

ORIGINAL ARTICLE

## Hydraulic conductance in seedlings of *Coffea arabica* L. accessions under contrasting nursery environments at Jimma, southwestern Ethiopia

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### ABSTRACT

The study was carried out with the objective to investigate the variations among *Coffea arabica* L. accessions in water conductance under contrasting nursery environments at the Jimma Agricultural Research Center, southwestern Ethiopia. The treatments included two shade (moderate shading and full sunlight) and two irrigation (well watered and water stressed) regimes, which were superimposed on seedlings of 12 accessions. The results depicted variations in water flow in the root and shoot of coffee seedlings due to shading, irrigation and accessions with varying levels of significance. The Haremma accessions had higher root and shoot hydraulic conductance as compared to others both for whole-plant as well as stem- and leaf- specific conductivity. Significant variations were observed in root, whole- shoot, leaf, petiole and primary branch due to shading regimes. Moderate shading significantly enhanced main stem conductivity on the first and 12 days after irrigation (DAI). Likewise, leaf- and stem- specific conductivities were significantly different among coffee accessions on eighth DAI. The interaction between shading and irrigation was highly significant on stem hydraulic conductivity at the beginning and eighth DAI of withholding watering. In all cases, significantly higher conductivities were measured in water-stressed seedlings. Overall, eight and 16 DAI were noted to be the respective threshold levels under full sunlight and moderate shade conditions, indicating twofold-advantages of shading to postponed the adverse effects of rapid soil drying. Our findings revealed peculiar water flow attributes of arabica coffee accessions and can be of interest in future breeding to characterize and utilize coffee genetic resources in Ethiopia.

**Keywords:** Arabica coffee diversity, drought tolerance, environmental stress, water relations

### INTRODUCTION

The high-altitude rainforests of Ethiopia are the center of origin and genetic diversity for the highland Arabica coffee which is highly demanded for its unique fruit quality standard in the global market. The country is thus endowed with favorable environment and huge genetic potentials for sustainable

production of specialty coffees, while conserving the forest genetic resources and environmental sustainability. Arabica coffee is thus a shade adapted plant in the natural multi-strata forest ecosystems with the occurrence of the wild Arabica coffee populations (Wintgens, 2004). However, these are fragmented forests and their coverage is shrinking from time to time, largely due to

anthropogenic activities. As a result, coffee is either replaced by other crops or its cultivation is expanding into less suitable open-sun conditions. These coupled with the increasing patterns of climate change are threatening the natural gene pools of arabica coffee and thus needs urgent actions before the genetic erosion reach an irreversible situation (Gole, 2003).

Water in soil facilitates absorption of minerals and helps in maintaining turgidity for growth and various synthesis processes (Larcher, 2003). Moisture deficit slows root growth and decreases water absorption. In this regard, roots are less sensitive than shoots to moisture-stress and the growth of leaves is more sensitive than root growth (Hopkins, 1995). The author also emphasized that moisture-stress indicates the demand for water within a plant and integrates the soil moisture tension in the rooting zone, the resistance to water movement within the plant, and the demand for transpiration imposed by the environment variables. According to Prasad (1997), the water status of plants has received much attention to provide baseline information for evaluating plant needs for water or how well plants adapt to their environment (site-plant matching), especially where water is a limiting factor. According to Sobrado (2003), investigation on the adaptation mechanisms of plant species is important to understand their ecological success and growth conditions. It is known that the degree of moisture-stress tolerance profoundly influences virtually all physiological and metabolic functions that are responsible for determining plant adaptation, growth and distribution. A practical measure of the hydraulic supply capacity of the xylem is leaf-specific conductivity (Zimmermann, 1983). Thus, the distribution of leaf-specific conductivity within a tree influences patterns of water potential throughout the crown and can impose constraints on such physiological processes as transpiration and photosynthesis (Yang and Tyree, 1993).

In Ethiopia, despite the multifaceted continuous threats there is still a huge potential of coffee genetic resources which have adapted to the various biotic and abiotic stress pressures (Taye, 2006). Yacob *et al.* (1996) reported that the released coffee varieties and local landraces in Ethiopia can be

broadly grouped into three canopy classes of open, medium and compact crown nature and their water relations can vary accordingly. So far, about 6385 coffee germplasm collections are *ex-situ* maintained for research purposes at the different research field genebanks in Ethiopia. Besides, among the potential coffee forest habitats, the Yayu and Kafa coffee forests were identified as UNESCO Biosphere Reserves for *in-situ* conservation and utilization of wild arabica coffee gene pools ([www.coffee.uni-bonn.de](http://www.coffee.uni-bonn.de)).

According to Bellachew and Sacko (2009), coffee genetic resources are believed to possess desirable traits, including high yielding, superior quality, resistance to diseases, tolerance to moisture-stress and other desirable agronomic traits. Nonetheless, the underlying adaptation strategies that take into account genetic and environmental factors remain little understood to fully exploit the wealth of coffee and ecological diversities in Ethiopia. In view of the fast adverse impacts of global warming and climate change on coffee genetic resources there is also an urgent need to develop suitable coffee cultivars for the development of the coffee sector in the globe. To this end, information on hydraulic conductance, a genetically fixed trait, would help as selection criterion towards indentifying drought tolerant Arabica coffee cultivars for specific geographical areas. Hence, in perennial crops like coffee knowledge on the early water flow to the various parts of coffee seedlings would also help in predicting the future field performances of coffee genotypes under varying environmental conditions. This study was therefore executed to examine the variations in hydraulic conductance among Arabica coffee germplasm accessions under contrasting sunlight and irrigation regimes at the Jimma Agricultural Research Center nursery site, southwestern Ethiopia.

## MATERIALS AND METHODS

### Description of the study area

The experiment was conducted in southwestern Ethiopia, at the Jimma Agricultural Research Center (JARC) (7°46'N and 36° E). The center nationally coordinates the coffee research in the country and about

6385 coffee germplasm collections are maintained at research field genebanks of the JARC, its sub-centers and sub-stations. JARC is situated within the temperate to cool humid highland agro-ecological zone at an altitude of 1,753 m a. s. l. The area receives a high amount of rainfall with a total of 1,556.88 mm per annum, which is unimodal in distribution pattern over several months of a year, the peak being between June and September, while the dry and cool months usually last from November to February. The annual mean maximum and minimum air temperatures are 26.7 and 12.8°C, respectively (Taye, 2006).

### Experimental procedure and design

Fully ripe red cherries were collected from coffee trees at three sites within four wild arabica coffee populations; viz, Harena, Bonga, Berhane-Kontir and Yayu. Except Harena in the southeast, the other three montane rain forests are located in the more humid southwest Ethiopia. Consequently, coffee seedlings from a total of 12 accessions: Harena (I-1, I-2, I-3), Bonga (II-1, II-2, II-3), Berhane-Kontir (III-1, III-2, III-3) and Yayu (IV-1, IV-2, IV-3), were *ex-situ* established and evaluated under controlled nursery settings. The recommended potting medium (Taye, 2006) was prepared from blends of topsoil and decomposed coffee husk compost at the respective ratio of 3:1 (v/v). The black plastic pots with a volume of 5.8 liter were perforated at the bottom, firmly filled with the so prepared soil medium, were arranged on nursery seedbeds. Coffee seeds were sown in each plastic pot and all post-sowing nursery operations were applied for about one-year according to the recommendations of the center (Yacob *et al.*, 1996). Then after, the coffee seedlings were arranged in two shade treatments (full sunlight and moderate shade) and managed for three-months between June and August 2005. The seedlings exposed to full sunlight were acclimatized to maximum sun light through gradual reduction of the shade cover so as to minimize the possible risks associated with a sudden change to a new and more stressful environment.

A factorial experiment arranged in a split-plot design of three replicates was used for the study. One-year-old coffee seedlings of the different accessions were screened

under contrasting sunlight and moisture regimes. Water application was withheld for 16 days from half of the seedlings (moisture-stressed, W0), while the other half were irrigated (well-watered, WW) at every four-day intervals. The irrigation treatment was performed on seedlings arranged under full sunlight (S0) and moderate shade (S1) conditions. In the case of well-watered seedlings, each plastic pot was irrigated in the late afternoon of the day before hydraulic measurements. In the soil drying plot, the seedlings were covered by a white plastic sheet at night and whenever there were clouds (rain) in the daytime.

### Hydraulic conductance measurement

The hydraulic conductance in root and shoot as well as leaf and stem hydraulic conductivity were examined in seedlings of wild coffee accessions using the transient method of the high-pressure-flow meter (HPFM) as previously described (Tyree *et al.*, 1995). This was made for two weeks at an interval of every four days (four, eight, 12 and 16 DAI). The first day after irrigation was also included and maximum care was taken to keep the seedlings remain dehydrated during the hydraulic measurements. Hydraulic conductances in root, whole shoot and shoot segments (leaves, primary branches, petiole and main stem) were recorded separately by sequential removal of each part. First, the HPFM was connected to the base of the debarked main stem cut at about 5 cm above the soil surface. The initial pressure was set and increased at 5 kPa s<sup>-1</sup> and flow rates were recorded at two seconds intervals. Root hydraulic conductance (reciprocal of hydraulic resistance) was measured by the transient method and hydraulic conductance was calculated from the slope of the change in the amount of water flow and applied pressure. Each plot consisted of 25 seedlings and 288 seedlings were sampled for hydraulic measurements at each moisture-stress period. Hence, a total of 1440 experimental coffee seedlings were used for hydraulic measurements in root, whole shoot and shoot segments throughout the study period. At the same time, seedling shoot growth parameters were also collected to determine hydraulic conductivities. The diameter of the debarked main stem was measured with a calliper and

the cross-sectional area was calculated. The water flow through a 20-cm long main stem was measured. Finally, leaf- and stem-specific conductivities were determined as described in Tyree et al. (1995) by dividing the amount of water conducted by the total leaf area supported by the main stem and by the basal area of the debarked main stem, respectively.

### Statistical analysis

Two-way analysis of variance (ANOVA) was carried out to investigate the variations in hydraulic conductance due to shade levels, irrigation regimes and coffee accessions. The main independent variables and interaction effects were examined at four-day intervals between the first day after irrigation (0 DAI) and subsequent soil moisture deficit periods (4, 8, 12 and 16-days after irrigation). All statistical analyses were performed using the SAS system for Windows Version 8.0 software (SAS Institute, Cary, NC). Treatment means were ranked according to Tukey's test at  $p = 0.05$ , whenever the F-test showed significant differences. Graphs of significant interactions were made with SigmaPlot v. 9.0 (SYSTAT Software Inc., TOWN, STATE).

## RESULTS

### Hydraulic conductance

The results showed differences ( $p < 0.001$ ) between shade levels on four and eight DAI and full sunlight exposed seedlings had higher whole-plant conductance. Thereafter, no statistically significant variations were observed, due neither to main nor to treatment interaction, except the significant ( $p < 0.01$ ) results between shade and irrigation occurring on eight DAI when moisture-stressed seedlings showed values that were significantly different to those of the other treatments. The results depicted significant differences ( $p < 0.05$ ) among accessions and between accession and irrigation on four DAI (Table 1). Except for Harena (I-1), Bonga (II-2) and Birhane-Kontir (III-1), in which conductance was significantly reduced, all accessions had higher whole-plant hydraulic conductance in drought-stressed than in the well-watered conditions. This was particularly true for drought-stressed accessions from Yayu (IV-1), Birhane-Kontir (III-2), Harena (I-

3, I-2) in that order, whereas whole-plant hydraulic conductance was lower in Yayu (IV-2), Bonga (II-1) and Birhane-Kontir (III-2) (Fig. 1).

Hydraulic conductance in roots and shoots revealed variations due to the main effect of shading, irrigation and accessions with varying levels of significance. Accordingly, the values were significantly higher for the full sunlight and moisture-stressed seedlings. However, interactions were not significant, except between shade and irrigation effect when all the lateral branches are removed. Except in the main stem cut, significant variations were observed in root ( $p < 0.05$ ), whole shoot ( $p < 0.05$ ), leaf ( $p < 0.05$ ), petiole ( $p < 0.05$ ) and primary branch ( $p < 0.05$ ) due to shade regimes. The full sun-exposed seedlings exhibited higher water flow both in root and shoot parts. Similarly, the influence of irrigation was significant ( $p < 0.05$ ) during the different days after watering, whereby root and shoot hydraulic flows were higher in moisture-stressed than in well-watered seedlings (Table 2).

On the other hand, accessions were comparable in the amount of water flow to root and shoot systems. Nonetheless, a significant difference ( $p \leq 0.05$ ) was found due to removal of all primary branches and reduction of the main stem length. Consequently, the highest and lowest hydraulic conductances for the stem-cut were measured for the Harena (I-2) and Yayu (IV-3) accessions, respectively. Root and shoot hydraulic patterns were inconsistent among accessions, though the overall average value was slightly higher in the whole-shoot than in the root part (Table 2). Likewise, treatment interactions were not significant for root and shoot hydraulic conductances. However, the removal of primary branches from seedlings exposed to soil moisture deficits significantly enhanced water flow in open sunlight and moderately shaded seedlings. In contrast, conductance tended to decline in well-watered plots both in full sunlight and moderate shade conditions.

Significant differences in hydraulic conductance in the different parts of the coffee seedlings were noted on the four and 16 DAI, where maximum average values were recorded in the roots and whole-shoots, respectively. Similarly, at the inception of

moisture-stress, the lowest hydraulic conductance was measured in the roots as compared to various shoot parts, though the values did not significantly differ. This was when maximum main stem hydraulic conductivity was also obtained from the 20-cm long stem cut, followed by the whole shoot. In addition, maximum root conductance was recorded between the four and eight DAI where the mean lowest and highest, respectively, was determined, with higher results in drought-stressed seedlings. The transition in root-shoot hydraulic conductance patterns was determined eight DAI when increased root hydraulic resistant was observed (data not shown). Furthermore, the contribution of shading in enhancing hydraulic conductance was greater at the inception of drought, i.e., up to eight DAI. This was when the conductance in shade seedlings began to surpass those grown in the full sun conditions. With extended drought period, however, the two irrigation regimes showed a more pronounced influence, though root and shoot showed insignificant variations in hydraulic conductance (Fig. 2). In moderate

shade conditions, hydraulic conductance in the roots and shoots did not show significant variations over the extended period of drought, except on four DAI ( $p < 0.05$ ). Conversely, significant hydraulic conductance variations in root and shoot segments were displayed on eight DAI and 16 DAI. Consistently lower root and shoot hydraulic conductance was measured in well-watered than in drought-stressed seedlings. The variations in shoot components particularly between leaves and petioles were also minimal and lowest even at the 16 DAI. The interaction between shade and irrigation was not significant at the first DAI and 12 DAI, possibly reflecting the different responses of the root and shoot systems in relation to the magnitude of water tensions in the soil-plant system. However, differences were measured during the other stress period when moisture-stressed seedlings showed maximum conductance as opposed to the well-watered ones both in full sun and shaded plots. At 16 DAI, however, well-watered seedlings had higher conductance than the water stressed seedlings under full sunlight (Fig. 2).

**Table 1.** Whole-plant hydraulic conductance ( $K_h$ , means $\pm$ SD $\times 10^{-5}$  kg s $^{-1}$  m $^{-2}$  MPa $^{-1}$ ) in seedlings of Arabica coffee accessions as affected by shade and irrigation levels during different days after irrigation (0 to 16 DAI)

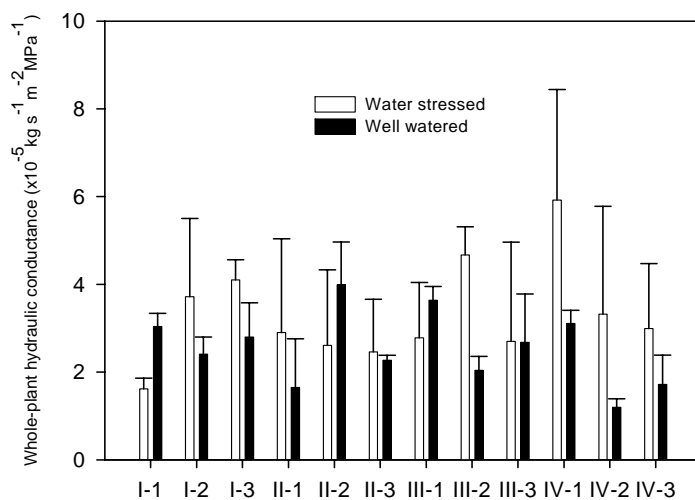
Treatment	0 DAI	4 DAI	8 DAI	12 DAI	16 DAI
<i>Shading</i>					
Moderate shade	3.16 $\pm$ 1.13	2.22 $\pm$ 0.93b	2.70 $\pm$ 0.64b	3.93 $\pm$ 1.74	3.39 $\pm$ 1.56
Full sunlight	2.92 $\pm$ 0.89	3.64 $\pm$ 1.51a	4.32 $\pm$ 2.15a	3.84 $\pm$ 1.73	3.21 $\pm$ 1.33
<i>Irrigation (Irr)</i>					
Well watered	2.70 $\pm$ 0.87b	2.54 $\pm$ 0.94b	2.53 $\pm$ 0.76b	2.52 $\pm$ 0.71b	2.08 $\pm$ 0.49b
Water stressed	3.39 $\pm$ 1.04a	3.31 $\pm$ 1.73a	4.49 $\pm$ 1.96a	5.25 $\pm$ 1.27a	4.52 $\pm$ 0.93a
<i>Accession (Acc)</i>					
I-1	4.21 $\pm$ 1.23	2.33 $\pm$ 0.85b	4.46 $\pm$ 2.72	4.81 $\pm$ 2.74	3.52 $\pm$ 1.25
I-2	3.41 $\pm$ 1.53	3.06 $\pm$ 1.29ab	4.38 $\pm$ 1.83	4.12 $\pm$ 1.66	3.95 $\pm$ 1.60
I-3	2.97 $\pm$ 0.66	3.45 $\pm$ 0.91ab	3.67 $\pm$ 1.42	4.49 $\pm$ 1.94	3.24 $\pm$ 0.98
II-1	2.89 $\pm$ 0.43	2.27 $\pm$ 1.57b	3.20 $\pm$ 1.40	3.80 $\pm$ 1.46	3.24 $\pm$ 1.56
II-2	2.73 $\pm$ 0.75	3.30 $\pm$ 1.39ab	3.22 $\pm$ 1.30	4.47 $\pm$ 2.22	3.00 $\pm$ 0.81
II-3	3.02 $\pm$ 0.66	2.37 $\pm$ 0.71b	4.02 $\pm$ 2.12	3.32 $\pm$ 1.01	2.75 $\pm$ 1.34
III-1	3.35 $\pm$ 0.97	3.21 $\pm$ 0.89ab	3.56 $\pm$ 1.30	3.39 $\pm$ 1.28	3.34 $\pm$ 2.46
III-2	2.80 $\pm$ 1.58	3.35 $\pm$ 1.57ab	3.29 $\pm$ 2.05	4.17 $\pm$ 1.36	3.50 $\pm$ 1.83
III-3	3.36 $\pm$ 0.72	2.69 $\pm$ 1.45ab	3.94 $\pm$ 3.39	3.63 $\pm$ 1.93	2.92 $\pm$ 1.50
IV-1	2.38 $\pm$ 1.33	4.51 $\pm$ 2.60a	2.64 $\pm$ 0.99	4.00 $\pm$ 1.54	3.34 $\pm$ 1.70
IV-2	3.00 $\pm$ 0.53	2.26 $\pm$ 1.88b	3.31 $\pm$ 1.76	3.19 $\pm$ 1.83	3.13 $\pm$ 1.63
IV-3	2.42 $\pm$ 0.98	2.35 $\pm$ 1.19b	2.44 $\pm$ 1.06	3.25 $\pm$ 2.61	3.66 $\pm$ 1.89
Mean	3.00	2.90	3.50	3.90	3.30
CV (%)	29.32	22.20	28.20	23.41	20.79
ANOVA					
Shading	NS	***	***	Ns	Ns
Irrigation	*	**	***	***	***
Accession	Ns	*	Ns	Ns	Ns
Shade * irr	*	**	**	Ns	Ns
Shade * acc	Ns	Ns	Ns	Ns	Ns
Irr * acc	Ns	**	Ns	Ns	Ns

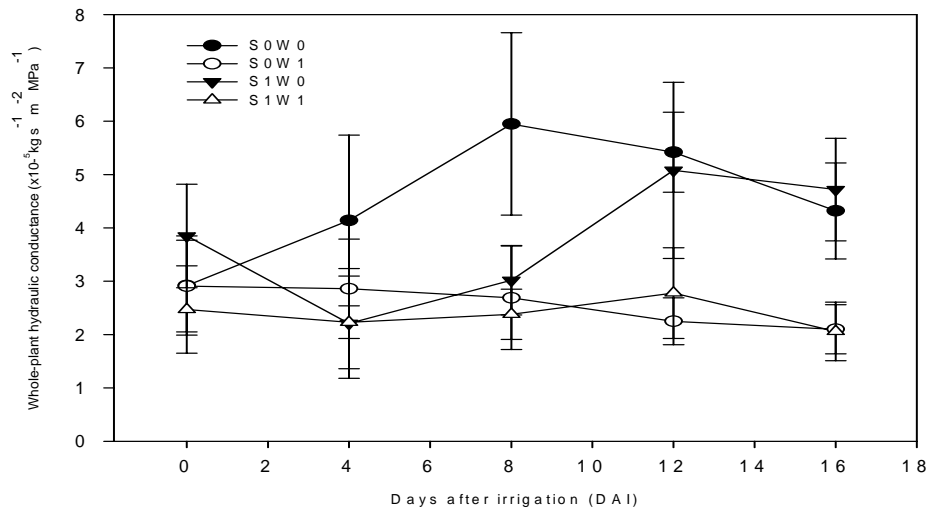
NS = Not significant; \*= $p < 0.05$ ; \*\*= $p < 0.01$ ; \*\*\*= $p < 0.001$ . Means with the same letter within a column are not significantly different according to Tukey's test at  $p = 0.05$ .

**Table 2.** Hydraulic conductance ( $K_h$ , means $\pm$ SD $\times 10^{-5}$  kg s $^{-1}$  m $^{-2}$  MPa $^{-1}$ ) in root and various shoot parts of Arabica coffee seedlings as influenced by shade, irrigation treatment and coffee accessions

Treatment	Root	Whole shoot	Leaf	Petiole	Branch	Stem cut
<i>Shading</i>	*	**	**	*	**	Ns
Moderate shade	3.11 $\pm$ 1.91b	3.61 $\pm$ 1.15b	2.67 $\pm$ 8.69b	2.56 $\pm$ 7.40b	2.94 $\pm$ 7.39b	3.50 $\pm$ 8.09
Full sunlight	4.01 $\pm$ 2.57a	4.15 $\pm$ 1.11a	3.22 $\pm$ 1.08a	2.98 $\pm$ 8.65a	3.4 $\pm$ 9.83a	3.66 $\pm$ 7.95
<i>Irrigation (Irr)</i>	***	***	***	***	***	***
Well watered	1.72 $\pm$ 7.95b	3.01 $\pm$ 7.30b	2.15 $\pm$ 3.84b	2.21 $\pm$ 4.07b	2.54 $\pm$ 4.53b	3.12 $\pm$ 5.73b
Water stressed	5.40 $\pm$ 1.73a	4.75 $\pm$ 7.68a	3.74 $\pm$ 7.75a	3.34 $\pm$ 7.47a	3.81 $\pm$ 7.58a	4.04 $\pm$ 7.26a
<i>Accession (Acc)</i>	Ns	Ns	Ns	Ns	*	*
I-1	4.53 $\pm$ 2.21	4.38 $\pm$ 1.03	3.14 $\pm$ 7.77	3.19 $\pm$ 7.36	3.90 $\pm$ 1.14a	4.20 $\pm$ 5.08ab
I-2	3.62 $\pm$ 2.22	4.00 $\pm$ 1.63	3.38 $\pm$ 1.39	3.39 $\pm$ 1.26	3.67 $\pm$ 1.08a	4.39 $\pm$ 1.03a
I-3	3.45 $\pm$ 2.93	4.54 $\pm$ 8.99	3.14 $\pm$ 7.77	3.01 $\pm$ 6.99	3.43 $\pm$ 7.52ab	3.70 $\pm$ 4.75ab
II-1	3.28 $\pm$ 1.98	3.29 $\pm$ 9.11	2.64 $\pm$ 9.39	2.35 $\pm$ 6.75	2.93 $\pm$ 1.14ab	3.32 $\pm$ 1.24ab
II-2	3.47 $\pm$ 1.83	4.11 $\pm$ 8.54	2.95 $\pm$ 6.92	2.81 $\pm$ 6.87	3.32 $\pm$ 8.30ab	3.78 $\pm$ 3.30ab
II-3	2.74 $\pm$ 1.80	4.10 $\pm$ 1.73	2.68 $\pm$ 8.72	2.50 $\pm$ 6.72	3.10 $\pm$ 1.05ab	3.13 $\pm$ 1.52ab
III-1	4.31 $\pm$ 2.57	3.62 $\pm$ 7.12	2.94 $\pm$ 9.75	2.80 $\pm$ 7.37	3.16 $\pm$ 5.87ab	3.85 $\pm$ 4.16ab
III-2	4.02 $\pm$ 2.98	4.11 $\pm$ 1.03	3.05 $\pm$ 9.27	2.89 $\pm$ 6.28	3.00 $\pm$ 8.20ab	3.38 $\pm$ 9.06ab
III-3	3.79 $\pm$ 4.23	3.85 $\pm$ 1.24	2.90 $\pm$ 1.38	2.70 $\pm$ 9.72	3.03 $\pm$ 9.07ab	3.49 $\pm$ 9.70ab
IV-1	3.66 $\pm$ 2.63	3.78 $\pm$ 1.20	3.35 $\pm$ 1.20	2.86 $\pm$ 1.04	3.23 $\pm$ 1.07ab	3.62 $\pm$ 7.77ab
IV-2	3.12 $\pm$ 1.82	3.53 $\pm$ 1.70	2.52 $\pm$ 1.20	2.40 $\pm$ 1.07	2.80 $\pm$ 1.04ab	3.21 $\pm$ 7.36ab
IV-3	2.75 $\pm$ 2.20	3.27 $\pm$ 1.37	2.65 $\pm$ 1.34	2.37 $\pm$ 9.77	2.52 $\pm$ 9.28b	2.91 $\pm$ 9.35b
Mean	3.60	3.90	2.90	2.80	3.20	3.60
CV (%)	37.80	14.08	18.65	18.18	12.66	14.18
<i>ANOVA</i>						
Shade * irr	Ns	Ns	Ns	Ns	*	Ns
Shade * acc	Ns	Ns	Ns	Ns	Ns	Ns
Irr * acc	Ns	Ns	Ns	Ns	Ns	Ns

Ns = Not significant; \* $p < 0.05$ ; \*\* $p < 0.01$ ; \*\*\* $p < 0.001$ . Means with the same letter within a column are not significantly different according to Tukey's test at  $p = 0.05$ .

**Figure 1.** Whole-plant hydraulic conductance of Arabica coffee accessions in moisture-stressed (four DAI) and well-watered seedlings.



**Figure 2.** Interaction effects of shade and irrigation on whole-plant hydraulic conductance of Arabica coffee seedlings during the different days after irrigation. S0W0 = no shade not watered, S1W0 = with shade not watered, S0W1 = not shaded watered, S1W1 = with shade watered.

### Leaf specific conductivity

The results of leaf-specific conductivity due to main and interaction effects showed that the contrasting shading regimes had significant influence on four DAI ( $p < 0.05$ ) and 8 DAI ( $p < 0.05$ ) (Table 3). Higher LSC values were recorded for the drought-stressed and for the sun seedlings. No differences were, however, detected on the first or after extended periods of soil drying. Besides, there was insignificant difference between sun and shaded leaves in the overall LSC, though a higher value was recorded in the full sunlight than in the shade conditions (Table 3).

In contrast, no differences were detected between irrigation levels up to the eight DAI. However, a significantly higher LSC was observed on 12 DAI ( $p < 0.05$ ) and 16 DAI ( $p < 0.05$ ). In addition, the overall result shows significantly ( $p < 0.05$ ) higher LSC in water stressed than in well-watered seedlings. Consequently, consistent and maximum values were measured for stressed compared to the well-watered seedlings throughout the drying period. The results also reveal that the accessions did not vary in LSC during the inception and persistent moisture-stress periods. The coffee accessions, however, significantly differed on the eight DAI ( $p < 0.05$ ), when the respective highest and lowest results were from the Harenna and Yayu

accessions. Similarly, the accessions displayed significant variations ( $p < 0.05$ ) in the overall results, which varied from  $1.75 \times 10^{-8} \text{ kg m}^{-2} \text{ s}^{-1} \text{ MPa}^{-1}$  to  $2.88 \times 10^{-8} \text{ kg m}^{-2} \text{ s}^{-1} \text{ MPa}^{-1}$  for the Harenna and Yayu accessions, respectively (Table 3). On the initial day of drying, the Harenna and Berhane-Kontir seedlings had the highest values in the full sunlight plots. This was unlike Bonga and Yayu accessions, which showed higher results under shade conditions. Similarly, most accessions had maximum results in the open sunlight on eight DAI. This was particularly the case for the Harenna and Yayu seedlings. In contrast, values were higher for the shaded seedlings of Harenna (I-3), Bonga (II-1) and Yayu (IV-4) accessions. On 12 DAI, most seedlings showed higher values in shade than in open sun plots. This was particularly observed for the Harenna (I-1, I-3) and Bonga (II-2) seedlings, but the Berhane-Kontir and Yayu seedlings that were kept in the sun plots revealed slightly higher values. At 16 DAI, the shaded Harenna (I-2) and Yayu (IV-3) accessions showed maximum values as opposed to the maximum values for the sun plot of Yayu accession (III-1). All accessions showed relatively maximum values under moisture-stressed plots of 12 and 16 DAI with the highest changes at 12 DAI. At this time, well-watered Yayu (IV-2) seedlings had higher

values than the Bonga (II-2) seedlings. Furthermore, the lowest and highest overall average values were measured from Yayu and Bonga accessions. Significantly higher LSC values were found in the Harenna accessions as opposed to the Yayu and Berhane-Kontir accessions (Table 3).

The results of the analysis of variance only showed no significant treatment interactions during the drought period due to the shade and irrigation on the first DAI ( $p < 0.05$ ) and eight DAI ( $p < 0.05$ ). In droughted seedlings in the full sun plots, the results ranged between  $1.88 \times 10^{-8} \text{ kg m}^{-2}\text{s}^{-1}\text{MPa}^{-1}$  and  $2.91 \times 10^{-8} \text{ kg m}^{-2}\text{s}^{-1}\text{MPa}^{-1}$  at the beginning and eight DAI, respectively. This is in contrast to the low values for the irrigated seedlings

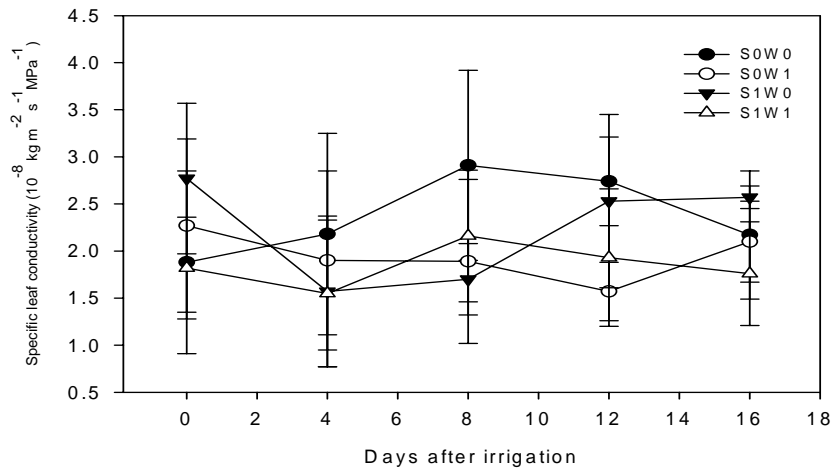
under moderate shade environments. When soil moisture was higher, moisture stressed and well-watered leaves showed increased and decreased trends from full sunlight to shade conditions. However, with progressive drought on eight DAI, a reverse pattern was observed and water stressed and well-watered seedlings revealed a declined and increased LSC in full sun and shade environments, respectively (Fig. 3). In droughted seedlings in the full sun plots, the results ranged between  $1.88 \times 10^{-8} \text{ kg m}^{-2}\text{s}^{-1}\text{MPa}^{-1}$  and  $2.91 \times 10^{-8} \text{ kg m}^{-2}\text{s}^{-1}\text{MPa}^{-1}$  at the beginning and eight DAI, respectively. This is in contrast to the low values for the irrigated seedlings under moderate shade environments (Fig. 3).

**Table 3.** Leaf specific conductivity ( $k_l$ , means $\pm$ SD $\times 10^{-8} \text{ kg m}^{-2}\text{s}^{-1}\text{MPa}^{-1}$ ) in Arabica coffee seedlings exposed to moisture-stress (0 to 16 DAI) in sun and shade conditions

Treatment	0	4	8	12	16 DAI	Overall mean
	<i>Shading</i>					
Moderate shade	2.30 $\pm$ 8.25	1.56 $\pm$ 7.72b	1.93 $\pm$ 5.97b	2.23 $\pm$ 8.65	2.16 $\pm$ 9.80	2.04 $\pm$ 5.27
Full sunlight	2.08 $\pm$ 9.43	2.04 $\pm$ 9.99a	2.40 $\pm$ 0.11a	2.15 $\pm$ 7.13	2.09 $\pm$ 5.62	2.17 $\pm$ 4.62
	<i>Irrigation (Irr)</i>					
Well watered	2.05 $\pm$ 7.70	1.72 $\pm$ 8.72	2.03 $\pm$ 7.80	1.75 $\pm$ 5.77b	1.88 $\pm$ 5.02b	1.89 $\pm$ 3.80b
Water stressed	2.33 $\pm$ 9.81	1.87 $\pm$ 9.72	2.31 $\pm$ 9.66	2.63 $\pm$ 7.19a	2.37 $\pm$ 9.52a	2.32 $\pm$ 5.06a
	<i>Accession (Acc)</i>					
I-1	2.86 $\pm$ 6.18	1.33 $\pm$ 6.78	3.25 $\pm$ 0.11a	2.67 $\pm$ 8.84	2.26 $\pm$ 3.39	2.48 $\pm$ 8.19ab
I-2	2.71 $\pm$ 0.14	2.87 $\pm$ 9.02	3.22 $\pm$ 9.46ab	2.32 $\pm$ 8.32	3.26 $\pm$ 0.14	2.88 $\pm$ 7.59a
I-3	2.03 $\pm$ 2.75	1.99 $\pm$ 5.97	1.97 $\pm$ 4.59abc	2.30 $\pm$ 7.10	1.79 $\pm$ 2.75	2.01 $\pm$ 2.01ab
II-1	2.23 $\pm$ 5.53	1.08 $\pm$ 8.70	1.65 $\pm$ 3.50c	1.85 $\pm$ 3.43	2.02 $\pm$ 6.31	1.91 $\pm$ 4.37b
II-2	2.17 $\pm$ 6.67	1.90 $\pm$ 3.88	2.30 $\pm$ 7.27abc	2.84 $\pm$ 0.11	1.90 $\pm$ 4.98	2.22 $\pm$ 0.14ab
II-3	2.31 $\pm$ 6.41	1.37 $\pm$ 2.05	2.13 $\pm$ 6.69abc	2.05 $\pm$ 3.87	1.78 $\pm$ 4.70	1.93 $\pm$ 0.19ab
III-1	2.45 $\pm$ 0.11	1.96 $\pm$ 9.81	2.44 $\pm$ 5.30abc	2.60 $\pm$ 9.36	2.14 $\pm$ 0.14	2.32 $\pm$ 2.98ab
III-2	2.08 $\pm$ 0.14	1.66 $\pm$ 6.81	1.89 $\pm$ 8.48c	2.02 $\pm$ 3.48	2.09 $\pm$ 6.79	1.94 $\pm$ 5.14ab
III-3	2.30 $\pm$ 7.16	1.64 $\pm$ 8.44	1.93 $\pm$ 6.15bc	1.80 $\pm$ 7.81	1.77 $\pm$ 5.36	1.89 $\pm$ 4.93b
IV-1	1.67 $\pm$ 0.11	2.59 $\pm$ 0.10	1.55 $\pm$ 6.87c	2.16 $\pm$ 3.86	2.15 $\pm$ 6.14	2.02 $\pm$ 5.80ab
IV-2	1.53 $\pm$ 2.85	1.13 $\pm$ 5.71	2.31 $\pm$ 0.11abc	1.91 $\pm$ 9.25	1.87 $\pm$ 2.31	1.75 $\pm$ 4.31b
IV-3	1.92 $\pm$ 0.13	2.08 $\pm$ 0.16	1.36 $\pm$ 3.96c	1.77 $\pm$ 0.13	2.47 $\pm$ 0.11	1.92 $\pm$ 6.10ab
Mean	2.19	1.80	2.17	2.19	2.12	2.11
CV (%)	36.22	37.46	21.27	23.05	27.55	15.88
	ANOVA					
Shading	Ns	*	**	Ns	Ns	Ns
Irrigation	Ns	Ns	Ns	***	*	**
Accession	Ns	Ns	*	Ns	Ns	*
Shade*Irr	*	Ns	***	Ns	Ns	Ns
Shade*Acc	Ns	Ns	Ns	Ns	Ns	Ns
Irr*Acc	Ns	Ns	Ns	Ns	Ns	Ns

Ns = Not significant  $p > 0.05$ ; \* $p < 0.05$ ; \*\* $p < 0.01$ ; \*\*\* $p < 0.001$ . Means with the same letter within a column are not significantly different according to Tukey's test at  $p = 0.05$ .





**Figure 3.** Leaf-specific conductivity in Arabica coffee seedlings as function of shade and watering treatments (S0W0= not shaded not watered, S0W1= not shaded watered, S1W0 = shaded not watered S1W1 = shaded watered) for the different days of withholding watering.

### Main stem conductivity

Reduced irradiance led to significantly enhanced main stem conductivity on the first DAI ( $p < 0.05$ ) and when there was severe soil drying on the 12 DAI ( $p < 0.05$ ) (Table 4). In contrast, seedlings in moderate shade showed higher average values than those in the sun. Moisture-stressed seedlings showed significantly higher main stem hydraulic conductivity values at the end of the drought period at 12 DAI ( $p < 0.05$ ) and 16 DAI ( $p < 0.05$ ). Similar to leaf specific conductivity, main stem conductivity was significantly different among accessions eight DAI, though the values did not differ before and after this date. Average values ranged from  $4.32 \times 10^{-5} \text{ kg m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$  to  $7.20 \times 10^{-5} \text{ kg m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$  in seedlings from the Yayu and Harena accessions, respectively, with minimum coefficient of variation (CV = 16.28%) among the accessions. The highest main stem conductivity values were measured for II-2 and III-1 seedlings, which resulted in the highest average value of  $6.50 \times 10^{-5} \text{ kg m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$ .

However, there was a decline after this date. In general, main stem conductivity was low in the Yayu seedlings (Table 4). The combined effect of shade and irrigation was significant on stem hydraulic conductivity at the beginning ( $p < 0.05$ ) and eight DAI ( $p < 0.05$ ) of withholding irrigation treatment.

Consequently, during the initial application of the treatments, shaded seedlings on the moisture-stressed plots exhibited higher main stem conductivity as compared with the other treatments, partly indicating the roles of shade levels, as this had a significant influence on main stem cross-sectional area ( $p < 0.05$ ) as well as on stem conductivity ( $p < 0.05$ ). In contrast, with extended time, moisture-stressed and well-watered seedlings showed significantly higher stem conductivity in sun and shade conditions, respectively. In other words, irrigated seedlings in the full sunlight and water stressed seedlings in the shade exhibited almost similar responses with the respective average stem conductivity of  $4.74 \times 10^{-5} \text{ kg m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$  and  $4.81 \times 10^{-5} \text{ kg m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$  (Fig. 4).

Moreover, seedlings of different accessions showed differences ( $p < 0.05$ ) in stem conductivity due to irrigation regimes. Accordingly, water stressed accessions from the Harena and Yayu populations revealed higher values than irrigated seedlings. On the other hand, seedlings from Bonga (II-2, II-3) and Yayu (III-1) accessions had higher stem conductivity when well-watered as opposed to soil moisture deficits and thus, a positive range of  $1.43 \times 10^{-5} \text{ kg m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$ ,  $1.21 \times 10^{-5} \text{ kg m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$  and  $3.11 \times 10^{-5} \text{ kg m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$  between the two irrigations levels, respectively. On the first day of irrigation, the

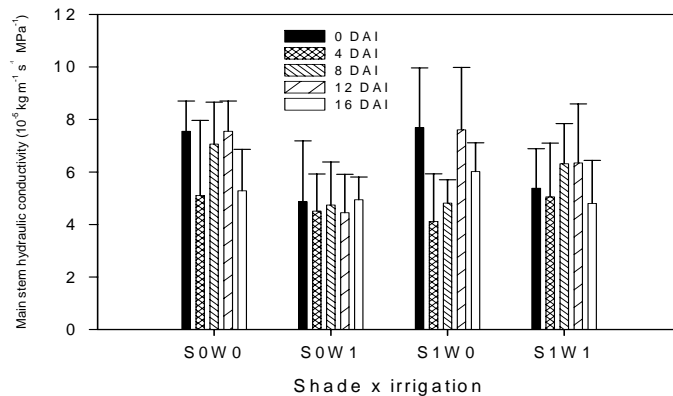
seedlings of Harenna (I-1, I-2) and Yayu (IV-3) had maximum conductivity as compared to the others. Consequently, accessions from Harenna exhibited lower stem conductivity in 16 DAI when most accessions from Bonga (II-1 and II-3), Berhane-Kontir (III-1, III-2 and III-3) and Yayu (IV-1 and IV-2) revealed slightly higher conductivity, the highest being from the Berhane-Kontir accessions. However, eight DAI the pattern changed and the water stressed seedlings of the Harenna accessions showed significantly higher values as compared to others. This was followed by the Yayu accessions.

All accessions, except Bonga (II-2, II-3) and Yayu (III-1), demonstrated higher stem hydraulic conductivity in the with irrigated plots than in those without. The Berhane-Kontir accessions showed only minimum differences between the irrigation regimes. The lowest stem conductivity was measured from Bonga accessions (III-1 and II-3) in both non-irrigated and irrigated plots. Thus, lowest and highest average stem conductivities were obtained for Bonga and Harenna coffee accessions (Fig. 5).

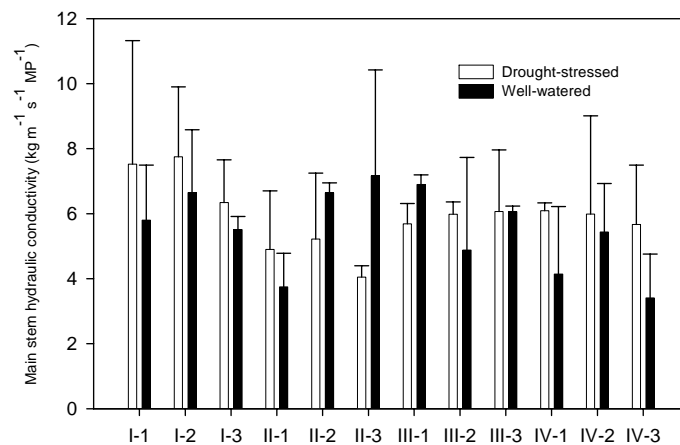
**Table 4.** Main stem hydraulic conductivity ( $k_s$ , means $\pm$ SD $\times 10^{-5}$ kg m<sup>-1</sup>s<sup>-1</sup>MPa<sup>-1</sup>) in seedlings of Arabica coffee accessions exposed to moisture-stress (between 0 and 16 DAI) in shade and full sunlight conditions

Treatment	0 DAI	4 DAI	8 DAI	12 DAI	16 DAI
<i>Shading</i>					
Moderate shade	6.54 $\pm$ 2.22a	4.58 $\pm$ 1.96	5.56 $\pm$ 1.45	6.97 $\pm$ 2.36a	5.41 $\pm$ 1.50
Full sunlight	4.47 $\pm$ 1.89b	4.80 $\pm$ 2.23	5.90 $\pm$ 1.98	6.00 $\pm$ 2.04b	5.11 $\pm$ 1.26
<i>Irrigation (Irr)</i>					
Well watered	5.13 $\pm$ 1.92	4.78 $\pm$ 1.75	5.53 $\pm$ 1.74	5.39 $\pm$ 2.10b	4.87 $\pm$ 1.29b
Water stressed	5.88 $\pm$ 2.60	4.60 $\pm$ 2.40	5.94 $\pm$ 1.71	7.57 $\pm$ 1.83a	5.64 $\pm$ 1.38a
<i>Accession (Acc)</i>					
I-1	5.82 $\pm$ 3.46	3.66 $\pm$ 2.14	6.66 $\pm$ 2.60ab	6.05 $\pm$ 2.29	5.67 $\pm$ 0.46
I-2	5.19 $\pm$ 2.37	5.34 $\pm$ 1.05	7.20 $\pm$ 1.79a	7.23 $\pm$ 2.17	6.60 $\pm$ 1.79
I-3	5.45 $\pm$ 1.93	5.50 $\pm$ 1.15	5.92 $\pm$ 0.93ab	7.56 $\pm$ 2.83	5.00 $\pm$ 0.93
II-1	4.98 $\pm$ 2.15	4.44 $\pm$ 4.35	4.32 $\pm$ 1.37b	5.53 $\pm$ 1.75	4.60 $\pm$ 1.27
II-2	6.10 $\pm$ 1.76	4.44 $\pm$ 1.09	5.93 $\pm$ 1.44ab	8.59 $\pm$ 3.46	4.68 $\pm$ 0.54
II-3	5.58 $\pm$ 1.66	4.45 $\pm$ 1.02	5.60 $\pm$ 2.60ab	6.69 $\pm$ 1.42	5.26 $\pm$ 2.53
III-1	5.79 $\pm$ 2.00	4.86 $\pm$ 2.36	6.29 $\pm$ 0.80ab	7.78 $\pm$ 2.38	6.30 $\pm$ 2.30
III-2	5.86 $\pm$ 2.15	5.48 $\pm$ 1.78	5.43 $\pm$ 1.78ab	6.39 $\pm$ 0.95	5.09 $\pm$ 0.50
III-3	7.29 $\pm$ 0.95	4.75 $\pm$ 2.41	6.06 $\pm$ 1.09ab	5.50 $\pm$ 2.31	5.37 $\pm$ 1.56
IV-1	4.21 $\pm$ 3.56	6.94 $\pm$ 2.31	5.12 $\pm$ 1.65ab	6.21 $\pm$ 0.99	5.07 $\pm$ 1.07
IV-2	4.15 $\pm$ 1.63	3.21 $\pm$ 1.44	5.71 $\pm$ 1.97ab	5.53 $\pm$ 2.44	4.94 $\pm$ 1.11
IV-3	5.65 $\pm$ 3.92	3.22 $\pm$ 1.02	4.54 $\pm$ 1.85ab	4.73 $\pm$ 2.39	4.50 $\pm$ 0.74
Mean	5.50	4.70	5.70	6.50	5.30
CV (%)	35.77	42.83	16.28	22.63	18.74
<i>ANOVA</i>					
Shading	**	Ns	Ns	*	Ns
Irrigation	Ns	Ns	Ns	***	*
Accession	Ns	Ns	*	Ns	Ns
Shade*Irr	*	Ns	***	Ns	Ns
Shade*Acc	Ns	Ns	Ns	Ns	Ns
Irr*Acc	Ns	Ns	*	Ns	Ns

Ns = Not significant, \*, \*\*, \*\*\* = significant at  $p < 0.05$ ,  $p < 0.01$  and  $p < 0.001$ , respectively. Means with the same letter within a column are not significantly different (Tukey's at  $p = 0.05$ ).



**Figure 4.** Main stem hydraulic conductivity in Arabica coffee seedlings with and without irrigation in full sunlight and moderate shade environments.



**Figure 5.** Main stem hydraulic conductivity in seedlings of Arabica coffee accessions under well-watered and water-stressed conditions for the period eight DAI.

## DISCUSSION

In full sunlight plus water stressed seedlings, the results at the beginning and eight DAI showed wide gap as compared to the minimum difference for the well irrigated seedlings under shade environments. The interaction between shade and irrigation significantly influenced the whole-plant conductance at the first, fourth and eighth DAI, possibly reflecting the different responses of the root and shoot growth in relation to the magnitude of water tensions in the soil-plant system. This was evident from the weak and indirect correlation between soil moisture and whole-plant hydraulic

conductance in moderately water stressed seedlings in a week of soil moisture deficits. This could be attributed, among others, to the variations in the microclimatic variables measured under the nursery conditions (Kufa and Burkhardt, 2011<sub>b</sub>). In contrast, highly significant variation was observed eight DAI in the open sun plots, indicating that Arabica coffee thrives best under partial shaded environments. This demonstrates that Arabica coffee has evolutionally adapted to forest habitats where shade can play important multiple roles (Wintgens, 2004), though the site-specific benefits of shade that take into account environmental and coffee genetic factors needs for rigorous research.

Similarly, the accessions displayed significant variations in the overall mean results with highest and lowest measured from Harena and Yayu accessions, respectively. The lowest hydraulic conductance was measured in the petiole of coffee leaves throughout the experimental period, except at the beginning of the drying treatment. The findings show a negative relationship between root and shoot hydraulic flows, where the respective maximum conductances were measured in drought-stressed and well-watered seedlings. This is in line with the *in-situ* hydraulic conductance of wild coffee population (Taye and Burkhardt, 2008), indicating that hydraulic conductance is a genetically fixed selection trait. Low conductance values were particularly noticeable with prolonged drying, when petioles showed the earliest drying symptoms and could be due to the blocked water flow via the stalk of the leaf blade to the distal leaf surface leading to water storage in the stem of the seedlings. There is substantial experimental evidence that stomatal conductance is positively correlated with the hydraulic conductance of the soil-root-leaf pathway in a wide range of plant species (Meinzer *et al.*, 1999). Therefore, in addition to the effect of path length, changes in crown architecture may determine whole-plant conductance (Becker *et al.*, 2000).

Our finding suggest provision of moderate shading to postpone the consequences of sever moisture deficits, optimize resource use efficiency and improve seedling growth. The results also indicated variations in moisture gradients and thus, the demand for water by coffee seedlings (Burkhardt *et al.*, 2006). It seems likely that stomatal conductance is adjusted to maintain xylem water potential above the critical point where runaway embolism would occur (Tyree and Sperry, 1988). These effects of hydraulic conductance on gas exchange were reported for intact plants by Meinzer *et al.* (1995). Tausend *et al.* (2000<sub>b</sub>) also described that differences in crown architecture can significantly influence plant gas exchange. In Arabica coffee, hydraulic conductance is positively correlated with total daily transpiration (Tausend *et al.*, 2000<sub>a</sub>). A major component of differential adaptation to drought among Arabica coffee appears to be

genetic factor, and may be governed by rates of water use or efficiency of extraction of soil water (Pinheiro *et al.*, 2005). Thus, genotypes with higher hydraulic conductance should have higher rates of water use. This means that they may deplete accessible soil water more rapidly and/or have a deeper root system than genotypes with lower hydraulic conductance. The strong association of total transpiration with hydraulic conductance might dampen variation in water potential with variation in water availability, which may help to avoid non-stomatal limitation to photosynthesis and xylem cavitations (Tausend *et al.*, 2000<sub>b</sub>). This would be advantageous with non-limiting soil water or with brief periods of water deficit, but disadvantageous with longer drought periods, since a high hydraulic conductivity would hasten the development of severe moisture-stress conditions.

According to Taye (2006), stem size and leaf growth were the strongest parameters related to hydraulic efficiency of arabica coffee seedlings. Consequently, leaf- and stem-specific hydraulic conductivities were calculated to describe the diversity in coffee accessions under contrasting light and soil water regimes. The results depicted that the full sunlight-exposed and water-stressed seedlings showed higher leaf specific conductivity than those in the shade and irrigated treatments. The seedlings significantly differed due to moderate drought not exceeding eight DAI; before and after this date no differences were detected. The same author also reported that soil moisture contents were in consistence with the patterns of stem hydraulic conductivity, which correlated positively, but weakly in seedlings eight DAI. This was also when highly significant gap was noted, suggesting that this is a minimum threshold level of moisture-stress in coffee seedlings managed under full sun conditions. This is when significant relationships between soil moisture content and leaf water potential measured in coffee seedlings (Kufa and Burkhardt, 2011<sub>b</sub>), indicating the moisture gradients in the soil-plant-air continuum under coffee nursery conditions.

Further, significantly higher overall average LSC values were found in the Harena accessions as opposed to the Yayu

and Berhane-Kontir accessions. This could be related to the wider stem diameter and increased total leaf surface area supported by the main stem segment, which may indicate the differences in functional xylem area and shoot morphological attributes. This is quite in agreement with the hydraulic conductance results of the Ethiopian wild coffee populations under field conditions (Taye and Burkhardt, 2008). Hence, the results demonstrate the inherent variations in growth habits and hydraulic architecture in the seedlings of different coffee accessions and the consideration of these traits in searching for suitable coffee varieties for specific locality, particularly moisture stress prone areas.

In the present study, the effect of irrigation levels was minimal under moderate shade, where little or no differences were observed particularly with prolonged moisture-stress. This shows the advantage of shade in reducing evapo-transpiration, thus helping to conserve the available soil moisture. To this end, Kufa and Burkhardt (2011a) also described similar results of leaf stomatal characteristics in coffee seedlings. According to Sperry *et al.* (2002), many aspects of plant water use, particularly in response to soil moisture deficits, may have as their basis the alteration of hydraulic conductance from soil to canopy. The same authors pointed out that the regulation of plant water potential by stomatal control and leaf area adjustment may be necessary to maximize water uptake on the one hand, while avoiding loss of hydraulic contact with the soil water on the other. Similarly, large differences in water use between species can be attributed in part to differences in their hydraulic equipment, which is presumably optimized for drawing water from a particular temporal and spatial niche in the soil environment. According to Meinzer (2002), components of dynamic variation in apparent hydraulic conductance in intact plants include exchange of water between the transpiration stream and internal storage compartments.

To this end, Tyree and Ewers (1991) described that trees growing in climates with high evaporative demand will have a low leaf to sapwood area ratio and thus, the expansion of the conducting area relative to transpiring area increases LSC. To support higher transpiration rates, a low leaf to sapwood area

ratio in desert versus montane trees could increase leaf-specific hydraulic conductance. Alternatively, a high sapwood volume to leaf area ratio in the desert environment may increase the contribution of stored water to transpiration (Maherali and DeLucia, 2001). Thus, the primary benefit of low leaf to sapwood allocation in progressively arid environments is to increase leaf specific hydraulic conductance and not to increase the contribution of stored water to transpiration.

The results indicated that shaded seedlings on the moisture-stressed plots exhibited higher main stem conductivity as compared with the other treatments, partly indicating the roles of shade levels, as this had a significant influence on main stem cross-sectional area as well as on stem conductivity. The lowest and highest average stem conductivities were obtained for the Bonga and Hareenna accessions, suggesting that the low main stem basal area of the accessions reduced the water flow. This corroborates with our findings on the water relations and growth performances of the same wild coffee populations in the mountain rainforests of Ethiopia (Taye and Burkhardt, 2008). The proportional decrease in leaf hydraulic conductivity and leaf photosynthetic rate with increasing wood density suggests that the biophysical structure of wood may constrain physiological functions to specific operating ranges and reflect life-history trade-offs at the whole organism scale. Wood density has been linked to support against xylem implosion by negative pressure (Hacke *et al.*, 2001), indicating that species with high density wood may better resist cell wall collapse, and are likely to withstand lower leaf potential (Santiago *et al.*, 2004). The substantial variations among coffee accessions in hydraulic movements under suboptimal nursery conditions are in agreement with the results of other physiological parameters (Kufa and Burkhardt, 2011a, 2011b) and in part underlined the diversity in adaptation mechanisms as pointed out by Sobrado (2003).

## CONCLUSIONS

In conclusion, knowledge of the characteristics of coffee germplasm and target environment is of prime importance for the success of coffee breeding programs. To this end, our present findings confirmed the contributions of moderate shading to postponed the occurrence of severe moisture stress effect in coffee seedlings by twofold over those in full sunlight conditions and the coffee accessions were noted to respond differently. Coffee accessions from the driest site, Harena, showed highest conductance, largely due to their extensive root system, high transpiration and biomass production as reported by Burkhardt *et al.* (2006). However, these germplasm were most vulnerable and they failed to withstand under persisting moisture deficits as opposed to others, especially the Bonga and Berhane-Kontir accessions. The results revealed peculiar hydraulic attributes in Arabica coffee germplasm accessions in coping with the imposed environmental stresses. This supports our previous findings on leaf stomatal characteristics (Kufa and Burkhardt, 2011a) and water potential (Kufa and Burkhardt, 2011b) in seedlings of the same coffee accessions, indicating the direct relationships among these traits to be considered for breeding improvements. This agrees with Burkhardt *et al.* (2006) who reported that the southeastern and southwestern coffee accessions were found to follow opportunistic and conservative ways of water use strategies, respectively. Thus, hydraulic properties can be used to characterize Arabica coffee genetic diversity. This calls, *inter alia*, for further ecophysiological and breeding works to identify and develop drought tolerant coffee cultivars for each geographical area and promote multi-site *in-situ* and/or on-farm conservation and utilization of Arabica coffee genetic resources in its home country, Ethiopia.

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