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Variations in Leaf Water Potential in the Wild Ethiopian *Coffea arabica* Accessions under Contrasting Nursery Environments

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Abstract: The study was conducted with the aim to compare the variability among the wild coffee germplasm accessions in diurnal leaf water potential (LWP, Ψ_L) under contrasting shading and irrigation environments. Twelve coffee accessions were evaluated under two shading (moderate shading and full sun radiation) and irrigation (well watered and water stressed) regimes at nursery site. The diurnal leaf water potential was measured with a pump-up pressure chamber twice a day (predawn and midday) at every 4-day intervals for a two week drought stress imposed period. The results depicted significantly maximum predawn ($\Psi_L = -0.66 \pm 0.43$ MPa) and midday ($\Psi_L = -1.35 \pm 0.24$ MPa) leaf water potential in shaded seedlings as compared with those in full sunlight conditions. Likewise, significant ($p < 0.05$) variation in midday LWP was measured on the 4th day after irrigation (4-DAI). The lowest ($\Psi_L = -1.54$ MPa) and highest ($\Psi_L = -1.32$ MPa) midday LWP were recorded for the Bonga and Berhane-Kontir coffee germplasm accessions, respectively. Moreover, relatively low ($\Psi_L = -0.87$ MPa) and high ($\Psi_L = -0.73$ MPa) predawn LWP were recorded for the Bonga and Berhane-Kontir coffee germplasm accessions with the lowest change in diurnal Ψ_L of -0.75 and -0.73 MPa, respectively. The two-way interaction effects revealed significant ($p < 0.0001$) variations in LWP due to shading by irrigation, shading by time of the day as well as irrigation by time of the day. Accordingly, coffee seedlings exposed to moisture deficits in full sun conditions exhibited minimum LWP on the 8th DAI, particularly in Harenna genotypes. Overall, the present findings demonstrated a two-fold advantage of shading coffee nurseries in optimizing water application and extending the occurrence of severe drought to damage coffee seedlings. However, the precipitation gradient of the geographical origins was not reflected in the LWP dynamics in coffee germplasm accessions, indicating the need for further research in understanding the underlying mechanisms involved in drought tolerance among the immense Arabica coffee genetic resources with the views to promote irrigated coffee farming and thus contribute to sustainable preservation and use of coffee gene pools at its original place of origin in Ethiopia.

Key words: Ethiopian wild coffee, coffee nursery, drought tolerance, irrigation, leaf water potential, shading, water relations

INTRODUCTION

Plant growth is controlled directly by drought stress and only indirectly by soil and atmospheric drought stress. The water status of plants has received much attention in recent years to provide baseline information for evaluating plant need for water or how well it is adapted to its environment (site-plant matching), especially where water is a limiting factor (Prasad, 1997). Water in soil facilitates absorption of minerals by plants and water in plants helps in maintaining the right type of turgidity for growth and various synthesis processes (Larcher, 2003). Hopkins (1995) emphasized that drought

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 (temperature, humidity, wind, etc.).

Investigation on the adaptation mechanisms of plants species is important to understand their ecological success and growth conditions (Sobrado, 1993). According to Turner (1979), drought tolerance in plants may result from either a reduction of water loss or maintenance of water uptake. It is known that the degree of drought stress tolerated profoundly influences virtually all physiological and metabolic functions that are

responsible for determining plant adaptation, growth and distribution (Ritchie and Hinckley, 1975). In this regard, measurements of leaf water potential can be a very dependable reading for small canopy plants managed under environments where there is only little transpiration water loss. Leaf water potential is always changing with the environmental variables and thus, the time of measurements should be considered in characterizing plant species or sites (Salisbury and Ross, 1992). This can be expressed in terms of predawn and midday leaf water potentials. If the soil is irrigated, the predawn leaf water potential values indicate the soil water potential, i.e., reduced water tensions around the root zone. The midday water potentials reflect the tension experienced by the plant as it pulls water from the soil to satisfy the water demand of the atmosphere, i.e., it shows the evaporation demand of the site and hence transpiration.

In general, there are three basic aspects of drought stress dynamics. These are atmospheric demands on the plant, plant regulation or how the plant reacts to drought stress and soil supply or the composition of the soil. The atmospheric demand includes radiation, air temperature, humidity and wind. The plant regulates drought stress by opening and closing the stomata, leaf flagging, rolling and shedding (Hale and Orcutt, 1987). Leaf water potential declines whenever the water balance in the plant becomes more negative due to insufficient water uptake to meet the required transpiration (Hale and Orcutt, 1987; Salisbury and Ross, 1992; Haniff, 2006). At predawn, reduced atmospheric demand for water slows down the water loss from the plant (Hopkins, 1995). The montane rainforests of Ethiopia are the known center of origin and genetic diversity for the highland arabica coffee (*Coffea arabica* L.), which is highly demanded for its unique quality standard in the global market. Ethiopian coffee is thus a shade-adapted plant in the natural multi-strata forest ecosystems with the occurrence of wild Arabica coffee genetic resources (Teketay, 1999). Ethiopia is endowed with wide ecological suitability and genetic diversity for sustainable production and export of known specialty coffee brands, while conserving friendly natural forest environments (Kufa, 2010). However, the fragmented forest areas with the occurrences of rich biodiversity is shrinking from time to time, largely due to the ever increasing population pressure, land use conflict, high deforestation, expansion of large-scale farms, crop replacement and fluctuating coffee prices (Teketay, 1999). As a result, the known coffee types are either replaced by other crops or their cultivation is expanding into less suitable and vulnerable areas. These coupled with the increasing patterns of climate change are threatening the natural gene pools of arabica coffee (Kufa, 2010) and thus calls for urgent reactions.

Drought is considered to be the main environmental factor limiting crop productivity, including Arabica coffee. The current climate change and limited availability of soil moisture, particularly at critical growth stages of coffee plant are among the major constraints (Kufa, 2010). According to Edjamo *et al.* (1996), the released coffee selections and landraces in Ethiopia can be broadly grouped into three canopy classes of open, medium and compact crown nature. They also differ in growth characteristics under field (Kufa *et al.*, 2004a) and experimental nursery conditions (Taye and Burkhardt, 2006), largely due to variations in shoot and root systems and thus, their water relations could vary accordingly. The existence of genetic variability has been evidenced from the hydraulic properties (Taye and Burkhardt, 2006) among the wild coffee populations, though their water storage response along soil moisture gradients under a controlled environment is little understood.

To this end, the possible fast adverse impacts of global warming and climate changes on coffee ecology and diversity demands urgent reactions before it reaches irreversible situations. It is speculated that the immense arabica coffee populations may have different coping mechanisms to environmental stress pressures (Kufa, 2010). To this effect, knowledge on soil-plant-water relations under diverse agro-ecologies and production systems would help, among others, in providing baseline information on useful traits that could be used as selection criteria for identifying desirable genotypes in coffee breeding program. This would contribute to sustainable conservation, management and utilization of natural coffee gene pool resources for the future development of the global coffee sector. It is, therefore, imperative to investigate the extent of variations in diurnal leaf water potentials in seedlings of wild arabica coffee germplasm accessions under contrasting sun light and irrigation regimes at the Jimma Research Center, southwestern Ethiopia.

MATERIALS AND METHODS

The study area: The experiment was undertaken during the dry season of 2005 under controlled nursery settings at the Jimma Agricultural Research Center (7° 46' N latitude and 36° 0' E longitude), southwestern Ethiopia. The area is located within the Tepid to cool humid highlands agro-ecological zone at an altitude of 1750 m above sea level. The area receives an average rainfall of 1595 mm per annum distributed into 173 days. The driest season lasts between December and January. The average maximum and minimum air temperatures are 25.9 and 11.2°C, respectively, the coldest month being December.

Experimental procedures: Fully ripe red and healthy coffee cherries were collected from the selected twelve- wild coffee mother trees in the montane rainforests of Ethiopia. These include Harena, Bonga, Berhane-Kontir and Yayu, which are dissected by the Great Fifty Valley with varying climate gradients (Burkhardt *et al.*, 2006). Except Harena in the driest southeastern part, the others are located in the southwestern Ethiopia. Hence, a total of 12 wild Arabica coffee germplasm accessions, three from each population, Harena (I-1, I-2, I-3), Bonga (II-1, II-2, II-3), Birhane-Kontir (III-1, III-2, III-3) and Yayu (IV-1, IV-2, IV-3), were used for the present *ex-situ* study.

The recommended nursery soil medium (Taye *et al.*, 2003) prepared from topsoil and decomposed coffee husk at the respective proportion of 3:1 (v/v) was firmly filled in black plastic pots perforated at the bottom and arranged on nursery seedbed. The coffee seeds were sown on March 30, 2004 in each plant plastic pot (volume = 5.8 liter) and all post-sowing nursery operations, including mulching, watering, shading, weeding, disease and insect control were uniformly applied according to the recommendations of the center (Institute of Agricultural Research, 1996; Edjamo *et al.*, 1996). The seedlings were uniformly managed under partial shade conditions and irrigation was applied at 4-day intervals during the dry season of 2005. In this way, the seedlings were uniformly managed for one-year until they attained the desired growth stage with four pairs of primary branches to impose the drought treatments.

The treatments and design: The treatments included shadings (moderate and full sunlight), irrigation regimes (well-watered and droughted) and 12 coffee germplasm collected from four wild arabica coffee populations. In this case, the treatment combinations involved not shaded and not watered (S0W0), not shaded and watered (S0W1), shaded and not watered (S1W0) and shaded and watered (S1W1). Moderate (50% light interception) overhead shade (at 2 m height) and side shades were constructed from the bamboo slants. Each treatment consisted of 25 seedlings per plot and maximum care was taken to avoid side-shading effects between the treatments. For this, the shaded plots were far apart from each other (12 m), while the spacing between irrigation and coffee germplasm accession plots was 2 and 1 m, respectively. The spacing between coffee seedlings was increased with ageing of the seedlings. At the beginning, it was 10×10 cm and later on arranged at 20×20 cm spacing. The water stressed plots were covered with white plastic sheet, whenever there is rain during day and night times throughout the study period. A factorial experiment in a randomized

complete block design of three replications was used to arrange the treatments. The blocks and the shading treatments were systematically oriented in east to west direction under controlled coffee nursery site.

Data collection

Microclimatic variables: The major microclimatic variables (air temperature, soil temperature and relative humidity) were monitored in potted coffee seedlings under full sunlight and moderately shaded plots using the Tinytag-Gemini Data Loggers (GLM version 2.8, UK). The probe of the Tinytag was inserted into the potting soil to about 15 cm depth to record soil temperature. The air and soil data were recorded from the same seedlings arranged in open sun and shaded nursery plots. Leaf temperature was measured using an infrared thermometer. For this, five seedlings per accession and two primary branches per seedling for each treatment were selected for repeated measurements. The data were recorded on the dorsal side of the leaf three times daily: morning (8:30-9:30 h), midday (12:00-13:00 h) and afternoon (15:00-16:00 h local time) from the same leaf spot. This was accomplished in the relatively dry month in May 2005 and cloudless hours of the day. In addition, ResiWin 0.12 (Gademann Instruments GmbH, Schweinfurt, Germany) was used to measure leaf microclimate variables and conductivity in shaded and full sunlight conditions. Maximum care was taken to ensure that leaves were not shaded by side seedlings. In addition, moisture drops and dust particles were cleaned from the sample leaves before recording leaf temperature.

Leaf water potential (Ψ_L): A pump-up pressure chamber (PMS Instrument Co., Corvallis, USA) was used to measure the leaf water potential (LWP, Ψ_L) in seedlings of different arabica coffee accessions studied under varying shading and irrigation treatment. The maximum capacity of the chamber is Ψ_L of -2.1 MPa. This is below the level where plants, including Arabica coffee can show typical drought symptoms such as closed stomata, stop in shoot growth and declining overall growth rate (PMS Instrument Co.). Mature and healthy true leaf pairs were used from the same node position and direction on a primary branch of coffee seedlings. LWP measurement was performed twice a day: predawn (05:30-06:30 h) and midday (12:00-13:00 h local time) at every 4-days interval between the first (0 DAI) and two weeks after irrigation (16- DAI). The dynamics in the diurnal LWP was compared, either singly or in combination, for the studied treatments.

Statistical analysis: Data analysis was performed with the default SAS 8.1 (SAS Institute Inc. Cary NC, USA) procedure. Two-way analysis of variance (ANOVA) was carried out to see the extent of variations in LWP due to

the main and interaction treatment effects. The diurnal LWP was assessed for a two-week period at every 4-day intervals to compare the variability between the shading and irrigation regimes and among coffee germplasm accessions as well as due to interaction effects. Moreover, treatment means were ranked according to Tukey test at $p = 0.05$, whenever the F-test showed significant differences. The relationships between the most relevant parameters were examined using regression analysis and graphs of two-way significant interactions were made with the SigmaPlot SPW9.0 (SYSTAT Software, Inc.).

RESULTS

Microclimatic variables: The results of microclimatic monitoring indicated significant differences between daylight and night in terms of relative humidity ($p < 0.05$) and air temperature ($p < 0.01$). Thus, significantly lower relative humidity (70.8%) and higher air temperature (20.47°C) were recorded during daytime. However, the difference between day and night soil temperatures was not significant, though it was higher during the day (23.83°C) time. The influence of shade level either singly or in combination with time of the day on microclimatic elements was not significant at coffee nursery site. Consequently, relative air humidity was 73.4 and 78.4% for the sun and shade plots, respectively. In addition, both air and soil temperatures were noted to be higher in full radiation exposed pots as compared with the shaded ones (Table 1).

Leaf water potential: The Analysis of Variance (ANOVA) for the leaf water potential (Ψ_L) in seedlings of arabica coffee germplasm over the imposed drought stress period is presented in Table 2. Accordingly, diurnal leaf water potential was significantly ($p < 0.001$) changed due to shading and irrigation regimes. The shade treatments exhibited highly significant differences in LWP on the 4 and 8-day after irrigation (DAI). This was declined and significant ($p < 0.05$) shading effect was manifested on the 12 and 16-DAI (Table 2).

The results show significantly maximum predawn ($\Psi_L = -0.66 \pm 0.43$ MPa) and midday ($\Psi_L = -1.35 \pm 0.24$ MPa) LWP in shaded seedlings as compared to those in full sun with mean predawn and midday Ψ_L values of -0.95 ± 0.70 and -1.52 ± 0.36 Mpa, respectively. However, the diurnal dynamics in the LWP was significantly lower ($\Psi_L = -0.70 \pm 0.22$ MPa) for shaded leaves as opposed to the sun exposed leaves (Table 3). Likewise, irrigation treatments showed highly significant variations throughout the induced drying period, except on predawn LWP at the beginning of the imposed drought stress

period. Hence, drought-stressed seedlings had significantly higher predawn ($\Psi_L = -0.26 \pm 0.02$ MPa) and midday ($\Psi_L = -1.16 \pm 0.12$ Mpa) LWP as compared to well-watered seedlings with a significantly lower change in diurnal leaf moisture potential ($\Psi_L = -0.89 \pm 0.12$ MPa). However, water stressed seedlings revealed significantly lower LWP in full sunlight (predawn $\Psi_L = -1.62 \pm 0.23$ and midday $\Psi_L = -1.90 \pm 0.27$) and shaded (predawn = -0.77 ± 0.45 MPa and midday $\Psi_L = -1.53 \pm 0.29$ MPa) environments on the 4 and 8-DAI, respectively (Fig. 1).

In contrast, except the significant ($p < 0.05$) variation in midday LWP on 4-DAI, there was no difference among accessions and their interactions with shade and irrigation regimes. Nonetheless, the lowest ($\Psi_L = -1.54$ MPa) and highest ($\Psi_L = -1.32$ MPa) midday LWP were recorded for the Bonga and Berhane-Kontir accessions, respectively. Similarly, relatively low ($\Psi_L = -0.87$ Mpa) and high ($\Psi_L = -0.73$ MPa) predawn LWP were obtained for the Bonga and Berhane-Kontir accessions with the lowest change in diurnal LWP values of -0.75 and -0.73 MPa, respectively, though the values were not significantly different from the others. The other accessions showed comparable Ψ_L with averages of -0.81 , -1.44 and -0.63 MPa determined for predawn, midday and change in LWP, respectively (Table 3). Although insignificant, the coffee accessions from the Harenna (I-1, $\Psi_L = -0.89$ MPa) and the Berhane-Kontir (III-1, $\Psi_L = -0.90$ MPa) wild coffee germplasm accessions exhibited the lowest LWP at the 4th DAI. This, however, declined after 8 DAI to the respective low LWP of -1.28 and -1.75 MPa. In this case, Bonga and Yaju accessions showed reduced Ψ_L from -0.78 to -1.98 MPa and from -0.63 to -1.98 MPa between 4 and 8 DAI, respectively. In addition, Harenna coffee seedlings had substantially lower predawn LWP when drought stressed in full sun radiations. Consequently, a higher diurnal change in LWP was observed in the Harenna accession. This is in contrast to the low midday values and reduced diurnal LWP of the drought stressed Berhane-Kontir accession. These accessions showed

Table 1: Microclimate variables in the full sunlight and shaded nursery conditions

Variable	RH (%)	Temperature (°C)	
		Air	Soil
Time of day	*	**	Ns
Night	80.97±9.97a	16.56±1.74b	19.10±7.16
Day	70.82±6.03b	20.47±2.01a	23.83±4.23
Shading level	Ns	Ns	Ns
Full sun	73.42±8.57	18.75±3.17	24.03±5.95
Shaded	78.36±9.52	18.28±2.46	18.90±5.60
Mean	75.89	18.51	21.46
CV (%)	3.17	3.58	30.42
Time×shade	Ns	Ns	Ns

Ns: Not significant; * $p < 0.05$; ** $p < 0.001$. Means were compared according to Tukey test at $p = 0.05$

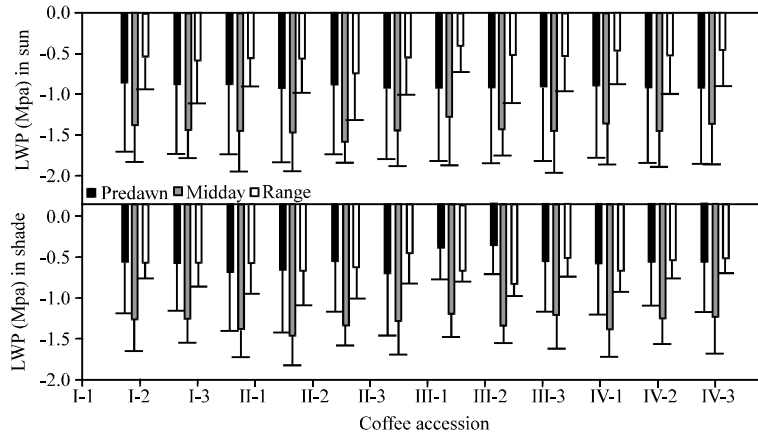


Fig. 1: Diurnal changes of leaf water potential in seedlings of coffee accessions in open sunlight and shaded nursery environments

Table 2: ANOVA for leaf water potentials in Arabica coffee seedlings for the different drought stress period (days after irrigation, DAI) under full sunlight and shaded environments

Source	Df	0-DAI			4-DAI			8-DAI			12-DAI			16-DAI		
		PD	MD	DD	PD	MD	DD	PD	MD	DD	PD	MD	DD	PD	MD	DD
Shade	1	Ns	Ns	Ns	***	***	Ns	***	***	***	*	*	Ns	Ns	*	Ns
Irrigation	1	Ns	***	***	***	***	Ns	***	***	***	***	***	***	***	***	***
Accession	11	Ns	Ns	Ns	Ns	*	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns
Shade×Irr	1	Ns	Ns	**	***	***	Ns	***	***	***	Ns	*	**	Ns	*	*
Shade×Acc	11	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns	**	Ns	Ns	Ns
Irr×Acc	11	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns

Ns = Not significant; *p<0.05; **p<0.01; ***p<0.0001. Df = Degree of freedom; PD: Predawn, MD: Midday, DD: Diurnal difference

Table 3: Diurnal leaf water potential (Ψ_L = MPa) in seedlings of wild arabica coffee accessions as influenced by contrasting shading and irrigation regimes

Treatment	Predawn	Midday	Difference
Shading			
Full sunlight	-0.95±0.70b	-1.52±0.36b	-0.57±0.37a
Moderate shade	-0.66±0.43a	-1.35±0.24a	-0.70±0.22b
Irrigation			
Water stressed	-1.35±0.32b	-1.72±0.16b	-0.37±0.18a
Well-watered	-0.26±0.02a	-1.16±0.12a	-0.89±0.12b
Coffee accession			
I-1	-0.78±0.65	-1.39±0.37ab	-0.61±0.28
I-2	-0.80±0.64	-1.43±0.29ab	-0.64±0.37
I-3	-0.85±0.68	-1.48±0.38ab	-0.63±0.30
II-1	-0.87±0.72	-1.54±0.35b	-0.68±0.37
II-2	-0.79±0.65	-1.54±0.27b	-0.75±0.42
II-3	-0.87±0.71	-1.44±0.37ab	-0.57±0.35
III-1	-0.73±0.67	-1.32±0.39a	-0.59±0.30
III-2	-0.73±0.67	-1.46±0.25ab	-0.73±0.44
III-3	-0.80±0.68	-1.41±0.41ab	-0.61±0.28
IV-1	-0.81±0.67	-1.44±0.36ab	-0.63±0.33
IV-2	-0.82±0.67	-1.43±0.35ab	-0.60±0.32
IV-3	-0.82±0.70	-1.38±0.40ab	-0.56±0.31
Mean	-0.81	-1.44	-0.63
CV (%)	11.94	4.22	14.41

Ns: Not significant (p>0.05), *p<0.05; *** p<0.001. Means with the same letter(s) in a column are not significantly different (Tukey's test at p = 0.05)

significantly higher predawn LWP than the Bonga germplasm accessions when examined in drought-stressed plots in moderately shaded nursery site.

With regard to interaction effects, the results depicted significant (p<0.0001) variations in LWP due to the interactions between shade and irrigation, shade and time of the day as well as irrigation and time of the day (Table 2). Hence, both predawn and midday LWP were significantly reduced in the sun as compared to the higher values in shade environments. Similarly, drought stressed seedlings had significantly lower predawn and midday LWP, particularly with the highest predawn LWP values in well-watered seedlings. The interaction between shade and irrigation was significant 4 and 8- DAI and tended to decline with extended soil drying periods. Accordingly, LWP was significantly reduced for seedlings subjected to water stress under full sun conditions with the lowest predawn (Ψ_L = -1.64 MPa) and midday (Ψ_L = -1.84 MPa) LWP values measured early in the drought imposed period. These values, however, declined as of the 8-DAI. This was followed by low predawn (Ψ_L = -1.06 MPa) and midday (Ψ_L = -1.58 MPa) LWP due to the combined effect of drought stress and moderate shade, where the lowest values were observed after 8 DAI (Fig. 2). In contrast, significantly high LWP were observed in well-watered seedlings both in the shaded and full sunlight conditions with a significantly higher change in LWP. The results of

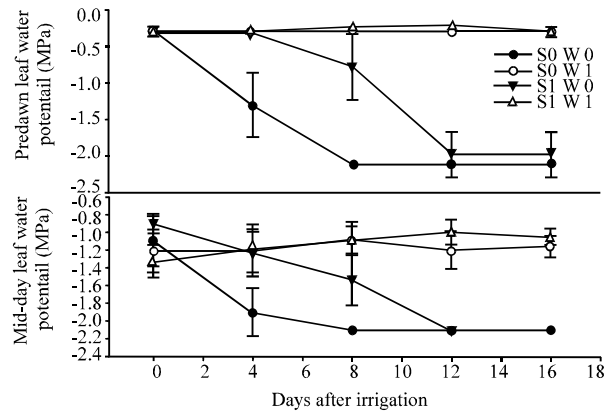


Fig. 2: Diurnal leaf water potential in arabica coffee seedlings as affected by shading and irrigation levels during the drought stress periods. (S0W0 = no shade not watered; S0W1 = no shade watered; S1W0 = shaded not watered; S1W1 = shaded watered)

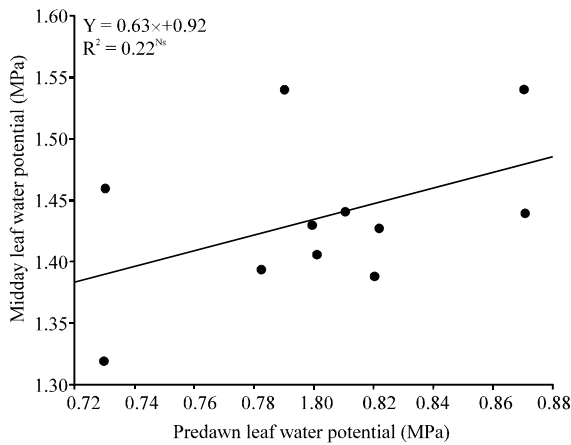


Fig. 3: Relationships between predawn and midday leaf water potential in seedlings of wild arabica coffee accessions

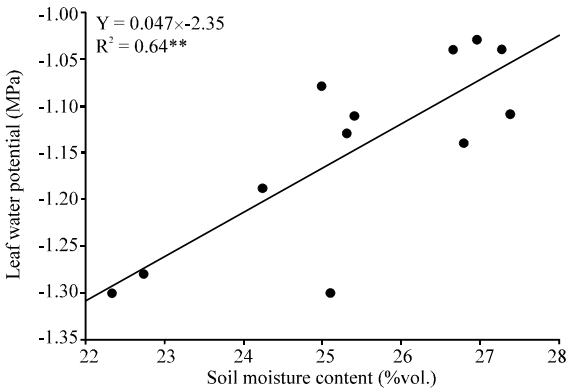


Fig. 4: Relationships between leaf water potential and soil moisture content in drought stressed Arabica coffee seedlings (8 days after irrigation)

the linear regression also demonstrated that coffee accessions from Bonga had low predawn and midday LWP as opposed to the Berhane-Kontir genotypes. The Harenna and Yayu accessions had intermediate reductions in LWP (Fig. 3). Moreover, the results revealed significant and direct relationships ($r = 0.80^{**}$) between soil moisture content and leaf water potential in droughted Arabica coffee seedlings for a week period (Fig. 4). Accordingly, the Yayu germplasm showed a higher LWP at higher soil moisture as compared with the other arabica coffee germplasm accessions, particularly those from the drier Harenna area.

DISCUSSION

The diurnal dynamics in the LWP was significantly lower for shaded coffee leaves as opposed to the full sunlight exposed seedlings. This is quite in line with the results of the nursery microclimate elements (Table 1) with a high loss of water vapor due to increased magnitude of the vapor pressure gradient between the leaf and the surrounding air. The increased moisture gradient between soil-leaf pathways and thus demonstrates the advantage of moderate shading before severe and irreversible drought stress occurs. The rate of transpiration can be naturally be influenced by factors such as humidity, temperature and wind speed, which influence the rate of water vapor diffusion between the substomatal air chamber and the ambient atmosphere (Salisbury and Ross, 1992; Sobrado, 2003). Hamiff (2006) also reported reduced leaf water potential (Ψ_l), leaf osmotic potential (Ψ_s) and leaf turgor potential (Ψ_p) response to the disruption in water supply.

With regard to coffee genotypes, the high leaf water contents in the Berhane-Kontir accessions as compared to the Yayu and Harena may be related to the variability in morphological growth natures (Kufa *et al.*, 2004a) and hence root water uptake capacity of the accessions in response to soil and atmospheric drought stress. Stomatal control of transpiration may decrease substantially as the rate increases from leaf to canopy. As the leaf transpires, water vapor tends to humidify the air nearby the leaves, thus decreasing the boundary layer conductance surrounding each leaf and uncoupling the vapor pressure at the leaf surface from that of the bulk air. To this end, Tausend *et al.* (2000), working with three Arabica coffee cultivars with contrasting shoot morphologies, showed that regulation of transpiration was governed by divergent hydraulic architecture rather than by stomatal physiology. This corroborates with empirical observations that compact coffee accessions with dense crowns (lower boundary layer conductance) are better able to postpone dehydration, which was not the case for the Harena germplasm, which have open crowns (Kufa *et al.*, 2004a; Taye and Burkhardt, 2006). At least partially, the findings could explain why the use of compact cultivars often results in the low productivity in lowland humid climates of the Berhane-Kontir region with high evaporative demand.

The LWP results are in harmony with the morphological and physiological (Kufa *et al.*, 2004a) and hydraulic characteristics of the same wild coffee populations under field conditions (Kufa and Burkhardt, 2010). This supports the maximum water loss rates (Becker *et al.*, 2000) and whole-plant hydraulic conductance (Tyree *et al.*, 1998) in pioneer as compared to succession forest species, which had low hydraulic conductance accompanied by better control over water use. According to Tyree *et al.* (1994), this implies low hydraulic efficiencies, although this trade-off is often weak. Another cost of developing a safe xylem could be the requirement of greater biomass allocation to the construction of that tissue (Hacke *et al.*, 2001). This is in line with the hydraulic conductance manifested in the same coffee accessions under nursery conditions (Taye and Burkhardt, 2006). The results are also in agreement with the work done by Sobrado (2003), who showed trade-offs between water transport and leaf water-use in pioneer and forest tree species. As reported by Haniff (2006), this could be due to the inhibited diffusion of CO₂ into the leaf, decreased the intercellular CO₂ level and reduction in photosynthetic rate under water stress conditions.

The results showed that most coffee accessions had relatively severe drought stress symptoms 8 and 12- DAI in the open sun and shade conditions, respectively. This was when the respective soil moisture contents were 8.4 and 21.5% vol and relative leaf water contents were about 50 and 57% in the full sun and shade plots, respectively (Fig. 4). The findings demonstrate that the sensitivity of the coffee seedlings to water deficits varied depending on soil conditions. This supports the findings of Maherali and DeLucia (2000) and corroborates with seedling growth in the shade and bright sunlight exposed plots, particularly with leaf and root parameters (Kufa *et al.*, 2004b). In this regard, implementing the theory of hydraulic limitation has been successful in predicting the regulation of transpiration in response to soil moisture and also the large differences in water-use efficiency between plant species and growth stages as reported by Tesfaye *et al.* (2008) among three grain legumes. The water potential regulation through stomata appears to be necessary for avoiding hydraulic failure and thereby maximizing the extraction of soil water. The pattern of water potential regulation and the particular thresholds of water potential that are controlled have to be tuned to the soil moisture regime and the hydraulic capability of the plant's root system and xylem. The extensive variation in water use between plants can be attributed in part to differences in their hydraulic equipment that is presumably optimized for drawing water from a particular temporal and spatial niche in the soil environment as it has been elucidated by Zewdie *et al.* (2007) in different enset clones. The response of the coffee seedlings, as evident from the soil-plant water contents and the regression results (Fig. 4), may be related to the diversity in growth characteristics (Taye and Burkhardt, 2006), reflecting their evolutionary adaptation and moisture deficit stress coping mechanisms.

There were significant variations in seedling water status between shade regimes and coffee accessions over the induced drought periods. The difference in water relation among the coffee accessions can be explained by the diurnal fluctuation in water relations. Accordingly, the reduced midday leaf water with a wider gap in the LWP for the Bonga accessions perhaps indicate their tolerance to low water potential. In contrast, coffee germplasm accessions from the Berhane-Kontir, Yayu and Harena coffee collections revealed significantly reduced midday LWP and diurnal fluctuations. This most likely indicates their distinct phenotypic growth and stomatal plasticity as drought stress avoidance strategies under limited soil moisture environments (Burkhardt *et al.*, 2006).

According to the results on the photosynthetic efficiency in these coffee accessions (Burkhardt *et al.*, 2005), those from Berhane-Kontir were found to exhibit a high midday transpiration decrease due to stomatal closure and were thus less productive even under optimal conditions. Hence, stomatal closure seems likely to be involved in such coffee accessions to cope with drought stress and as a conservative water saving strategy. This agrees with the findings of Tesfaye *et al.* (2008) in different grain legumes in the arid-part of Ethiopia. Moreover, the reduced predawn LWP and midday leaf water contents in the Bonga as opposed to the Berhane-Kontir coffee accessions could reflect their ability to re-equilibrate at the maximum LWP at night. The significant drop in LWP for the Yayu and Harena coffee accessions could be attributed to their maximum root contact with the soil and high shoot surface (Taye and Burkhardt, 2006), possibly they are more water demanders. According to Bashar *et al.* (2003) leaf water potential was significantly and positively correlated with root thickness, root volume, root length, plant height and leaf area, but negative relationship was found with shoot dry weight.

Moreover, the decrease in leaf water content could have triggered stomatal closure to reduce transpiration water loss. Besides, the relatively low stomatal frequency in the shade environments could be associated with low photosynthetic rates. This in turn could be linked to the reduced transpiration and thus vapor pressure gradients between the leaf surface and the saturated air layer above and the CO₂ concentration (Haniff, 2006). According to Woodward and Bazzaz (1988), stomatal frequencies decrease with increased CO₂ concentrations. On the other hand, conditions of extreme drought stress should override the plant, immediate photosynthetic needs and lead to closure, protecting the leaf against the potentially more damaging effects of desiccation. The extent of stomatal opening and its impact on both photosynthesis and water loss will be determined by the sum of all the factors mentioned and not by any one alone.

Arabica coffee seedlings displayed symptoms of water stress on the 8 and 12-DAI in bright sun radiation and shade environments, respectively. Similarly, the midday LWP of -1.42 and -1.60 MPa were measured in open sun and shade plots, respectively. This is in line with the high rating of minimum leaf water potential causing reduced metabolic processes and hindering growth (Joly, 1985). Further, according to the guidelines for selected agricultural crops, coffee is classified as one of the less drought-tolerant crops. The estimated minimum (predawn) and maximum (midday) plant drought stress was -1.2 and -1.4 MPa, respectively. This is the level

where plants show typical drought symptoms such as closed stomata, stop in shoot growth and declining overall growth rate (PMS Instrument Co.). Depending on plant species, this is when wilting and decline in the vigor of most plants can be observed, primarily because of the sensitivity of plants to changes in stomatal opening and CO₂ assimilation (Salisbury and Ross, 1992). In the present study, there were differences according to Arabica coffee accessions showing an early drop in leaf water potential of -2.1MPa, particularly in the severe drought induced treatment (no watering plus full sun).

Coffee plants retain high relative leaf water content under dehydrating conditions and are considered water saving rather than drought-tolerant species (Da Matta *et al.*, 2002). This may be attributed to (i) an efficient stomatal control on transpiration (Nunes *et al.*, 1993) and/or (ii) low cell-wall elasticity (Meinzer *et al.*, 1990; Da Matta *et al.*, 2002). A small water loss, therefore, causes a shift in turgor so that leaves tend to maintain high relative water content to retain a high symplast volume. Thus, it appears that under water deficit conditions, the maintenance of high relative leaf water content is more important than osmotic adjustment per se in conferring drought tolerance to the coffee plant (Da Matta *et al.*, 2002). The present results on the water relations of coffee seedlings are in agreement with the work done by Tausend *et al.* (2000) on the water utilization of three Arabica coffee cultivars. According to the results, coffee accessions from the same wild coffee populations responded differently to the induced water and radiation pressures, demonstrating their distinct adaptive strategies (Burkhardt *et al.*, 2005). Pinheiro *et al.* (2005) quoted researchers who described that these mechanisms involve maximization of water uptake by deep, dense root systems and/or minimization of water loss by stomatal closure and reduction of leaf area. These improve plant water status, particularly turgor maintenance, which may be achieved through osmotic adjustment and/or changes in cell elasticity and is essential for maintaining physiological activity for extended periods of drought. This corroborates with the findings on the succession of local coffee types along soil moisture gradients (Kufa *et al.*, 2004a). The results may also reveal substantial variations in the stomatal opening among coffee accessions, perhaps due to osmotic uptake of water by the guard cells and the consequent increase in hydrostatic pressure, as indicated by Hopkins (1995). The decline in leaf water potential in the Harena seedlings was in agreement with the increased carbon assimilation capacity and total biomass productivity of the accessions as opposed to the southwest accessions

(Burkhardt *et al.*, 2006). According to Burkhardt *et al.* (2006), the Harena populations might find their way out of serious droughts by putting their main effort into seed production, while trees from other populations seem to be more oriented to ensure survival of the individual coffee plant. This might indicate a trade-off between productivity and vulnerability to xylem embolism in Arabica coffee seedlings under sub-optimal environments.

In this regard, Zewdie *et al.* (2007) have also found variations in physiological traits between two onset clones due to irrigation regimes. This was reported in wheat (Subhani *et al.*, 2000), in peanut (Puangbut *et al.*, 2009), in corn (Khalatbari *et al.*, 2007) and in sesame (Hassanzadeh *et al.*, 2009), suggesting that desirable genotypes can be developed for stress or non-stress environments.

CONCLUSIONS AND PERSPECTIVES

The present results demonstrate the benefits of partial shading at coffee nurseries in appreciably extending the effects of drought in coffee seedlings and reduce reduction in the frequency of water application and associated costs. The *ex-situ* study showed that the precipitation gradient was not reflected in a simple way by drought stress tolerance of coffee genotypes (Burkhardt *et al.*, 2005). The findings depict the existence of genetic diversity among the wild Ethiopian coffee germplasm accessions in leaf water potentials. The results may demonstrate the conservative features behavior of the Berhane-Kontir accessions in contrast to the relatively vulnerable and opportunistic Harena collections to declined soil moisture in full sun conditions. This was, however, more detected by microclimatic elements at nursery site, indicating the contributions of partial shading in optimizing irrigation and production of healthy coffee seedlings. This variability could demonstrate the need for further multi-site *in situ* on farm preservation approach of coffee genetic resources. The study would provide information on the use of LWP as useful traits in soil-plant-water investigations and coffee breeding program. However, developing desirable arabica coffee cultivars and effective water management approach for irrigated coffee production system call, *inter alia*, detail studies on ecological, molecular, ecophysiological and biochemical aspects both under controlled and field conditions. This would contribute towards sustainable utilization and conservation of Arabica coffee genetic diversity at its place of origin and genetic diversity in Ethiopia.

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