African Journal of Agricultural Research Vol. 5(15), pp. 2066-2072, 4 August, 2010
Available online at http://www.academicjournals.org/AJAR
ISSN 1991-637X ©2010 Academic Journals

Full Length Research Paper

Dry matter partitioning and physiological responses of *Coffea arabica* varieties to soil moisture deficit stress at the seedling stage in Southwest Ethiopia

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Accepted 2 July, 2010

Dry matter partitioning, leaf chemical contents and morpho-physiological responses of six *Coffea arabica* varieties were tested in 15 and 30 days water stress followed by 15 days re-watering at seedling stage in Jimma, southwest Ethiopia. Repeated measures analysis revealed that differences among varieties depended on water stress and recovery periods for leaf P content and shoot mass ratio (SMR). Regardless of stress and recovery periods, significant differences among varieties were found for root fresh weight (RFW), leaf dry weight (LDW), leaf mass ratio (LMR), root mass ratio (RMR) and root to shoot ratio (RSR). Varieties 7440, 7487, 74140 and 74148 showed relatively high biomass allocation to roots whereas variety 741 allocated more to shoots. Variety 7487 had higher RFW and LDW. Significant differences among stress and recovery periods were also obtained; leaf K, Ca and Mg contents and SMR significantly increased whereas leaf P content, LMR, RMR and RSR decreased during stress. Higher leaf and root biomass fraction, and fresh weights were obtained after 15-day stress and recovery, respectively but similar root biomass fraction after 30-day stress and 15-day recovery and fresh weights during stress. Significantly higher leaf folding, stomatal resistance, leaf temperature and wilted seedlings and the lowest relative water content were observed after 30-day water deficit. Overall, variable coffee plant responses to drought stress periods, and faster recovery of the seedlings after re-watering were observed.

Key words: Leaf chemical contents, morphological responses, repeated measures, water deficit stress.

INTRODUCTION

Coffea arabica L., whose centre of origin and diversity is Ethiopia, accounts for more than 62% of the world coffee production (Dias et al., 2007) and 90% of the world coffee market. It accounts for more than 60% of Ethiopia's foreign exchange earnings and 25% of the population's employment opportunity. The national average yield (250 - 475 kg $ha^{-1}annum^{-1}$) is very low due to several production constraints including adverse climatic factors (MOA, 2003). Drought is a major climatic factor that limits coffee production in Ethiopia by inhibiting growth, yield and quality. This problem is expected to become more challenging due to the changes in global climate.

Many perennial plant species growing in drought prone areas have developed mechanisms to cope with restricted water supply. Some plant species avoid drought stress by maximizing water uptake or minimizing water loss. Others tolerate drought stress by increasing either osmotic-c/elastic adjustment or osmoprotective substances or both (Kozlowski et al., 1991). Similarly, coffee plants showed variable responses (e.g., Leaf shape change, fruit shedding, leaf senescence, branch die-back and leaf folding) to cope with drought stress under field conditions (Anon, 1987; Yakob et al., 1995). Drought stress decreased total leaf area, leaf water potential, transpiration rate, relative growth rate and total biomass of coffee (Meinzer et al., 1992; Dias et al., 2007). Drought stressed coffee plants tend to have greater biomass allocation to the root than to the shoot, lower leaf area, and heavier leaves than well - watered

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plants (Ludlow, 1989).

Species/varieties more tolerant to drought generally differ morphologically and/or physiologically with mechanisms that allow them to produce comparable yield under limited water supply (DaMatta, 2004). The ability of coffee varieties to survive and maintain productivity in moisture deficit areas also varies. Some varieties of coffee were found to differ in their morphological responses to water deficit in Uganda (Dancer, 1963), Zimbabwe (Anon, 1987), and Colombia and Brazil (Carr, 2001). Differences among arabica coffee genotypes in adaptation mechanisms to drought have been reported by many authors; e.g., stomatal control, soil water extraction efficiency (DaMatta and Ramalho, 2006), plant water use, biomass allocation to the stems and leaves (Dias et al., 2007) and tissue water potential (DaMatta, 2004). Tolerant varieties display adaptation mechanisms to drought including stomatal closure, osmotic adjustment, non-radiative energy dissipation and leaf area reduction (Cai et al., 2007). Drought-tolerant coffee genotypes are better to maintain higher tissue water potential and plant water use than drought-sensitive ones under water-deficit conditions (DaMatta, 2004; Dias et al., 2007). Burkhardt et al. (2006) postulated various strategies for drought tolerance among wild coffee populations growing in different agro-ecologies of Ethiopia. They observed coffee plants with extensive root system but vulnerable to drought due to their hydraulic system and stomatal behavior. However, a study on robusta coffee showed deeper root system (Pinheiro et al., 2005) and larger root dry mass (Ramos and Carvalho, 1997) in drought tolerant clones than in drought sensitive ones.

Despite these facts, there has been little work to examine the extent and pattern of responses of various *C. arabica* genotypes to water deficit in Ethiopia. Thus, the objectives of this study were to test (i) morphological and physiological traits that contribute to varietal differences in water stress responses; (ii) the impact of water stress on dry matter partitioning, leaf chemical concentration and relative water content; and (iii) differences among genotypes differing in their canopy architecture in the extent of their responses to water stress and recovery periods.

MATERIALS AND METHODS

The study site

The experiment was conducted at Jimma Agricultural Research Center (JARC), southwest Ethiopia. JARC is located at 7°46‘N and 36°E, 1753 m a.s.l. with 1580 mm mean annual rainfall, 66% RH and 26.3°C maximum and 11.5°C minimum temperature.

Experimental materials and procedures

Six coffee berry disease resistant varieties (741, 744, 7440, 7487, 74140 and 74148) selected from three types of canopy classes (CC) were tested for their responses to water stress in a randomized complete block design (RCBD), with the six varieties completely randomized within each of the 4 blocks. Each experimental plot contained 36 plants, and the total number of plants in the experiment was 864. The canopy nature of the selected varieties is: 741 and 744 open CC, 7440 and 7487 medium open CC and 74140 and 74148 compact CC. As per nursery recommendations for JARC (IAR, 1996), each seedling of these varieties were grown in a mixed growth medium of topsoil, compost and sand (6:4:1, v/v/v) contained in an 1884 cm^3 (10 cm diameter, 24 cm height) black polythene bag. Watering at 4 day interval and all other routine nursery management activities were based on nursery recommendations from JARC until eight months of age. Eight months old seedlings were subjected to water stress by withholding watering under open sunlight for one month in March 2004, and by protecting them from rain (if any) with transparent white plastic sheets. Following moisture stress, 24 seedlings left from destructive data measurements for stress responses were re-watered for 15 days to observe the recovery capacity of the varieties.

Response measurements

Response measurements were made (i) after 15 and 30 days of moisture stress period, and (iii) at the end of 15 days recovery period for four seedlings uprooted at around 9:00 AM and separated into leaves, stems and roots. The roots were carefully excavated and cleaned with tap water. The fresh and oven-dry weight (70°C for 24 h) of leaves, shoots, roots and total dry matter were measured. Using these data, leaf mass ratio (LMR = leaf dry weight/total dry matter), shoot mass ratio (SMR = shoot dry weight/total dry matter), root mass ratio (RMR = root dry weight/total dry matter) and root to shoot ratio (RSR = root dry weight/shoot dry weight) were calculated to assess the effect of drought on dry matter partitioning. Some physiological responses, namely number of wilted seedlings (WS), percentage of rolled leaves (LF), stomatal resistance (SR), relative water content (RWC) and leaf temperature (LT) were also measured between 10:00 and 11:00 AM. SR, LT and RWC were estimated from the same fully-grown leaves using Delta T Porometer AP3 and Infrared Thermometry, respectively according to Baker (1984). Leaf chemical (P, K, Ca and Mg) concentrations were determined according to the standard laboratory procedures of the Ethiopian National Soil Laboratory Research Center (Sahlemedhin and Taye, 2000). The P concentration was determined colorimetrically by spectrophotometer at 460 nm wavelength and that of K by flame photometer at 766.5 nm wavelength. The concentration of Ca and Mg were determined by atomic absorption spectrophotometer at wave lengths of 422.7 and 285.2 nm, respectively.

Gravimetric water content of the pot soil was determined at each measurement day according to FAO (1971) by taking soil samples from each pot from which sampled seedlings were harvested (Table 1).

Statistical methods

The experimental design for all response measurements was a RCBD with varieties as the factor of interest and four blocks. Since water deficit stress was induced for 15 or 30 days, followed by a recovery period of 15 days, and measurements were taken on day 15, 30 and 45, the measurements were effectively repeated measures, and hence repeated measures analysis was completed. The error terms were assumed to have a normal distribution with constant variance, but not independent. The most appropriate covariance structure that represents the type of dependence was identified (Littell et al., 1998) to be compound symmetry (CS). For all responses, the normal distribution and constant variance assumptions on the error terms were verified by examining the residuals (Montgomery, 2009). When variety and/or stress and recovery

Table 1. Mean pot soil water content (%) on different measurement days during water stress and recovery periods.

Variety	Stress period (days)			Recovery period (days)
	0	15	30	15
741	50.9	29.7	21.3	44.6
744	51.5	30.7	22.3	38.0
7440	48.4	29.8	22.9	44.1
7487	50.4	31.8	23.7	45.2
74140	51.1	30.8	23.4	45.2
74148	50.0	32.3	23.0	46.1

period (day) effect was significant ($P < 0.05$), the least squares means of the varieties and/or days were compared, and letter groupings generated at the 5% level of significance. The analysis was completed using the MIXED Procedure of SAS (SAS Institute Inc., 2003).

RESULTS

Analysis of variance results (Table 2) indicated significant effect of day for all measurements, main effect of variety for some responses and interaction effect between variety and day for two responses.

Interaction effect of *variety and day*

The interaction effect of variety and day was significant for leaf phosphorus (P) content and shoot mass ratio (SMR). Multiple means comparison for the variety by day treatment combinations shown in Figure 1 indicates that the mean leaf P content for all varieties decreased during the stress and recovery periods with lower rates of reduction during recovery except for varieties 74148 and 744 that exhibited a constant reduction rate across the study periods. The mean leaf P content for variety 7440 stayed lower during the stress periods, but the lowest P after the recovery period was of varieties 74148 and 744.
Multiple means comparison of SMR (Figure 2) revealed a significant increase during water deficit stress period for varieties 741 and 7440. All other varieties also showed increasing trend (though not statistically significant) during stress period. However, the changes in SMR among varieties during recovery were inconsistent. For example, the SMR for variety 741 showed a decreasing trend while that of variety 744 significantly increased. Varieties 741 and 74148 maintained higher and lower mean SMR, respectively during the stress and recovery periods.

Main effects of *variety and day*

For those responses which showed non-significant interaction effects, either the main effect of variety or day or both was significant (Table 2).

Multiple means comparison of the six varieties indicated that varieties 7440, 7487, 74140 and 74148 allocated more dry matter to roots than to shoots, showing the largest RMR and RSR. Varieties 744, 7487, 74140 and 74148 also showed the highest LMR, whereas variety 741 allocated more biomass to shoots (Figure 2) than to leaves and roots showing the lowest LMR, RMR and RSR values (Table 4). Varieties 744, 7440 and 7487 maintained the highest root fresh weight, whereas variety 74148 had the lowest. Varieties 744 and 7487 also had the highest leaf dry weight whereas varieties 7440, 74140 and 74148 had the lowest. Although there was some inconsistency, the intermediate (7440 and 7487) and compact (74140 and 74148) varieties generally showed higher biomass allocation to roots and leaves compared to open (741 and 744) varieties (Table 4).

Analysis of variance also showed a significant main effect of day on all responses (Table 2). This indicated that the dry matter accumulation and partitioning, leaf chemical contents and some physiological responses of coffee were affected differently by 15 and 30 days of water deficit stress and 15 days of recovery. Average leaf chemical contents (K, Ca and Mg) and dry weights of leaves, shoots and roots significantly increased at each 15-day period; but fresh weights stayed the same during the 30-day water deficit period, and increased during the recovery period (Table 3). Significantly higher root dry matter proportion (RMR and RSR) was observed after 15-day water deficit period, but similar after 30-day deficit and 15-day of recovery (Table 3). A significant decrease in LMR was observed during water deficit and recovery periods with the highest decrease after 15-day deficit and the lowest decrease after 15-day recovery. Significantly higher leaf folding (LF), stomatal resistance (SR), leaf temperature (LT) and number of wilted seedlings (WS), and the lowest relative water content (RWC) were observed after 30-day water deficit period. However, these responses, except LF, were well recovered after rewatering period (Table 3). The result showed that 30-day water deficit brings significant morphological and physiological changes to coffee, and that coffee plants cope with drought stress by both morphological and physiological mechanisms.

DISCUSSION

The significant interaction effect of variety and day suggests that the varieties responded differently to water stress and recovery periods. For the responses with significant day effect but non-significant interaction effect (Table 2), it means the differences among the days (Table 3) were applicable to all varieties. For the other responses that showed non-significant interaction effect, but significant main effect of variety (Table 2), the implication is that the differences among varieties (Table 4) were consistent regardless of water stress and recovery

Table 2. P-values for the main and interaction effects of variety and day on leaf phosphorous (P), potassium (K), calcium (Ca) and magnesium (Mg) contents; leaf folding (LF); stomatal resistance (SR); relative water content (RWC); leaf temperature (LT); leaf fresh weight (LFW); shoot fresh weight (SFW), root fresh weight (RFW), number of wilted seedlings (WS), leaf dry weight (LDW), shoot dry weight (SDW), root dry weight (RDW), leaf mass ratio (LMR), shoot mass ratio (SMR), root mass ratio (RMR) and root to shoot ratio (RSR). Effects that require further multiple means comparison are shown in bold.

Source of variation	P	K	Ca	Mg	LF	SR	RWC	LT	LFW	SFW
Block	0.893	0.016	0.040	0.001	0.622	0.240	0.175	0.001	0.005	0.011
Variety	0.012	0.360	0.566	0.891	0.128	0.508	0.068	0.620	0.069	0.140
Day	0.001	**0.001**	**0.001**	**0.001**	**0.001**	**0.001**	**0.001**	**0.001**	**0.001**	**0.001**
Variety*Day	**0.006**	0.081	0.281	0.957	0.153	0.666	0.295	0.964	0.568	0.138
Source of variation	**RFW**	**WS**	**LDW**	**SDW**	**RDW**	**LMR**	**SMR**	**RMR**	**RSR**	
Block	0.017	0.002	0.001	0.020	0.004	0.010	0.095	0.255	0.255	
Variety	**0.018**	0.071	**0.009**	0.191	0.146	**0.011**	0.001	**0.032**	**0.035**	
Day	**0.001**	**0.001**	**0.001**	**0.001**	**0.001**	**0.001**	0.001	**0.038**	**0.041**	
Variety*Day	0.104	0.410	0.762	0.188	0.854	0.095	**0.045**	0.546	0.573	

Table 3. Means for leaf potassium (K), calcium (Ca) and magnesium (Mg) contents; leaf folding (LF); stomatal resistance (SR); relative water content (RWC); leaf temperature (LT); leaf fresh weight (LFW); shoot fresh weight (SFW); root fresh weight (RFW), number of wilted seedlings (WS), leaf dry weight (LDW), shoot dry weight (SDW), root dry weight (RDW), leaf mass ratio (LMR), root mass ratio (RMR) and root to shoot ratio (RSR) for the three measurement days (day). For each response, means followed by the same letter are not significantly different at the 5% level.

Day	K (ppm)	Ca (ppm)	Mg (ppm)	LF (%)	SR (sm^{-2})	RWC (%)	LT (^0C)	LFW (g)	SFW (g)
15	38973 c	1921 c	1256 c	34.5 b	9.6 b	83.6 b	29.9 c	4.24 b	1.67 b
30	42478 b	3581 b	1718 b	44.9 a	20.9 a	63.7 c	34.4 a	3.96 b	1.80 b
45	56421 a	6072 a	2177 a	41.7 a	9.1 b	90.5 a	33.5 b	6.06 a	3.02 a
Day	**RFW (g)**	**WS**	**LDW (g)**	**SDW (g)**	**RDW (g)**	**LMR ($g\ g^{-1}$)**	**RMR ($g\ g^{-1}$)**	**RSR ($g\ g^{-1}$)**	
15	1.80 b	2.33 b	0.98 c	0.51 c	0.38 c	0.53 a	0.21 a	0.26 a	
30	1.71 b	9.21 a	1.18 b	0.71 b	0.47 b	0.51 b	0.20 b	0.24 b	
45	3.18 a	0.00 c	1.87 a	1.12 a	0.72 a	0.50 c	0.20 b	0.24 b	

Table 4. Means for root fresh weight (RFW), leaf dry weight (LDW), leaf mass ratio (LMR), root mass ratio (RMR) and root to shoot ratio (RSR) for six Coffea arabica varieties. For each response, means followed by the same letter are not significantly different at the 5% level.

Variety	RFW (g)	LDW (g)	LMR ($g\ g^{-1}$)	RMR ($g\ g^{-1}$)	RSR ($g\ g^{-1}$)
741	2.16 bc	1.33 bc	0.49 c	0.18 c	0.23 c
744	2.45 ab	1.51 ab	0.52 a	0.19 bc	0.24 bc
7440	2.28 ab	1.26 c	0.50 bc	0.21 a	0.27 a
7487	2.78 a	1.54 a	0.51 ab	0.20 ab	0.26 ab
74140	2.02 bc	1.23 c	0.52 a	0.20 ab	0.26 ab
74148	1.69 c	1.20 c	0.52 a	0.20 ab	0.25 ab

periods. Overall, the data support the hypothesis that all measurements were significantly affected by days (stress and recovery periods) and varieties.

The significant difference observed in characteristics including physiological responses (RWC, SR and LT), morphological responses (LF and WS), dry weights, dry matter partitioning and leaf chemical contents among the measurement days (Table 2) showed that coffee performances are influenced by drought stress and recovery. Similarly, a siginificant effect of drought on morphological variables (Guridi et al., 1987) and incipient wilting and accumulation of different solutes (Venkataramanan and Ramaiah, 1987) for coffee seedlings was reported. Variable drought stress responses that maximize water uptake or minimize water loss or both, and keeps physiological activities for coffee plants were also observed by different authors (Anon, 1987; Meinzer et al., 1992; Yakob et al., 1995; Dias et al., 2007). Similarly, the variable responses to drought and recovery, regardless of variety (e.g., an increase in leaf K, Ca and Mg contents, SMR, dry weights, LF, LT, SR and WS; a decrease in leaf P content, LMR, RMR, RSR and RWC; and no change in fresh weight – Table 3, Figures 1 and 2) indicate that drought response of coffee plants is complex, involving different modifications following soil drying. This suggests that different varieties of coffee follow

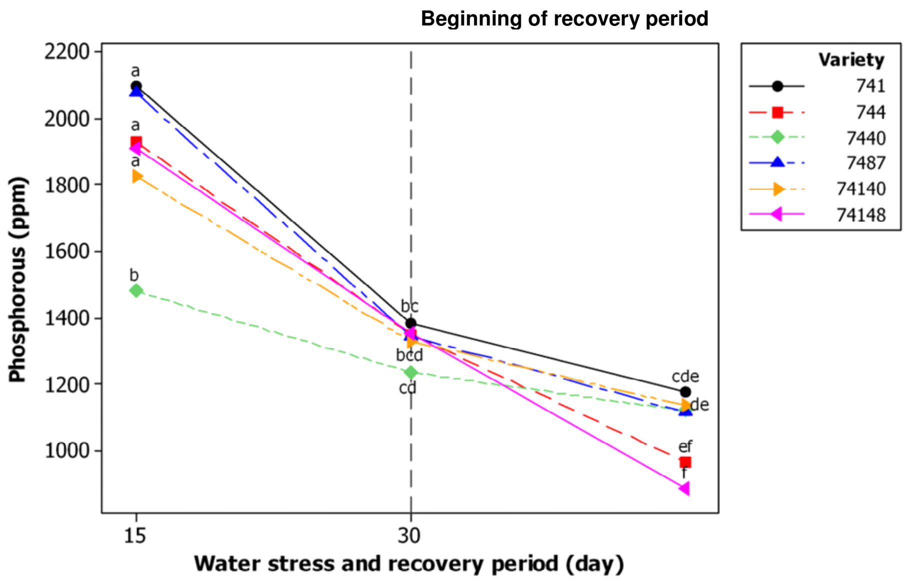

Figure 1. Mean leaf phosphorous content (ppm) versus water stress and recovery period (in days) for the six varieties of *Coffea arabica*. Means sharing the same letter are not significantly different at the 5% level of significance.

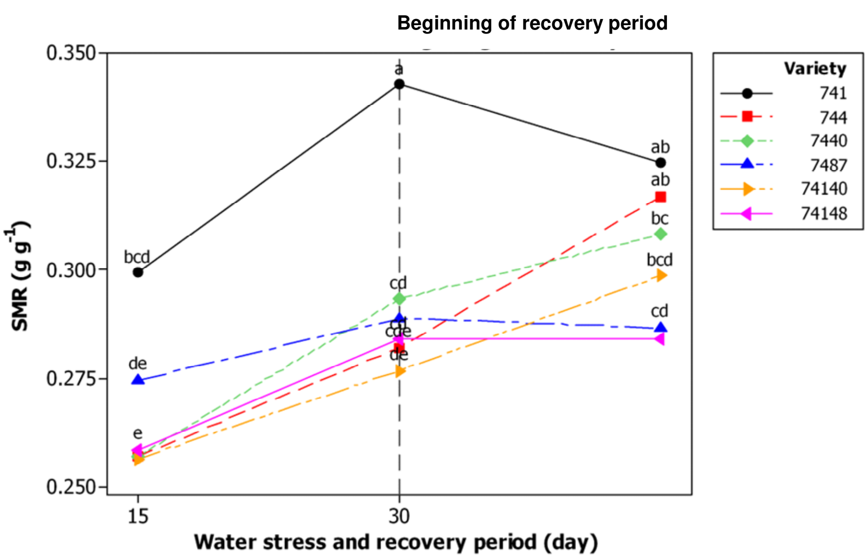

Figure 2. Mean shoot mass ratio (SMR in g g^{-1}) versus water stress and recovery period (in days) for the six varieties of *Coffea arabica*. Means sharing the same letter are not significantly different at the 5% level of significance.

different strategies to cope with soil moisture deficit stress.

A significant increase in leaf K and Ca during water stress periods observed in this study is in agreement with Venkataramanan and Ramaiah (1987) who reported higher accumulation of Ca and K but lower Mg in the wilted coffee plants. The accumulation of nutrients in plant tissues is generally considerd as an indicator of water use eficiency and drought stress tolerance. K and Ca provide water stress tolerance capacity to the plant by promoting K uptake, increasing cell protoplasm viscosity, maintaining cell membrane integrity, stabilizing chlorophyll membrane, increasing osmotic adjusment and reducing stomatal opening (Kumar, 1979; Taiz and Zeiger, 1998). Higher LF and SR after 30 days of stress showed that the varieties reduced transpiration by leaf rolling and stomatal closure. Such phenomena (minimizing of drought effects by leaf folding and high correlation of leaf folding with leaf area, leaf dry weight and leaf water content) for CBD resistant varieties was also observed by Yakob et al. (1995). Progressive closure of the stomata with increasing water stress and leaf temperature (Martin et al., 1983), and closure of the stomata at 18 to 30% foliar water deficit (Coste, 1992) was also reflected in this study (Table 3). The highest RWC and fresh weight, and the lowest WS after 15 days of recovery indicated that coffee cell turgidity is well recovered after moisture deficit stress.

A significant increase in dry matter (leaf, stem and root) during stress and recovery periods with higher increment after recovery showed coffee plants responded differently to 15- and 30-day stress; and to a greater extent to recovery compared to stress. This confirms that coffee growth is faster after drought stress alleviation (Table 3). It was reported that plants growing under drought stress altered photosynthate allocation from leaves and stems to roots to increase root: shoot ratio (Setter, 1992), but dry matter partitioning in this study and investigation by Dias et al. (2007) did not confirm this, showing that coffee plants may not shift biomass allocation to roots as response for drought stress.

Relatively more biomass was allocated to roots than to stems for intermediate and compact varieties, and to stems than to leaves and roots for the open varieties, particularly for variety 741. These show differences between coffee populations (canopy classes) for dry matter partitioning. Differences between open and dense crown coffee cultivars in total daily transpiration and consideration of crown architecture for selection of cultivars for drought-prone environments was also found by DaMata (2004).

The finding of a significant variety by day interaction effect for leaf P content and SMR showed that the tested varieties responded to drought stress and recovery differently, supporting the initial hypothesis of this study and the potential of these traits for selecting drought stress tolerant coffee varieties. It is also supported by various findings of previous researches on morpho-physiological drought stress responses of coffee varieties (Dancer, 1963; Anon, 1987; Venkataramanan and Ramaiah, 1987; Carr, 2001; Burkhardt et al., 2006). Relatively higher responses (an increase or a decrease) in P content and dry matter partitioning to shoots and roots for the majority of coffee varieties during drought stress than during the recovery period (Table 3, Figures 1 and 2) indicate stronger effect of drought stress compared to that of stress recovery. The reduction of P concentration during the stress period is contrary to the findings of Venkataramanan and Ramaiah (1987), but further reduction after rewatering is in agreement with the findings of this study. Regardless of variety, significantly higher dry matter partitioning (increase in SMR) to the shoots, and lower to the roots and leaves (decrease in RMR, RSR and LMR) during stress period showed that coffee plants reserve photosynthates more in the stems than in the leaves and roots when responding to moisture deficit stress.

In conclusion, the adaptation of coffee plants to soil water deficits in general was both morphological and physiological, manifested by higher proportion of biomass allocation to the stems, and increasing of leaf K, Ca, and Mg contents, dry weights, leaf folding and stomatal resistance, thereby keeping fresh weight. On the other hand, varieties responded to stress recovery by fast plant turgidity and fresh weight resumption, and higher rate of dry matter and leaf K, Ca, and Mg accumulation. This showed that coffee plants may be using a combination of mechanisms to postpone dehydration and minimize drought effects while growing in low and unpredictable precipitation environment. The open canopy varieties (e.g. 741) allocate more biomass to stem. The variety by water deficit and re-watering period interaction effect on SMR and leaf P content indicated the potential of these traits for selecting water deficit stress tolerant varieties of coffee.

ACKNOWLEDGEMENTS

This research was sponsored by Agricultural Research Training Project (ARTP) and Ethiopian Institute of Agricultural Research (EIAR). T. R. Rathore and Nigussie Dechasa are acknowledged for their cooperation during the various stages of this research.

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