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Review Article

Mechanisms of Drought Tolerance in Coffee (*Coffea arabica* L.): Implication for Genetic Improvement Program: Review

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Abstract: Drought is a limiting factor of coffee production and industry worldwide which result 40-80% yield loses. The most substantial solution for this factor is developing tolerant coffee variety. In order to design genetic improvement program, understanding the mechanisms exhibited by drought tolerant and desirable traits involved in coffee genotypes under drought stress is priority issue. Thus, the present review article was conducted with the intension to assess and to understand the drought tolerance mechanisms revealed in coffee for further genetic improvement program. So far, the achieved research results on drought tolerance mechanisms of coffee such as morphological, physiological, biochemical and molecular mechanisms were clearly discussed in this article. Drought tolerant coffee genotypes exhibited deep root, reduce leaf area and even shade leaf, control on stomatal conductance and leaf transpiration under water deficit. Under drought stress, several biochemical accumulation such as sugar, amino acid, carbon metabolism enzymes *Viz* sucrose synthase and phosphofructokinase were confirmed in drought tolerant coffee which favor osmoregulation and enable desiccation tolerance. Coffee breeders' experts should be conscious these desirable traits during coffee genetic improvement for drought tolerance. In Arabica coffee, CaERF017 is the most expressed gene under low temperature and drought stress. Generally, many genes identified in *Coffea arabica* and *Coffea canephora* that response to drought stress which are essential for intra and inter- cross for genetic enhancement and developing drought tolerant coffee variety.

Keywords: Biochemical, Coffee, Drought Tolerance, Molecular, Morphological, Physiological

1. Introduction

Coffee is a perennial evergreen [1] cash crop and predominantly under production in African, Latin American and Asian countries. About 124 coffee species are identified among which only two species are predominantly produced in the world [2]. From these species, *Coffea arabica* L. and *Coffea canephora* F. together contributing 99% to world coffee production [3]. The former species is highly demanded and consumed worldwide than all species; it shares 65% of world coffee production. Ethiopia is well known in the world for home land and center of diversity for this noble coffee species viz *Coffea arabica* L.

Coffee has immense roles in social culture, economy, job opportunity creation and input for beverage industries in coffee producing countries and worldwide. Brazil is the leading country in the world in coffee production [1]; but Ethiopia is the fifth in the world and the leading country in Africa in coffee production. Ethiopia produces sole Arabica coffee which is organic in quality. Despite its principal contributions in many sectors of producing countries, Arabica coffee productivity and production is highly fluctuating and decreasing in the world [4, 5] including Ethiopia. Among the factors that feeble its production is climate change from which drought is the current alarming issue.

Drought prone areas of the world is increasing which estimated to be 16.2 to 41.2% of cultivated land in the 20 century [6, 7]. Drought is among the devastating natural hazard that affects crops at all stages; thus, it severely affects crops' production and quality [7-10]. Drought resulted from climate change, deforestation, over grazing and overexploiting water surface [7]. Under drought condition, water scarcity, high temperature and heat are expected to be happen most frequently and adversely affect crop production and productivity including *Coffea arabica* L. [11, 12]. The protracted period of shortfall precipitation adversely decreases crops production and quality such as coffee [13-16].

Drought become a bottleneck for sustainable crop production, and it reduces crop yielding potential up to 74% [9, 17]; also, it decreases from 40-80% yield in coffee [3, 4]. Thus, protracted drought and high temperature are among the predominant factors affecting coffee growth and production [18, 19]. High temperature and water deficit during flowering and fruit development lead to defoliation of flowering and defoliation of developing fruit; whereas, extreme drought may cause complete death of coffee trees [20]. Additionally, it reduces the physical characteristics of the coffee fruits (shape and size) and the biochemical compositions such as sugar, protein and caffeine, which finally deteriorates the quality of the beverage [13, 14, 21].

The morphological, physiological, biochemical and molecular mechanisms of plant responses to drought is complex; the dynamic soil water depletion and not meet the water demand by coffee plant growth and phenological state are sources of wide variation in plant responses to drought. Some findings authenticated that the existence of genetic variability among coffee genus for drought tolerance [22-24].

Drought tolerance is a desirable trait in crop improvement due to agricultural productive areas are suffer heavily from recurring and intensive drought across the globe. Drought tolerance is polygenic in its nature [7]; thus, for successful coffee improvement for drought tolerant, one has to be conscious about the tolerance mechanisms identification, identified gene/s that involved in drought tolerant materials and selection of desirable traits of the crops for drought tolerance. Plants have different mechanisms that enable them to survive and perform better under drought including Arabica coffee [19]; for instance, they increase water uptake via growing root and reduce leaf transpiration via stomatal conductance. Coffee integrates multiple mechanisms to survive and gives significant yield under protracted water deficit; thus, in this drought tolerance approach morphological traits, genetic, physiological, and metabolism pathway are involved [17, 25]. Thus, to mitigate drought problem on coffee production and quality, priority has to be given for developing drought tolerant coffee variety [26]; also, well developed breeding strategy is extremely momentous issue for further genetic improvement [27] and to realize sustainable coffee production. Thus, this review was conducted to assess the research results so far achieved in Coffee for drought tolerance mechanisms in physiological, morphological and molecular patterns to apply comprehensive improvement methods for the next Arabica coffee breeding programs.

2. Morphological and Physiological Mechanisms

2.1. Leaves Morphological and Physiological Traits

Identification of desirable phenotypic and physiological traits that associated to drought tolerance is prerequisite for improvement using different breeding methods [7, 28]. Coffee tolerates drought using different strategies which are observed at morphological and molecular level; among these, the morphological traits expressed on leaf for extreme drought response is significant traits. Different crops including coffee design their leaf shape, stomatal conductance and even shade their leaf or leaf abscission which enables them withstand drought period (Figure 1 A and B); some genotypes curled their leaves to resist water stress (Figure 1C). Similarly, Simkin et al. [29] reported that the coffee leaves color change under osmotic stress during soil moisture stress. Also, some findings confirmed that leaves have role in drought tolerance by dehydration postpone via stomatal closure and decrease leaf areas [4, 5, 30-32]; thus, it improves crop water status and turgor maintenance. Also, the findings confirmed that the existence of significant decrease of stomatal conductance which leads transpiration rate reduction in drought tolerant coffee clones under drought stress [30, 31]. The highest leaf cuticle thickness was recorded for drought tolerant Arabica coffee cultivar (IAPAR59 = 1.98 ± 0.19 μm) than drought sensitive (Rubi = 1.73 ± 0.28 μm) [33]. Additionally, stomatal closure with leaf growth inhibition protect plants from excessive water loss which leads cell dehydration, xylem cavitation and death during water deficit [34].

Among the mechanisms used by coffee to cope up with drought: leaf folding (Figure 1C) and inclination to reducing leaf surface area, water loss by transpiration and exposure to high irradiance were observed on tolerant coffee genotypes [22, 31, 35, 36]; leaf abscission and a rapid recovery of vegetation with return rain fall is another desirable traits. In agreement, Vu et al. [37] reported that highest leaf area reduction recorded for Arabica coffee than *Coffea canephora* coffee species under water deficit.

Drought tolerant coffee genotypes showed balanced root mass to leaf area ratio relative to drought sensitive genotypes [35]. Also, drought tolerant coffee showed slow or late and low leaf xylem pressure potential than sensitive to drought. For successful drought tolerant coffee variety development, one has to be conscious these desirable traits of morphological and physiological traits. Relative to Arabica coffee genotypes, Robusta coffee showed less reduction of specific leaf area and high bulk modulus of elasticity under water deficit [38]; this implies that Rabusta coffee species is more drought tolerant comparative to Arabica coffee [39, 40]. Under water deficit, high relative water content (RWC) in leaf was recorded for *Coffea liberica* than Arabica coffee [37] indicating genetically variable of coffee species in drought tolerance. Also, high relative water content in leaf and chlorophyll content were observed in grafted Arabica coffee (*C. arabica* as scion and *C. robusta* as root stock) than non-grafted under drought stress [36]. There is genetic variability among Arabica coffee accessions in leaf water potential retention under moisture deficit. In agreement, Kufa and Burkhardt [11] finding confirmed that Arabica coffee collected from Berhane-Kontir, Harenna and Yayo forest showed less leaf water potential reduction than those collected from Bonga forest under drought stress.

The maintenance of leaf water potential has direct relation with hydraulic conductance [41]. The decreases of leaf water potential resulted from water loss by transpiration upsurges, physical tension in xylem and plant hydraulic conductivity under water deficit [42]. Under drought, the close of stomata was authenticated for Robust and Arabica coffee [32, 43]; drought tolerant coffee clone recorded 52% reduction of transpiration rate; but, for drought sensitive clone transpiration rate declined by 39% [4]. The physiological function such as net carbon assimilation rate, stomatal conductance, transpiration rate are processed in very well managed manner in drought tolerant coffee species, but these activities lowered faster in sensitive genotype which leads to complete death of coffee trees [20]; also, better photosynthesis rate observed in drought tolerant Arabica coffee genotypes under water deficit [32]. In line with this, Joshi et al. [44] confirmed that even though drought adaptation mechanisms are available among sensitive genotypes, the tolerant genotypes, however, developed additional regulatory mechanisms that enhance them to manage severe abiotic stresses. Also, Menezes-Silva et al. [45] reported that 33% and 66% gas exchange reduction relative to control for drought tolerant and sensitive clones respectively under serious drought condition.

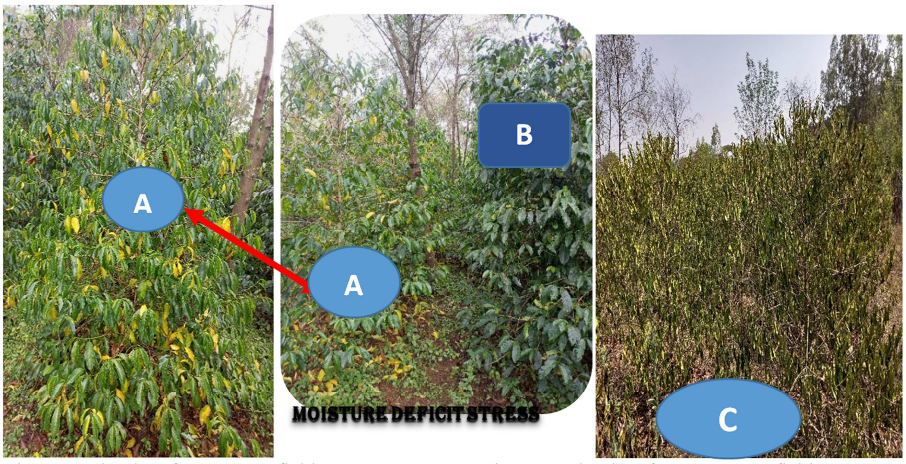

Photo graph taken from JARC field (2022) Photo graph taken from HARSC field (2021)

Figure 1. *Leaves morphological mechanisms for moisture deficit tolerance in Arabica coffee.*

Hint. Figure A and B were taken from Jimma Agricultural Research Center (JARC) field at the beginning of moisture stress season in 2022 in Ethiopia. Photo graph of figure C was taken from Haru Agriculture Research Sub-center (HARSC) field at severe drought season in 2021 in Ethiopia (taken by Asfawu Adugna).

2.2. Root Morphological and Physiological Traits

Some crops show postpone drought tolerance mechanism by having deep root growth in the soil; likewise, DaMatta [5] and Blum [46] reported that plants characterized with deep and vigorous root systems are drought tolerant. Due to their deep root trait, the 120 robusta clones showed drought tolerance with minimum leaf area decreasing per tree; but, for 46 clones having shallow root, drought sensitivity was observed under moisture deficit [4, 47]. Similarly, finding elucidated that root length, root thickness and root volume were positively correlated with leaf water potential under water deficit [48]. Also, deep root and dense root system together with stomatal closure and leaf area reduction enhanced in maximizing water uptake which improve plant water status especially by turgor maintenance and important for maintaining physiological activity in extended drought stress [35, 50]. Moisture deficit tolerant coffee genotypes showed narrow conducting xylem, high wood density (D_w) and fiber wall thickness [1, 49] which increase water use efficiency, control hydraulic conductance and lessening water leaf potential tension [51]. Drought stress tolerant genotypes stay green under sever soil water deficit due to their deep root and water saving ability [52].

In coffee, the larger root dry mass has relationship with drought tolerance [18, 53]. The finding clearly indicated that the deeper root for drought tolerant coffee genotypes and shallow root for drought sensitive genotypes [35]. Also, some findings confirmed that plant water stress developed faster in drought sensitive than tolerant coffee genotypes [35, 54]. In contrast, Burkhardt et al. [55] found the drought sensitivity of deep rooted coffee genotypes which might be due to their feebleness in hydraulic conductance and stomatal control on transpiration. Also, this may be due to Arabica coffee genetic variability in responses to drought stress even though exhibited deeper root trait. In *Coffea arabica* L., hydraulic conductance showed positive correlation with total daily transpiration [56]. Thus, coffee breeder has to be aware how to select coffee genotypes having deeper root with high wood density, low hydraulic conductance and stomatal limiting on transpiration under postpone drought during improvement for drought tolerance.

3. Coffee Growth Habits

Coffee species including *Coffea arabica* L. are genetically different in their growth habits or crown architecture. Accordingly, coffee grouped in to compact, intermediated and open depending on their crown architecture. These essential traits aid coffee responses differently to abiotic and biotic stress in addition to their vital gift for coffee producers such as intercropping with other compatible crops and increase production via increasing population per unit area.

Experimental observation showed that dwarf cultivar having crown dense (compact) are better to postpone dehydration than cultivar having open growth habit [4, 49, 50]; also, the authors confirmed that the stomatal control on transpiration may decreases as the scale increases from the leaf to the crown of the plant. In line with this, Kufa and Burkhardt [11] reported that stomatal control on transpiration reduced as the rate upsurge from leaf to crown. In contrast, Tausend et al. [57] found that the regulation of transpiration governed by divergent hydraulic architecture than stomatal physiology using three Arabica coffee having contrast in morphological growth habits. Hence, one has to be conscious to select coffee genotypes possessing desirable crown, deep root with important stomatal hinder on transpiration simultaneously during improvement for drought tolerance breeding program.

4. Biochemical Mechanism

The biochemical mechanism is another technique that plants use for drought tolerance. Plants including coffee produce and accumulate several biochemical such as sugar, amino acid, polyol and amide to maintain their homeostasis under water deficit condition [58, 59]. The induction of hydrolytic enzyme such as α-amylases or invertases have been detected in plants under water deficit stressed [60]; in agreement, Menezes-Silva et al. [45] found high accumulation of enzymes of carbon metabolism such as sucrose synthase, phosphofructokinase, enolase, pyruvate kinase and aldolase in coffee clone under water deficit condition than control/irrigated. Also, Praxedes et al. [54] suggested that the association of sucrose-phosphate synthase activity with the assimilate export which might be contributed for some additional root growths of plant under drought stress; this enables drought tolerant coffee genotypes to keep its productivity under drought prone areas.

Despite lower rate of carbon assimilation, soluble sugar conserved in leaf of water stressed crop [34] which favors osmoregulation and enables desiccation tolerance. Also, in plant polyols (reduced form of aldose and ketones sugar) and cyclitols stored in leaves reaction to drought stressed [61]. Under water deficit, plants accelerate production of phytohormone abscisic acid (ABA) either at leaf level or root system level to make stomatal closure and reduce transpiration rate that potentiate the crops drought tolerant [31].

The *Coffea canephora* clones showed increasing level of soluble amino acid and glucose under drought condition than ample irrigation [45] which induce osmoregulation. The author and his colleagues confirmed that the drought tolerant clones improve their photosynthetic performance coupled to an accumulation of huge osmoregulators response to drought than susceptible clones.

5. Molecular Mechanisms

The identification of gene responsible to drought tolerance is important to understand the molecular mechanism of crops to withstand water stress [62]; also, it has a key roles in perennial crops such as coffee genetic improvement application via marker assisted selection or gene transfer. Thus, to combat the impact of drought on crop production, it is emphasized to identify gene response for drought tolerance; this is crucial to realize sustainable production and food security in the world through genetic improvement for water stress tolerance [63, 64]. Rubisco is an enzyme in plant chloroplast which has vital role in fixing atmospheric CO_2 during photosynthesis and in oxygenation during photorespiration [65, 66]; it also, contributes for large nitrogen storage in leaf which is remobilized under water stress [66, 67]. Thus, RBSC1 is identified gene in *Coffea arabica* L. and *Coffea canephora* that regulates the function of Rubisco under drought stress [68] and contributes to the non-stomatal control of photosynthesis under water deficit [69]. Thus, Marraccini et al. [24] reported that higher total expression of RBSC1 gene for drought tolerant coffee genotypes than sensitive genotypes under water stress.

Gene such as CcPSBO, CcPSBP and CcPSBQ are identified genes which contribute for proteins accumulation of PSII under drought stress [20, 70]. In agreement, the oxygen-evolving complex (OEC) of PSII protected by extrinsic proteins found in lammina side under high heat stress was reported in Pea, Tomato and Tobacca [71, 72]. From *Coffea canephora*, twenty eight (for instance from 28 CGs CcTRAF1, CcPDH1, CcUNK8, CcDH3, CcEDR1, CcHSP1, CcMPR1 and CcUBQ10 were identified by screening of macroarrays) candidate genes (CGs) were identified that response to drought tolerance [20]. Also, the expression of CcPYL7 which induced by drought in drought tolerant (clone 14) and encodes the ABA signalling pathway in coffee response to drought [20, 73] via controlling on stomatal conductance.

Under drought stress, it was authenticated that the expression carotenoid genes in leaf tissue from osmotically stressed coffee plants [29]. Rapid expression of the DREB1D genes in transgenic *Coffea arabica* was clearly indicated under water deficit [74, 75]. Likewise, Torres et al. [76] confirmed that in Coffea arabica, CaERF017 is the most expressed gene under low temperature and low humidity and high temperatures; also, under moisture deficit the authors authenticated that the most expressed genes *Viz* CcDREB1B, CcRAP2.4, CcERF027, CcDREB1D and CcTINY in leaves of drought-tolerant C. canephora. In agreement, Santos et al. [77] found genes CaMYB1, CaERF017, CaEDR2, CaNCED, CaAPX1, CaAPX5, CaGolS3, CaDHN1 and CaPYL8a in Arabica coffee which contribute to efficiency of the photosynthesis in drought tolerant progenies.

Table 1. *Genes identified for drought tolerance in coffee.*

Gene	Gene Function	Abiotic stress tolerance	Coffee species	Reference
RBCS	Rubisco regulation and antioxidative of photorespiration	Control on photosynthesis and photorespiration under drought stress	*Coffea arabica* & *Coffea canephora*	[24]
CcCA1	Change/activate a chloroplast carbonic anhydrase in response to changes in environmental conditions	Encoding carbonic anhydrase (CA) that transmitting signal to response under drought stress	*Coffea canephora*	[20, 78]
CcPSBQ, CcPSBO and CcPSBP	Protect Oxygen- evolving complex of PII and increased amount of protein under stress	Encode stability of extrinsic protein of PII for regulation of PII activity under moisture stress	*Coffea canephora*	[20, 72]
CcUBQ10 and CcGAPDH	Housekeeping genes/reference gene	Response to drought stress	*Coffea arabica* & *Coffea canepora*	[79]
CcPYL3 and CcPYL7	Encoding the ABA signal pathway	Involved in ABA signaling pathway by control on stomatal conductance under drought stress	*Coffea canephora*	[20, 29, 73]
CaDREB1D	Controlling responses to abiotic stress via ABA pathway	Response to cold and moisture deficit	*Coffea arabica* (transgenic)	[74, 75]
CcDREB1D	Controlling responses to abiotic stress via ABA pathway	Response to cold and moisture deficit	*Coffea canephora*	[74, 75]

6. Conclusion

Abiotic stress particularly drought is a devastating factor that cause great loses on coffee production and quality in coffee producing countries including Ethiopia. Coffee utilizes different drought tolerance mechanisms to gives economical yield and acceptable quality under severely soil moisture stress. The most important mechanisms are morphological, physiological, biochemical and molecular (gene) which were elaborated in this article. Drought tolerant coffee genotypes have desirable traits in crown architecture, root and leaf that enable them better performance over susceptible under water deficit environment. Under water limit, drought tolerant coffee genotypes control on hydraulic conductance, leaf transpiration and stomatal conductance which retain leaf water potential for better physiological process to give yield without losing their inherent quality.

As biochemical mechanism, accumulation of soluble sugar and protein observed in drought tolerant coffee to avoid desiccation problem via osmoregulation under drought stress. Enzymes of carbon metabolism such as sucrose synthase contributed for additional root growth under drought stress and enhanced productivity under drought prone areas. Huge number of genes were identified and highly expressed in drought tolerant coffee genotypes under water stress which are momentous in genetic improvement using different breeding techniques.

Competing Interests

Authors have declared that no competing interests exist.

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