor**	**Tupi**
Leaves	*Total leaf blade thickness (L_TBT, µm)*	211.1±29.5	193.8±11.9	251.6±26.5	196.2±13.5	225±21.7	202.2±10.5
	Total leaf mesophyll thickness (L_MT, µm)	175.4±30.0	160.7±13.0	215.3±26.3	160.2±14.1	185.3±20.1	161.2±8.8
	Leaf superior epidermis thickness (L_SET, µm)	**25.0±0.6 ab**	**22.7±1.1 b**	**24.1±1 ab**	**22.8±0.5 b**	**26.2±0.2 a**	**27.6±0.3 a**
	Palisade parenchyma thickness (L_PPT, µm)	50.6±7.4	55.5±6.5	47.8±5.7	48.8±2.5	51.9±0.2	35.6±3.0
	Spongy parenchyma thickness (L_SPT, µm)	119.8±22.8	101.7±6.4	164.4±20.1	107.2±11.9	129.1±19.8	124±10.2
	Leaf inferior epidermis thickness (L_IET, µm)	15.3±0.4	15.2±0.9	15.9±0.8	17.6±0.5	17.5±2.3	16±1.3
	Specific leaf area (SLA, $cm^2\ g^{-1}$)	**118.8±2.5 ab**	**125.2±4.4 b**	**112.8±1.4 c**	**170.5±6.1 a**	**116.4±4.3 b**	**171.6±9.0 a**
Petiole	*Petiole total cross section area (P_TCS, μm^2)*	72901.9±8012.2	60306.6±3678	70272.5±5951.3	63239.4±5943.9	68093.3±4109.5	61740.6±3528.1
	Petiole vascular tissue cross section area (P_VTCS, μm^2)	**43823.9±4958.9 a**	**27680.5±1897.6 bc**	**40840.5±5126.2 ab**	**35765.9±3088.1 abc**	**35665.2±1479.1 abc**	**28030.8±5743.4 bc**
	Petiole epidermis and fundamental tissue cross section area (P_EFCS, μm^2)	29078.0±4190.1	32626±2123.8	29432.0±5924.3	27473.5±2984.8	32428.1±5518.9	33709.8±8941.3
	Petiole phloem and procambium cross section area (P_PCCS, μm^2)	**26310.6±2692.8 a**	**16819.2±1149.5 b**	**25484.2±3295.0 a**	**21341.8±1603.9 ab**	**21199.1±648.5 ab**	**17677.3±2170.9 b**
	Petiole xylem cross section area (P_XCS, μm^2)	**17513.3±2267.9 bc**	**10861.3±1259.8 bc**	**15356.3±1831.7 b**	**14424.1±1514.9 bc**	**14466.0±948.5 bc**	**10353.5±3767.8 bc**
	Petiole number of vessel elements per area (P_NVA, VE μm^{-2})	23956.5±1328.2	34157.2±4827.0	25251.5±1912.8	32844.6±3921.2	22851.7±789.9	69666.2±34363.6
	Petiole average of vessel element per diameter (P_AVED, VE μm^{-2})	6.4±0.2	6.6±0.3	6.1±0.1	6.5±0.5	5.8±0.1	6.7±0.7
Root	*Total cross section area (R_TCS, μm^2)*	447475.0±116028.3	129991.5±6544.9	412124.0±85298.3	256945.4±81151.6	107151.5±18295	194857.5±52935.1
	Stele cross section area (R_SCS, μm^2)	28242.8±6970.5	6472.1±775.3	27503.0±6928.9	21651.8±8244.0	6521.7±849.4	11399.6±3034.3
	Epidermis cross section area (R_ECS, μm^2)	46508.4±8435.1	25118.4±1188.0	51269.3±8517.2	33071.2±7185.2	22448.3±3393.8	32083.0±3984.5
	Cortex cross section area (R_CCS, μm^2)	372723.8±101716.9	98401.0±5600.3	333351.7±70935.4	202222.4±65826.9	78181.5±14344.9	151374.9±46515.9
	Pericycle (R_Pe, μm^2)	6824.3±1519.4	1947.4±221.3	5774.6±1039.9	4527.6±1592.8	1692.8±248.2	3110.0±796.9
	Phloem and procambium cross section area (R_PCCS, μm^2)	11236.4±3013.3	2376.5±301.9	10907.1±2568.4	7423±2586.8	2208.2±276.8	4248.7±1050.9
	Xylem cross section area (R_XCS, μm^2)	10182.2±2519.9	2148.3±297.2	10821.3±3374.9	9701.3±4121.5	2620.7±358.3	4055.6±1239.4
	Number of protoxylem poles (R_NPX, unitless)	**6.0±0.5 a**	**3.4±0.2 c**	**5.0±0.3 ab**	**5.6±1 ab**	**4±0.3 bc**	**4.4±0.5 bc**
	Number of cell layers in the cortex (R_NCC, unitless)	10.6±1.2	6.2±0.1	10.0±0.6	8.8±1.3	6.2±0.5	7.5±0.8

Supplementary Table 3. Cont.

Organ	Tissue (abbreviature, unit)	Tolerant-drought							*F* or *KW*§	R^2	*P*
		X5B9P1	**X7B13P14**	**Acauã**	**Catiguar MG2**	**Catuaí SH3**	**IPR100**	**Sagarana 19**			
Leaves	*Total leaf blade thickness (L_TBT, µm)*	209.7±28.9	241.8±9.8	172.0±12.7	206.8±11.6	197.7±18.7	212.4±15.1	215.7±14.7	1.24	0,36	n.s.
	Total leaf mesophyll thickness (L_MT, µm)	175.9±28.4	206.6±9.2	132.2±12.4	169.5±12.9	161.7±16.4	178.8±14.6	179.8±16.6	1.33	0,38	n.s.
	Leaf superior epidermis thickness (L_SET, µm)	**20.5±1.2c**	**22.8±0.9 b**	**26.0±0.1 a**	**24.6±0.3 ab**	**22.5±0.7 b**	**22.2±1.3 b**	**25.1±0.5 a**	**29.3**§	---	***
	Palisade parenchyma thickness (L_PPT, µm)	54.2±6.0	47.8±1.6	39.7±4.8	50.1±6	42.8±1.2	51.1±1.5	54.3±8.8	1.41	0,39	n.s.
	Spongy parenchyma thickness (L_SPT, µm)	121.4±26.6	155.7±7.6	88.5±11.1	114.6±6.7	114.8±15.9	123.2±13.3	120.7±9.1	1.73	0,44	n.s.
	Leaf inferior epidermis thickness (L_IET, µm)	14.5±1.1	16±0.7	18.3±0.7	19±0.4	18.5±2	16.2±0.4	15.3±0.8	1.69	0,44	n.s.
	Specific leaf area (SLA, $cm^2\ g^{-1}$)	**136.1±8.2ab**	**115.7±7.5 b**	**174.4±9.7 a**	**127±11.3 b**	**161.8±5.7 a**	**142.5±3.9 ab**	**150.1±3.0 ab**	**32.5**§	---	***
Petiole	*Petiole total cross section area (P_TCS, μm^2)*	70269.2±5685.5	68490.8±10709.3	53265.7±8857.2	54587.0±3033.9	40507.4±344.8	46241.4±6088.9	64323.7±4039.7	20.7§	---	n.s.
	Petiole vascular tissue cross section area (P_VTCS, μm^2)	**36651.8±4345.8abc**	**47990.2±7166.4 a**	**25969.3±2641.8 b**	**28061.3±1538.0 b**	**23834.4±309.4 b**	**17993.5±6786.2 c**	**31386.5±2720.9 ab**	**27.2**§	---	***
	Petiole epidermis and fundamental tissue cross section area (P_EFCS, μm^2)	33617.4±1340.0	20500.6±3619.1	27296.4±6671.6	26525.6±1671.8	16673.0±644.7	28247.9±8361.5	32937.3±1428.0	1.1	0,34	n.s.
	Petiole phloem and procambium cross section area (P_PCCS, μm^2)	**22450.0±3343.9a**	**26785.4±3811.1 a**	**14830.1±1489.2 c**	**18629.7±1785.0 b**	**14355.7±368.4 c**	**10016.9±3601.1 c**	**19011.9±1818.2 b**	**27.5**§	---	***
	Petiole xylem cross section area (P_XCS, μm^2)	**14201.8±1238.7bc**	**21204.9±4453.6 a**	**11139.2±1385.3 b**	**9431.6±675.4 bc**	**9478.7±675 bc**	**7976.5±3185 c**	**12374.6±904.9 bc**	**22.3**§	---	***
	Petiole number of vessel elements per area (P_NVA, VE μm^{-2})	23257.1±1997.6	22488.8±3173.6	35248.5±4751.9	26990.5±1158.7	38309.6±3484.8	70347.0±37629.4	22725.5±1921.8	1.34	0,38	n.s.
	Petiole average of vessel element per diameter (P_AVED, VE μm^{-2})	6.4±0.8	7.0±0.4	6.2±0.3	6.2±0.5	5.8±0.6	5.6±0.4	7.1±0.2	1.08	0,33	n.s.
Root	*Total cross section area (R_TCS, μm^2)*	170892.4±34041.2	264578.8±69821.1	2292141.6±2085568.1	288157.3±111254.8	137480.1±61913.6	165037.2±11669.5	218875.1±55766.7	1.36	0,16	n.s.
	Stele cross section area (R_SCS, μm^2)	10735.2±2277.3	19046.9±5253.9	155326.5±139939.1	16347.2±5758.6	10094.6±4825.1	12615.3±151.3	17949.0±6432.9	1.39	0,16	n.s.
	Epidermis cross section area (R_ECS, μm^2)	27999.6±2418.6	36352.5±8099.4	170836.2±138089.4	35461±8606.5	20685.1±6867.8	31207.7±413.9	31474.2±3062.7	1.4	0,16	n.s.
	Cortex cross section area (R_CCS, μm^2)	132157.6±29901.8	209179.4±56648.2	1965979.0±1807612.2	236349.1±97121.6	106700.4±50410.7	121214.2±11242.4	169451.9±46676.3	1.36	0,15	n.s.
	Pericycle (R_Pe, μm^2)	3465.5±889.5	4300.9±1032.1	50989.0±47411.3	4603.4±1611.7	2880.1±1531	3764.3±764.4	3918.5±1266.5	1.37	0,16	n.s.
	Phloem and procambium cross section area (R_PCCS, μm^2)	3812.4±732.0	7919.8±2370.3	55245.0±49165.7	6485.6±2417.7	4166±2060.3	4734.4±284.1	6281.2±2307.9	1.41	0,16	n.s.
	Xylem cross section area (R_XCS, μm^2)	3457.2±765.0	6826.2±1920.1	49092.5±43379.5	5258.2±1771.2	3048.5±1281	4116.5±604.4	7749.3±2921.5	1.39	0,16	n.s.
	Number of protoxylem poles (R_NPX, unitless)	**4.1±0.5bc**	**4.8±0.5 b**	**4.5±0.7 ab**	**4.8±0.7 b**	**4.6±0.6 ab**	**4.7±0.3 ab**	**4.9±0.5 ab**	**22.0**§	---	***
	Number of cell layers in the cortex (R_NCC, unitless)	6.9±0.7	8.9±1.2	9.0±2.1	8.7±2	7.4±1	7.0±0.4	8.0±0.8	1.8	0,20	n.s.

Supplementary Table 4. Percentage of thickness of the tissue layers that constitute the leaf, petiole and root of 13 coffee genotypes.

Organ	Tissue (abbreviature, unit)	Susceptible-drought					
		Bourbon	**Geixa**	**IAC125RN**	**Obatã**	**Sarchimor**	**Tupi**
Leaves	*Percentage of superior epidermis (pL_SET, %)*	12.4±1.8	11.8±1.2	9.7±0.8	11.8±1.1	12±1.1	13.6±0.7
	Percentage of palisade parenchyma (pL_PPT, %)	24±0.3	28.3±1.8	18.9±0.5	25±1.1	23.8±2.4	17.6±1.9
	Percentage of spongy parenchyma (pL_SPT, %)	**56.1±2.9b**	**52.1±0.4b**	**64.9±1.4a**	**54.2±2.5b**	**56.5±3.2b**	**60.8±2.2ab**
	Percentage of inferior epidermis (pL_IET, %)	**7.6±1.2b**	**7.9±0.9b**	**6.5±0.8c**	**9±0.5ab**	**7.7±0.3b**	**7.9±0.3b**
Petiole	*Percentage of vascular tissue cross section area (pP_VTCS, %)*	60.3±3.2	45.9±1.3	58.3±6.5	56.7±1.2	53±5	46.7±11.9
	Percentage of epidermis and fundamental tissue cross section area (pP_EFCS, %)	39.7±3.2	54.1±1.3	41.7±6.5	43.3±1.2	47±5	53.3±11.9
	Percentage of phloem and procambium cross section area (pP_PCCS, %)	36.3±2	28±1.9	36.4±4.2	33.9±0.6	31.5±2.7	29.2±5.4
	Percentage of xylem cross section area (pP_XCS, %)	24±1.3	17.9±1	21.9±2.3	22.8±0.9	21.5±2.4	17.4±6.8
Root	*Percentage of stele cross section area (pR_SCS, %)*	6.5±0.2	4.9±0.5	6.4±0.7	7.2±1.2	6.4±0.4	5.7±0.4
	Percentage of epidermis cross section area (pR_ECS, %)	**13.2±1.5c**	**19.6±1a**	**13.3±0.6c**	**15.4±2.2bc**	**21.4±0.9a**	**19.6±1.5a**
	Percentage of cortex cross section area (pR_CCS, %)	**80.3±1.6a**	**75.5±0.9b**	**80.4±0.9a**	**77.3±1.2ab**	**72.2±1.1b**	**74.7±1.5b**
	Percentage of pericycle (pR_Pe, %)	1.7±0.1	1.5±0.1	1.5±0.1	1.6±0.2	1.7±0.1	1.6±0.1
	Percentage of phloem and procambium cross section area (pR_PCCS, %)	**2.5±0.1b**	**1.8±0.2c**	**2.6±0.3b**	**2.6±0.4b**	**2.2±0.2b**	**2.2±0.2b**
	Percentage of xylem cross section area (pR_XCS, %)	2.4±0.1	1.6±0.2	2.4±0.4	3±0.7	2.6±0.2	1.9±0.1

Supplementary Table 4. Cont.

Organ	Tissue (abbreviature, unit)	Tolerant-drought							*F* or *KW* (§)	R^2	*P*
		5B9P1	**7B13P14**	**Acauã**	**Catiguar MG2**	**Catuaí SH3**	**IPR100**	**Sagarana 19**			
Leaves	*Percentage of superior epidermis (pL_SET, %)*	10±0.8	9.4±0	15.3±1.2	11.9±0.8	11.6±1.2	10.5±0.8	11.8±0.9	19.5§	---	n.s.
	Percentage of palisade parenchyma (pL_PPT, %)	26.6±4.5	19.8±0.7	23.1±2.6	23.8±1.5	21.9±1.6	24.2±1.3	25±3	2.08	0,49	n.s.
	Percentage of spongy parenchyma (pL_SPT, %)	**56.3±5.5b**	**64.2±0.7a**	**51±3.2b**	**55±0b**	**57.3±2.8b**	**57.6±2.6b**	**56.1±2.3b**	**21.1§**	---	***
	Percentage of inferior epidermis (pL_IET, %)	**7.1±0.8b**	**6.6±0.1b**	**10.7±0.4a**	**9.3±0.7ab**	**9.3±0.4ab**	**7.7±0.6b**	**7.1±0.4b**	**23.2§**	---	***
Petiole	*Percentage of vascular tissue cross section area (pP_VTCS, %)*	51.9±1.9	70.3±1	49.9±4.6	51.4±1	58.9±1.3	39.7±13.1	48.7±1.3	1.87	0,46	n.s.
	Percentage of epidermis and fundamental tissue cross section area (pP_EFCS, %)	48.1±1.9	29.7±1	50.1±4.6	48.6±1	41.1±1.3	60.3±13.1	51.3±1.3	1.87	0,46	n.s.
	Percentage of phloem and procambium cross section area (pP_PCCS, %)	31.6±2.1	39.6±2.6	28.7±3.8	34.1±2.2	35.4±0.6	22.1±7	29.4±1	1.93	0,47	n.s.
	Percentage of xylem cross section area (pP_XCS, %)	20.2±1	30.7±3.1	21.2±0.9	17.4±1.4	23.4±1.9	17.6±6.1	19.2±0.3	1.55	0,42	n.s.
Root	*Percentage of stele cross section area (pR_SCS, %)*	6.1±0.2	7±0.3	7±0.8	6.2±0.3	7±0.7	7.7±0.4	6.8±0.6	1.62	0,18	n.s.
	Percentage of epidermis cross section area (pR_ECS, %)	**18.6±1.5ab**	**15.6±1.5bc**	**17.3±2.7ab**	**16.4±2.2bc**	**17.1±1.9ab**	**19.1±1.1a**	**17.8±1.4ab**	**27.2§**	---	***
	Percentage of cortex cross section area (pR_CCS, %)	**75.3±1.4b**	**77.4±1.3ab**	**75.7±2.7b**	**77.4±2.4ab**	**75.9±1.8b**	**73.2±1.6b**	**75.4±0.9b**	**24.1§**	---	***
	Percentage of pericycle (pR_Pe, %)	2±0.1	1.8±0.1	2±0.1	1.8±0.1	1.9±0.2	2.3±0.5	1.7±0.1	1.78	0,19	n.s.
	Percentage of phloem and procambium cross section area (pR_PCCS, %)	**2.2±0.1b**	**2.8±0.2a**	**2.7±0.3ab**	**2.4±0.1b**	**2.9±0.2a**	**2.9±0.1a**	**2.4±0.2b**	**22.8§**	---	***
	Percentage of xylem cross section area (pR_XCS, %)	1.9±0.2	2.5±0.2	2.3±0.4	2±0.1	2.3±0.4	2.5±0.5	2.8±0.4	1.47	0,17	n.s.

Despite data on coffee roots are available (Pinheiro et al., 2005; Silva, 2010), the integration of root traits, distribution, depth, among others, is of paramount importance (Tajima, 2021) to the water deficit resistance in coffee genotypes. But, what can we tell from the lateral primary root anatomy? It is tempting to outline possible roles of coffee plants primary roots on water deficit resistance strategies. Lateral roots are at the front line for water and nutrient acquisition, and there are clues of cyclic loops among root differentiation, xylem sap transport, mineral nutrition, and water deficit environmental triggers. The study of the root underground, under controlled water deficit conditions, may uncover differences and history of nutrient acquisition throughout the root length, architecture, diameter, length, chemical features and development of vascular tissues, cortex, and root hairs. There is a range of primary roots anatomical features in coffee genotypes that may contribute to water deficit tolerance or be assigned to coffee genotypes that harbor higher water deficit tolerance based on the available empirical data. Aside it seems that that there are inborn traits of derived from coffee plants phenotypic plasticity, it should be thoughtfully examined under controlled water drought experiments. Nevertheless, these spoilers are a start!

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