

Hydraulic characteristics of wild *Coffea arabica* populations in natural forests of Ethiopia

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Abstract

The montane rainforests of Ethiopia are the known centres of origin and genetic diversity for *Coffea arabica*. However, the remnant rainforests with the spontaneously grown wild coffee populations are under continuous threat, largely due to population pressure, indiscriminate deforestation and extensive disturbance of the natural forest habitats, and associated global climate changes. This demands urgent action for sustainable environmental management, utilization and conservation of forest biodiversity for global benefits. This study was conducted with the aim of investigating the diversity in hydraulic characteristics among the wild coffee populations in forest environments of Ethiopia. To this end, in-situ investigation was made within four rainforests along a rainfall gradient in the South Eastern and South Western parts of the country. These include, the specific sites of Berhan-Kontir, Yayu, Bonga, and Harena, with the driest site, Harena, situated in the South East. A high-pressure flow meter was employed to measure hydraulic flows in root and shoot segments of mature coffee trees. In addition, saturated hydraulic resistance components were recorded along with root and shoot parameters to examine the extent of possible drought damage and recovery rates. Hydraulic conductance of stems and branches differed highly significantly among wild arabica coffee populations and the results followed the order of Harena>Berhan-Kontir>Yayu>Bonga, both for whole branches as well as length specific. The juvenile primary branches showed the lowest hydraulic conductance within the tree crowns. The subsequent removal of growth parts significantly reduced hydraulic resistance components in the primary branches of the coffee trees and shoot of the coffee trees. In general, the Harena wild coffee populations exhibited significantly higher root and shoot hydraulic conductance, as compared to those from the moist areas in the South West, demonstrating their increased water use efficiency and productivity under sub-optimal environments. Overall, our results revealed significant variability in hydraulic properties and underline the importance of the four natural coffee forests as gene pools, and the need for multi-site in-situ conservation strategy for sustainable conservation and use of coffee genetic resources at their centre of origin and genetic diversity in Ethiopia.

Key words: Conservation, drought stress, hydraulic properties, natural forests, wild coffee diversity

Introduction

Coffea arabica is indigenous to the montane rainforests of Ethiopia, where it is largely produced by smallholders who are most vulnerable to the adverse impacts of global warming and climate changes. Human-induced forest losses are still the major threats to the world forest resources, including coffee environments and coffee genetic diversity. The main driving forces behind deforestation are increasing population pressure, the expansion of agricultural land, urbanization, uncontrolled exploitation of forest resources, overgrazing, seasonal fire, non-forestry investment, mining and establishment of new settlements in the forested lands (Gole, 2003). The management of wild coffee under the forest canopy has considerably affected and will continue to affect the diversity, composition and structure of the populations of wild coffee and the forests, as well.

In Ethiopia, there are immense arabica coffee cultivars materials with desirable traits (yield, quality, disease resistance, drought stress tolerance, etc). The local coffee landraces are known by vernacular names and growth characteristics in the different localities. According to Yacob et al. (1996), they are broadly grouped into three canopy classes of open, intermediate and compact types. These arabica coffee species could be bourbon or typical cultivars as they are quite different in shoot and root growth systems as well as adaptation to specific site and respond to management inputs. They also vary in frequency of occurrence along rainfall gradients and soil profile depths (Taye et al., 2004), indicating the existing variability among the cultivated coffee landraces in their adaptation strategies under specific environments.

But, most coffee farmers have replaced coffee by other high priority monoculture crops and/or there has been a shift in coffee cultivation from productive to marginal sites. The regional climatic change and drought is becoming one of the major problems for the coffee industry and the existence of wild coffee gene pools in Ethiopia. Drought stress during critical growth stages can result in poor growth and development, reducing the life span or completely drying the coffee trees and aggravating the genetic erosion of local coffee types. However, there are still immense diversities of wild and cultivated arabica coffees in Ethiopia. According to Dullo et al. (1998) and Bellachew and Labouisse (2006), there are about 21,407 coffee germplasm in the different field gene banks of some African countries, of which around 89.85% is arabica coffee, which is found in Ethiopia. This corroborates with the reports of Surendra (2008), indicated that Ethiopia alone possesses around 99.8% of the world total arabica's genetic diversity. Up to now, a total of around 11,691 arabica coffee germplasm accessions have been collected from the different areas and conserved ex-situ at different field gene banks in Ethiopia (Taye, 2010).

With regard to the possible effects of global warming and climate change on coffee environment and genetic diversity, nowadays, it is not uncommon to observe drying symptoms on new coffee trees in Ethiopia due to physiological disorders between vegetative and reproductive growths. This is associated with continues flower blooming and heavy crop load, as a result of change in weather pattern with erratic rainfalls. The situation is more aggravated with the outbreak of insect pests and diseases, requiring new corrective strategies to protect the Arabica gene pools from the subsequent possible fast and irreversible losses. In spite of this, there is lack of adequate knowledge on the drought stress adaptation mechanisms among the genetically diverse arabica coffee genetic resources and various production systems in Ethiopia.

The internal water balance in coffee trees is influenced by soil moisture, soil type and root resistance (Coste, 1992; Wrigley, 1988). Plants attempt to maintain water balance at decreasing soil moisture by stomatal closure, increasing permeability to water in the root zone, or both. The specific morphological differences of coffee reflect the hydraulic architecture of the plants by their influence of the boundary layer resistance, as well as by the determination of the hydraulic resistance for the soil-root-shoot-leaf resistance (Tausend et al., 2000a, 2000b). The well-documented decline in leaf size with increasing altitude in tropical mountains has defied definitive explanation (Tyree and Ewers, 1991). However, there studies are totally lacking in Ethiopia.

The potentials, constraints and recommendations for the conservation of the Ethiopian coffee genetic resources are presented by Girma et al. (2008). In view of the importance of coffee, its high genetic erosion in the centres of its origin and the observed minimal conservation efforts, Bellachew and Sacko (2009) strongly

emphasized on the need for immediate intervention of all the concerned bodies to undertake aggressive conservation measures to warrant sustainability of the global coffee industry.

In this study, we hypothesized that a climatic gradient would promote regional differentiation pressure in ecophysiological traits that would allow the identification of drought-tolerant coffee populations. In this regard, there are many indications of genetically based traits in the coffee plants for adaptation to stress environments. The hydraulic conductivity of the roots and shoots are among the key elements for identifying drought-tolerant coffee cultivars. This study will help to identify some of the most important functional traits and the underlying mechanisms for coping with environmental stress in wild coffee populations. Therefore, this study would provide highlight on the prevailing extent of variability among the wild coffee populations in hydraulic properties, thereby provides insights on adaptation and mitigation strategies against the upcoming adverse effects of global climate changes. The specific objective of the study was, therefore, to determine the diversity in the in-situ hydraulic characteristics of wild Arabica coffee populations in four natural forests of the South Eastern and South Western parts of Ethiopia -its centre of origin and genetic diversity.

Materials and Methods

The study area

The study was carried out in the natural forests of southeast and southwest Ethiopia with the occurrence of diverse indigenous plant species including wild *Coffea arabica* populations. The study montane rainforests are Hareenna, Bonga, Berhane-Kontir and Yayu. Except Hareenna in the southeast, the other three forests are located in the southwest Ethiopia. Experimental measurements were made at three sites within each natural forest. They are separated by the Great East African Rift Valley, which dissects the country into southeast and northwest highlands (Fig. 1). According to Paulos and Demel (2000), these forests differ in area coverage (Hareenna 15000 ha, Bonga 5000 ha, Berhane-Kontir 1000 ha and Yayu 1000 ha), agro-ecological zones, physical characteristics and forest vegetation. The rainfall gradients follow the decreasing order of Berhane-Kontir > Yayu > Bonga > Hareenna with the average annual precipitation of 2200, 1800, 1700 and 1000 mm and average air temperatures of 18, 18, 22 and 21°C, respectively (Paulos and Demel, 2000). Taye (2006) also described the characteristics of the study montane rainforests (Table 1).

Data measurements

Uniform sample trees and branches were selected from the wild coffee population and used for hydraulic measurements. From each tree, three primary branches were used along the positions of a tree crown (bottom, middle and top); thus, representing different age groups. Subsequent to recording all growth parameters, in situ hydraulic measurements were made in the field using a high-pressure flow meter (HPFM). Hydraulic conductances (Kh) in root and shoot parts. Besides, hydraulic resistance (Rh) in primary branch segments (Dynamax Inc., Houston, TX, USA) of the coffee trees were also measured following the procedures adopted by several authors (Tyree and Dixon, 1986; Tyree et al., 1993; Martinez et al., 2002). The flow meter consisted of a water reservoir that could be pressurized with compressed air from a pressure regulator.

Water flow rate from the reservoir to the base of the excised plant part was computed from the measured pressure decrease across a capillary tube interposed between the reservoir and root (Tyree et al., 1994). The bases of the main stem and the branch were re-cut under water and connected to the HPFM. Root and shoot hydraulic conductance were measured using the transient method of the HPFM. Measurements were done while the whole shoot was attached and by consecutive removal of the shoot segments (branches, leaves, fruits and petioles) and main stem cut (30 cm). On the main stem, hydraulic conductivity was measured with the methods described by Sperry et al. (1988). For this, a 30-cm long main stem segment (a conventional stumping height in Ethiopia) was cut and immediately filled with water to prevent air from entering into the xylem. The segment was connected to the plastic tubing of the

HPFM supplied with degassed and de-ionized water at a pressure of 0.2 MPa. Root conductance was measured by forcing distilled water into the base of the root system (opposite to the normal direction of water flow during transpiration). The computer connected to the HPFM recorded values of the parameters for the different parts of the coffee trees.

The selected primary branches were labeled, removed and immersed in pure water. Then, saturated whole-branch hydraulic resistance and its components were measured using the steady state flow meter method of the HPFM as described by Tyree et al. (1995). The hydraulic architecture of the branch was measured by recording the conductance or resistance of the distal portions. This was performed by consecutive removal of the other growth components (leaves, fruits, petioles and branches), followed by reduction of the branch length to 20 cm. The resistance of each component part was viewed as resistances in parallel and related to the total resistance in a similar inverse fashion as described by Tyree et al. (1994, 1995). The total leaf area on a branch was measured using leaf dimensions and a constant ($K = 0.66$) developed by Yacob et al. (1998) and leaf area-specific hydraulic conductivity was calculated. Leaf-area hydraulic conductivity (k_h) was calculated by dividing the hydraulic conductance to the total leaf area of the branch segment. All root and shoot growth parameters were simultaneously measured and their relationships with hydraulic characteristics were examined (Taye 2006).

Statistical analysis

Analysis of variance (ANOVA) in a nested design was performed to compare the variability among and within wild coffee populations. In this case, the sub-sites and coffee trees were nested under the four populations. Moreover, the relationship between stem growth and hydraulic flow was assessed from regression analysis plotted using the pooled data of the whole study sites. The means were compared using the Tukey test at 0.05% probability level whenever the F-test declared significant differences. Data analysis was performed with the default SAS 8.1 (SAS Institute Inc. Cary NC, USA) procedure. Graphs of two-way interactions were made with the SigmaPlot SPW9.0 (SYSTAT Software, Inc.).

Results

Hydraulic conductance

Wild arabica coffee trees from the four wild coffee populations did not reveal significant differences in whole-plant, root and/or shoot hydraulic conductance. Significant variations ($P < 0.01$) were, however, detected in main stem hydraulic conductance and stem-specific hydraulic conductivity (Table 2). In addition, whole-plant conductance showed significant differences ($P < 0.05$) within the Harenna sites, and between coffee trees at Berhan-Kontir and Yayu. At Bonga, this did not show any change due to sites and coffee trees. Hydraulic conductance in the various parts of the coffee plant did not change within sites, except for the significant variations ($P < 0.05$) observed in the hydraulic conductance of lateral branches and reduced stem length (30 cm). Accordingly, Harenna exhibited significantly higher values in contrast to Bonga and Yayu, while Berhan-Kontir had intermediate stem results (Table 2). In other words, the magnitude of changes between whole-shoot and stem-cut conductance varied among populations. Consequently, the coffee trees from Harenna (41%) and Bonga (54%) showed high percent increments as compared to Berhan-Kontir (15%) and Yayu (18%).

At all the study sites, higher conductance were measured in the whole-shoot than in the root part, though the percent share varied among wild coffee populations. As a consequence, the contribution of root conductance was high in Harenna (46%) and Bonga (44%), as compared to that of Berhan-Kontir (37%) and Yayu (33%) (Fig. 2). In addition, whole-plant hydraulic conductance showed increasing patterns with the reduction of shoot components. The greatest increment over whole-shoot conductance was recorded with leaf defoliation with values ranging from 21 to 35% at Harenna and Berhan-Kontir, respectively. This is in contrast to a slight reduction at Bonga due to leaf defoliation. Consecutive removal of fruits and petioles was noticed to enhance conductance with the least (5%) and maximum (16%) percent increments over the

whole-shoot conductance determined from the coffee trees at Yuyu and Berhan-Kontir, respectively (Fig. 3). The coffee trees from the Berhan-Kontir and Harena forest stand revealed high hydraulic conductance, both with regard to the root and whole-shoot parts, as compared to those from Bonga and Yuyu. The overall mean of whole-plant hydraulic conductance was significantly ($P < 0.05$) higher at Harena and Berhan-Kontir, as opposed to the least value recorded for Bonga. The results follow the order of Harena ($2.69 \times 10^{-4} \text{ kg s}^{-1} \text{ m}^{-2} \text{ MPa}^{-1}$) > Berhan-Kontir ($2.30 \times 10^{-4} \text{ kg s}^{-1} \text{ m}^{-2} \text{ MPa}^{-1}$) > Yuyu ($1.36 \times 10^{-4} \text{ kg s}^{-1} \text{ m}^{-2} \text{ MPa}^{-1}$) > Bonga ($1.13 \times 10^{-4} \text{ kg s}^{-1} \text{ m}^{-2} \text{ MPa}^{-1}$) (Fig. 4). The results of main stem diameter and main stem hydraulic conductance of the wild coffee population showed a similar pattern. Consequently, the values were higher for Harena followed by the Berhan-Kontir coffee trees, while they gave the least records for the sample trees from Bonga and Yuyu (Fig. 5). Furthermore, the influence of stem size on hydraulic flow was confirmed by the strong positive linear regression recorded in the study (Fig. 6).

Hydraulic resistance

There were no significant differences in branch hydraulic resistances (reciprocal of conductance) among populations, sites and coffee trees. Except at Bonga, where remarkable reductions in branch hydraulic resistances were noted with the removal of leaves, fruits and petioles. Therefore, resistances tended to increase with the reduction of lateral branch parts at Bonga, which is mostly associated with the differences in branch growth characteristics. The average hydraulic conductance increased (Fig. 3) and the hydraulic resistance in the various branch segments of the wild coffee trees declined in the order of Bonga > Yuyu > Berhan-Kontir > Harena (Fig. 7). Furthermore, the highest ($6.91 \times 10^5 \text{ MPa m}^2 \text{ s kg}^{-1}$) and lowest ($0.45 \times 10^5 \text{ MPa m}^2 \text{ s kg}^{-1}$) hydraulic resistance values from a 20-cm long branch were recorded from the wild coffee trees of Bonga and Harena, respectively. These same orders were maintained in branch- and leaf-specific resistances evaluated in this study. Thus, based on branch resistances, Bonga and Harena were grouped into the highest and lowest extremes, while Yuyu and B-Kontir were found to be intermediate (Fig. 7).

An independent analysis of variance was carried out for each population when sites, trees and branches were nested, which depicted significant ($P < 0.001$) differences in whole-branch hydraulic resistance patterns on the samples collected from Bonga, Berhan-Kontir and Yuyu forests, but not from Harena. However, no variations were observed due to the selected coffee trees at all sites, except at Yuyu, where reduced whole-branch hydraulic resistances were recorded from the middle canopy position. The values (Fig. 8) generally revealed increased resistances with decreased branch age and the uppermost branches exhibited the highest values at Bonga ($10.9 \times 10^5 \text{ MPa m}^2 \text{ s kg}^{-1}$) and Berhan-Kontir ($6.52 \times 10^5 \text{ MPa m}^2 \text{ s kg}^{-1}$). Hence, the reduction in branch hydraulic resistances between bottom (old) and middle (medium age) branches were 8, 25 and 48% at Berhan-Kontir, Bonga and Harena forests, respectively. At Harena, the resistance patterns in various branch segments were indirectly and significantly ($P < 0.05$) correlated to the length of internodes in the young growing part of the branch. At Yuyu, however, it tended to reduce from middle to top primary branches.

On the other hand, the reduction of hydraulic resistances in the various component parts of primary branches was only significant at Harena, where the removal of leaves significantly ($P < 0.05$) reduced whole-branch resistance. However, leaf defoliation from the varying branches within a tree crown was noticed to reduce resistances at all sites. An exception to this was the slight increment observed on the top juvenile branches of the Bonga forest. The percent hydraulic resistance reductions due to leaf cut were 47, 36 and 33% at Harena, Yuyu and Berhan-Kontir, respectively. There was a direct highly significant correlation between the patterns of whole-branch resistances and leaf removal (data not shown). Whole-branch hydraulic resistance was significantly related to old and young branch growths, though the correlations were positive and negative, respectively. Unlike this, there was a slight increment (10%) in resistance due to leaf removal from the Bonga trees. In addition, decreased resistance was observed due to subsequent removal of leaf petioles. The resistance contribution of petioles was higher at Harena (19%) compared to the rest three populations (Bonga = 3%, Berhan-Kontir and Yuyu = 5%).

At Bonga and Berhan-Kontir, branches showed significant ($P < 0.05$) differences in

branch cut (20-cm long) resistances. The lowest resistances (highest conductance) were measured from the shortest branch free of side growths. Hence, the values increased from bottom to top positions and ranged from $1.40 \times 10^5 \text{ MPa m}^2 \text{ s kg}^{-1}$ to $17.5 \times 10^5 \text{ MPa m}^2 \text{ s kg}^{-1}$ for Bonga, and from $0.79 \times 10^5 \text{ MPa m}^2 \text{ s kg}^{-1}$ to $4.40 \times 10^5 \text{ MPa m}^2 \text{ s kg}^{-1}$ for Berhan-Kontir. The hydraulic resistance difference between whole branch and branch cut was higher at Berhan-Kontir (21%) and Hareenna (19%), as compared to Yayu (13%) and Bonga (15%). At all sites, branch cut was found to decrease resistances (increase conductance) with increased branch ages (bottom position), except for the middle branches from the Yayu forest. In general, the mean resistance values followed the descending order of Bonga>Yayu>Berhan-Kontir>Hareenna; while the reverse holds true for branch hydraulic conductance from the experimental sites.

At Bonga, branch- and leaf- specific hydraulic resistances were significantly ($P < 0.05$) higher for the upper branches, as compared to the bottom and middle branches. That means, there were reductions in branch- and leaf-specific resistances (highest branch- and leaf-specific conductance) in the medium-aged primary branches of the middle crown position, where most of the coffee trees carried fruits. Nevertheless, no significant variations were detected among the selected primary branches from the rest three study sites. On the other hand, at Hareenna and Berhan-Kontir, branch- and leaf-specific hydraulic resistances were negatively correlated along the crown of coffee trees. Accordingly, resistances tended to decline with increased branch aging, although there was an increase in leaf-specific hydraulic resistance from bottom ($3.66 \times 10^2 \text{ kg s m}^{-2} \text{ MPa}^{-1}$) to top ($1.30 \times 10^3 \text{ kg s m}^{-2} \text{ MPa}^{-1}$) canopy positions (Fig. 8). From each population, relatively low values of hydraulic resistance from branch segments and branch-specific hydraulic resistances were recorded for Hareenna, Bonga, Berhan-Kontir, and Yayu. In contrast, coffee trees at most sites in the montane rainforests were noted to display maximum values for whole-branch hydraulic resistances and branch- and leaf- specific hydraulic resistance patterns. High branch-specific resistance ($4.13 \times 10^5 \text{ kg s m}^{-2} \text{ MPa}^{-1}$) was found at Hareenna (Fig. 8), where the lowest whole-branch resistance (highest conductance) was recorded, which in turn would be ascribed to the increased leaf area records of the same site.

Discussion

Hydraulic conductance

The relatively high root, whole-shoot and leaf conductance values were recorded for the same sites of each population, which may be related to the weak growth performances of coffee trees under heavy shade cover and thicker plant density (Taye and Burkhardt, 2006). The magnitude of changes between whole-shoot and stem-cut conductance varied among wild coffee populations, where coffee trees from Hareenna and Bonga showed high percent increments as compared to Berhan-Kontir and Yayu. This could be associated to stem size and vegetative growth responses of the coffee trees under the prevailing heterogeneous forest environments.

The difference in the intensity of light interception and photosynthetic rates could be the reason for the variations in growth vigor, hydraulic architecture and hence, hydraulic characteristics of the wild coffee trees evaluated in this study. The hydraulic conductance corresponded with branch hydraulic resistances, as well as with the morphological growth parameters (Taye et al., 2004). The differences observed in water flow patterns within a relatively saturated main stem could suggest the inherent growth variability and impacts of environmental factors, particularly between the geographically distant forest habitats. The enhanced water transport in the stem segments of the wild coffee trees at the Berhan-Kontir and Hareenna sites indicate their high water-use rates, although this could be limited with low leaf conductance. The mechanism explaining this follows Ohm's law analogue for water flow in plants (Yang and Tyree, 1993; Tyree, 2003). Quantitatively, the argument is that the product of stomatal conductance and driving force of water vapor diffusion determines the change in the water use of leaves.

Of the four study sites, the contribution of root conductance to the whole-tree at Hareenna and Bonga was observed to be lower than that of the whole shoot. Consequently, tree hydraulic conductance on either leaf area or dry weight basis might follow the same trend, as elucidated by Tyree (2003). The capacity of the stem water

storage status could demonstrate that the coffee trees might have experienced some degree of drought stress during the past recurring droughts. Therefore, the hydraulic condition of forest coffee trees seems to be influenced by multi-variables, which needs further investigations. The present finding is in agreement with similar other reports conducted on other tropical forests (Lawton, 1984; Borchert, 1994; Sobrado, 1993 and 2003; Tausend et al., 2000b). According to Lawton (1984), wood density values are the measure of mechanical support and appear to be negatively correlated with the rates of growth and mortality. Wagner et al. (1998) found that species with heavier mechanical stress are associated with relatively low stem specific hydraulic conductivity. The authors have also reported twofold higher values of leaf specific conductivity in pioneer compared to forest species. However, Sobrado (2003) reported that specific hydraulic conductance was species-specific and independent of the differences in wood density.

There is evidence for a plastic response of plants to their growth environment, which causes changes in plant conductance. Hence, it would be of interest to know if slow-growing species and fast-growing species still exhibit differences in whole-plant conductance even when all are grown in the same environment. This issue was addressed in an investigation by Tyree et al. (1998) that involved five species of tropical seedlings grown in a similar environment. If low hydraulic conductance is manifested at the sapling stage and if all low-conductance saplings are slow growing, then early selection of coffee genotypes with high hydraulic conductance could save time in breeding or tree selection programs.

Hydraulic resistance

The difference among the wild coffee populations in hydraulic resistance could be largely attributed to the variations in branch age and growth responses in the contrasting forest conditions. Accordingly, resistances tended to decline with increased branch aging, although there was an increase in leaf-specific hydraulic resistance from bottom to top canopy positions (Fig. 7). This is quite in line with leaf growth characteristics on primary branches (Taye, 2006). Similar effects were observed in declining oak crowns, since in addition to changes in the shoot structure the crown becomes much more open. These changes in crown architecture might be even more important reasons for the reduction of wood production and height growth with age than tree height (Becker et al., 2000).

Moreover, the increased crop to leaf ratios at Berhan-Kontir could be among the reasons for leaf senescence from the fruit-bearing parts of the coffee trees, because fruits are among the strongest sinks for water and assimilates (Coste, 1992; Wrigley, 1988). The greatest resistances with decreased branch age in Bonga and Berhan-Kontir corresponded with the significantly lowest diameters recorded on top branches. On the other hand, both branch- and leaf-specific hydraulic resistances were highest for lateral branches at the middle canopy of the coffee trees. This could also be related to the significantly small branch diameter ($P < 0.001$) recorded for the top juvenile branches. Furthermore, the observed significantly ($P < 0.01$) higher total leaf area from the middle branches (Taye, 2006) could lead to enhanced water transport. This is the position where maximum total leaf areas were estimated, especially for Harena and Bonga. This is in contrast to the observed considerable reduction of leaf production in the middle canopy branches at Berhan-Kontir and Yayu (Taye, 2006). This supports the findings of Rust et al. (2004), who identified two bottlenecks to water transport in the shoots of old oak trees, namely nodes and abscission zones. In young twigs, vessel diameter and vessel density in nodes with abscission zones were significantly reduced compared with internodes. They described that in nodes without abscission zones, vessel density was significantly reduced. The reduction of hydraulic conductance was especially severe in the smallest and most juvenile shoots. The highest and lowest branch specific resistances were from Bonga and Harena, respectively. Similarly, maximum specific leaf hydraulic resistances were measured for Bonga, Yayu, Berhan-Kontir and Harena coffee trees in that order, demonstrating that the Harena coffee trees would thus be more vulnerable to embolism than the other coffee trees.

In this regard, several studies (Machado and Tyree, 1994; Tyree et al., 1991) showed a correlation between stem segment hydraulic conductivity and tree growth rates. However, such studies are based on the assumption that stem segment conductivity is a proxy for whole-plant conductance. There are ample evidences regarding how

drought and frost cause xylem dysfunction and loss of stem and root hydraulic conductivity, and hence loss of plant conductance (Tyree and Zimmermann, 2002). Tyree (2003) indicated that several factors can bring about changes in whole-tree hydraulic conductance and hence influence whole-tree performance. These include tree size, xylem dysfunction, growth conditions with little xylem dysfunction, and genetics within species and between species.

Tropical montane forests are among the least understood of humid tropical forest ecosystems as far as the water and nutrient dynamics are concerned. Although it has long been suggested that a suppression of transpiration due to high humidity and cloud cover and a consequent limitation of mineral supply could explain the reduced forest height with altitude (Leigh, 1975), available in-situ observations of transpiration and leaf water relations are rare and contradictory. Cavellier et al. (1996) found no evidence for reduced transpiration rates among cloud forest tree species in Colombia. Therefore, they proposed a possible difference of cloud forest species from lowland species in their hydraulic architecture, which in turn may lead to limitations of transpiration under sunny conditions. Consequently, they had suggested that hydraulic conductance of cloud forest trees to be not high enough to compensate for the high water losses that occur during sunny weather.

Conclusions and conservation implications

At its center of origin and diversity in Ethiopia, *Coffea arabica* is under a severe threat of genetic erosion and irreversible loss largely due to increasing population, expansion of large farms, crop replacement, and climate change, among others. The additional stresses imposed by climate change can also aggravate these problems as they can disrupt the ecosystem and coffee diversity. The destruction of original coffee habitats coupled with changes in weather patterns can adversely affect coffee genetic resources and thus the livelihoods of millions of people in the world. .

Arabica coffee is known to evolve under the multi-strata of forest ecosystem in Ethiopia. Hence, it is an evergreen and shade-loving tree crop suitable for agriculture and forestry practices in different agroforestry systems. Therefore, its production and conservation approach needs to be fully embedded into any climate agreement and compensated for its multiple eco-services as carbon sinks in coffee producing countries taking into account, inter alia, the different production systems.

The present findings provide the first detailed hydraulic analyses and demonstrate inter- and intra-regional variability among wild coffee populations. This variability underlines the importance of the natural coffee forest environments and coffee gene pools for future improvement programs, and the need for multi-site in-situ conservation strategy, though its environmental, social and economical sustainability calls for further studies. This in turn would help a lot in implementing appropriate conservation and management strategies for coffee genetic resources for future breeding works, which would be of great benefit to the global coffee sub-sector. Overall, our findings would contribute towards indentifying drought tolerant coffee genotypes and their adaptation and mitigation mechanisms against the current global climate changes. This would have a practical conservation and management implications of the wild arabica coffee genetic resources at its place of origin in the montane rainforests of Ethiopia.

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Table 1 Characteristics of the four montane rainforests in Ethiopia

Variable	Harena	Bonga	Berhane-Kontir	Yayu
District	Mena-Angetu	Gimbo	Sheko	Yayu-Hurumu

Latitude (N)	6°23′-6°29′	7°17′-7°19′	7°04′-7°07′	8°23′
Longitude (E)	39°44′-39°45′	36°03′-36°13′	35°25′-35°26′	35°47′
Altitude (m a.s.l)	1420-1490	1520-1780	1040-1180	1400
Slope (%)	2-3	3-6	4-18	1-8
Rainfall (mm year-1)	950	1700	2100	1900
Max temperature (oC)	34.4	29.9	31.4	34.7
Min temperature (oC)	10.4	8.7	13.8	7.6
Mean temperature (oC)	22.2	18.2	20.3	19.7
Minimum RH (%)	37.9	45.0	50.8	41.8
Maximum RH (%)	84.3	95.2	85.4	98.5
Mean RH (%)	63.2	80.4	68.9	80.9
Wind speed (m h-1)	0.93	0.64	0.43	0.35

Table 2 Variations in hydraulic conductance (means±SDx10⁻⁴ kg s⁻¹ m⁻² MPa⁻¹) and stem conductivity (khx10⁻⁴kg s⁻¹m⁻¹ MPa⁻¹) in coffee trees of the four wild populations in montane rainforest of Ethiopia

Plant part	Hareenna	Bonga	B-Kontir	Yayu	Pr>F
Root system	1.76±0.65	0.62±0.05	1.57±0.73	0.78±0.28	Ns
Whole shoot	2.21±1.03	0.81±0.26	3.09±1.66	1.60±0.33	Ns
Leaves	1.75±0.71	0.98±0.09	2.01±1.57	1.09±0.20	Ns
Fruits and petioles	1.59±0.51	0.85±0.31	1.59±0.86	1.01±0.21	Ns
Branches	2.49±1.04	1.28±0.62	2.06±0.57	1.30±0.34	Ns
Stem cut (30 cm)	6.33±1.22a	2.24±1.24b	3.50±1.00ab	2.40±0.39b	**
Stem conductivity	1.73 ±0.37a	0.90±0.38 b	1.16±0.34ab	0.82±0.26b	**

Ns = Not significant; ** significant at $P < 0.01$; Mean values followed by the same letter within a row are not significantly different from each other

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Figure 1 Map of Ethiopia and location of the studied montane rainforests (Hareenna, Bonga, Berhane-Kontir and Yayu)

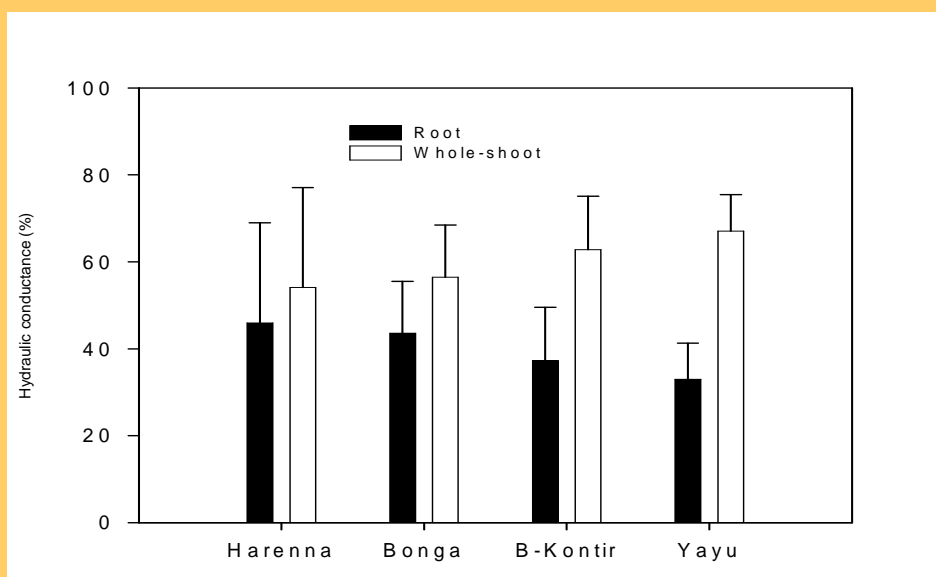


Figure 2 Percent whole-plant hydraulic conductance in root and whole shoot of coffee trees of the four montane rainforests of Ethiopia.

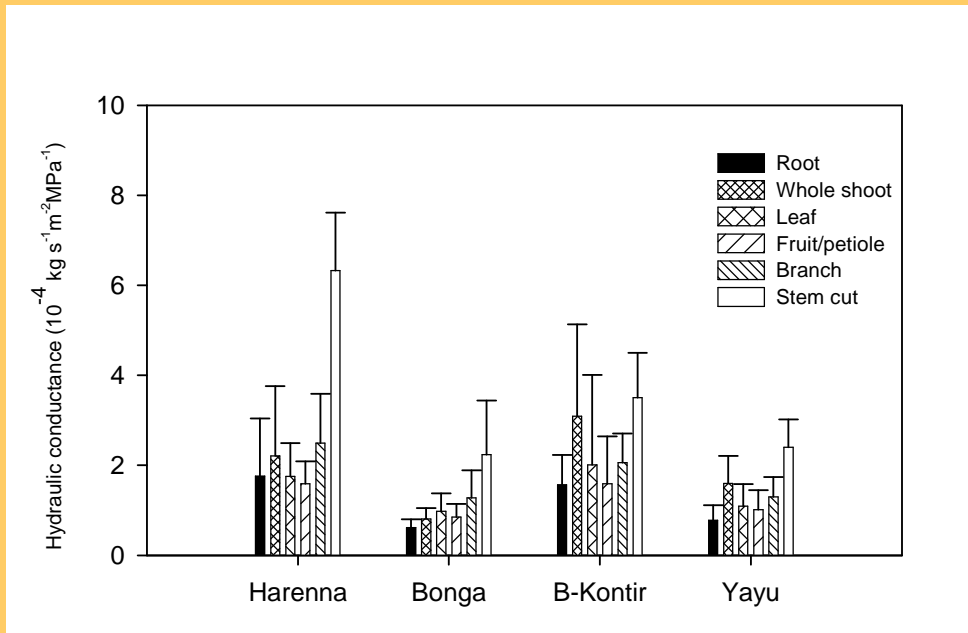


Figure 3 Hydraulic conductance in components of the wild coffee trees at the four montane rainforests of Ethiopia

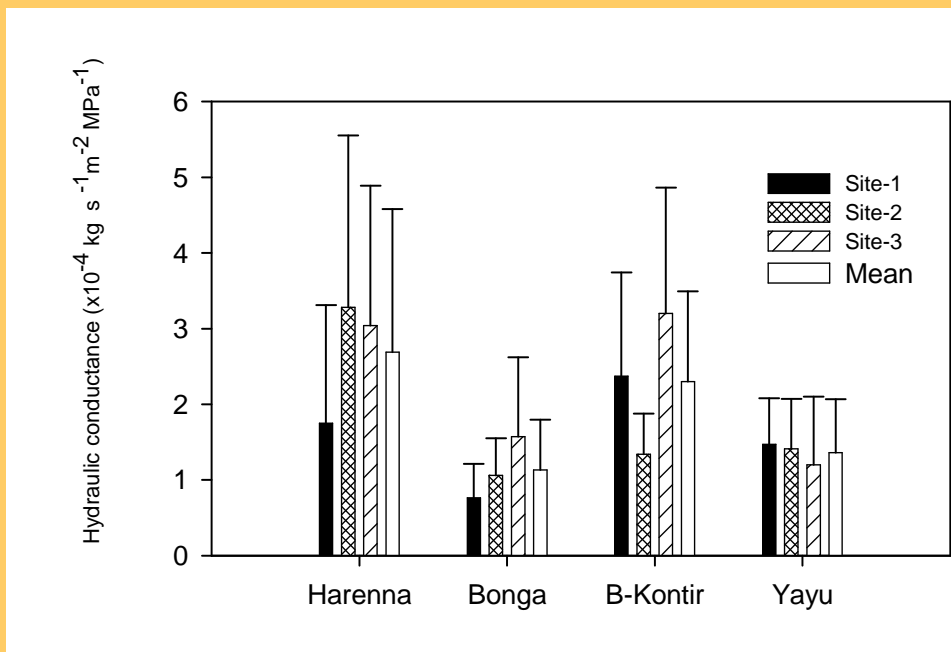


Figure 4 Variations in whole-plant hydraulic conductance of coffee trees within sites of each montane rainforest of Ethiopia

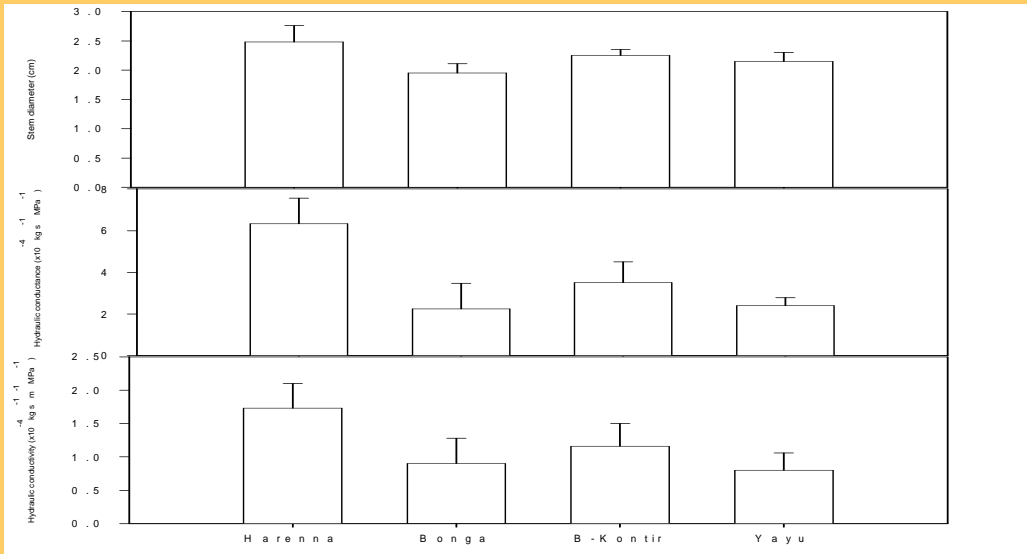


Figure 5 Diameter of main stem cut and hydraulic conductance of wild coffee trees at the four montane rainforests of Ethiopia

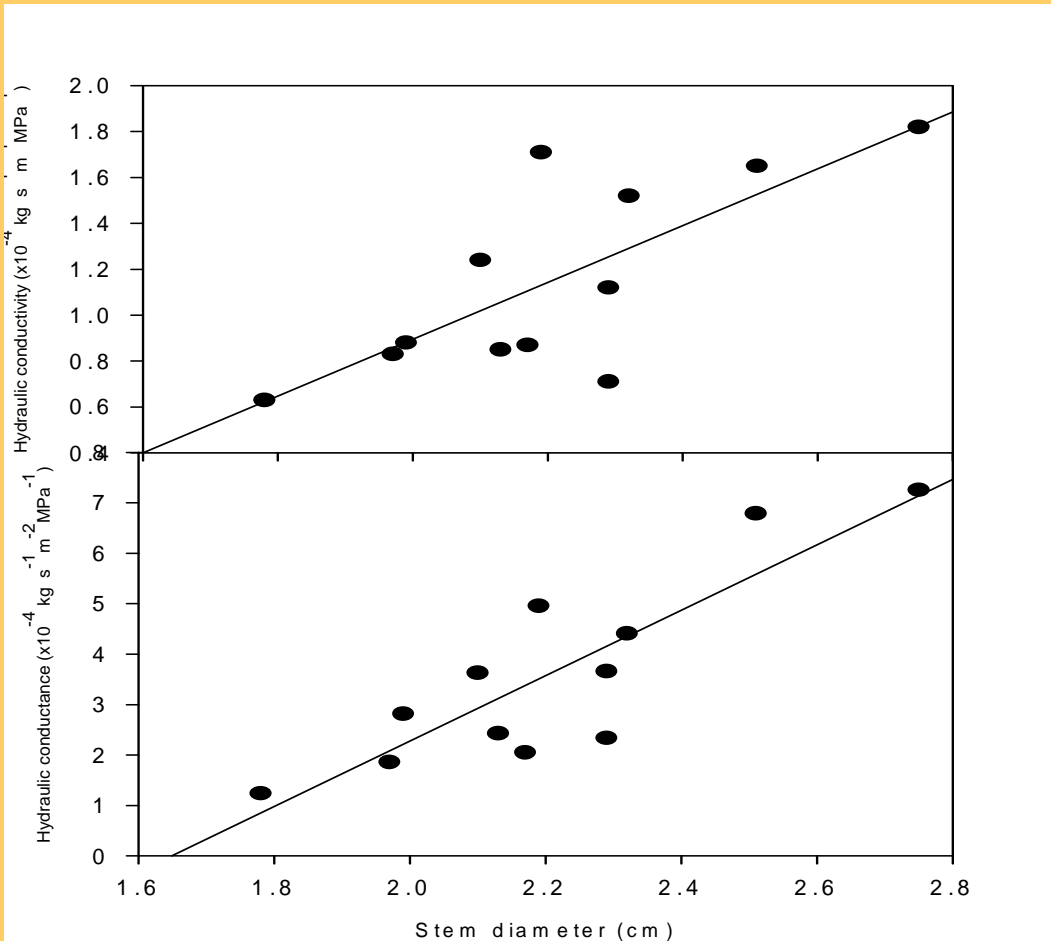


Figure 6 Hydraulic conductance and specific hydraulic conductivity of main stem cut (30 cm) plotted against debarked main stem diameter of wild coffee trees using pooled data from the study sites (n =12)

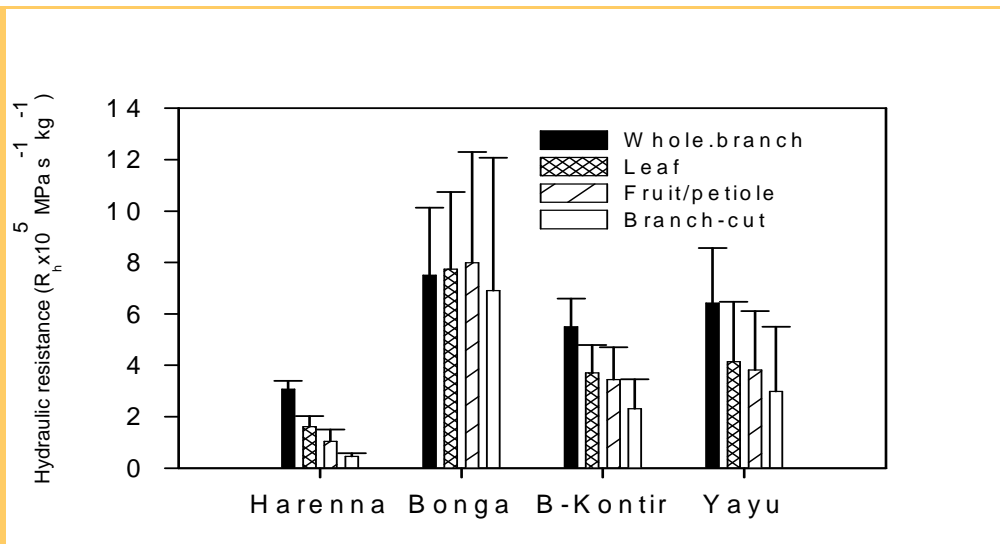


Figure 7 Branch hydraulic resistance components in the wild coffee trees at the study montane rainforests of Ethiopia

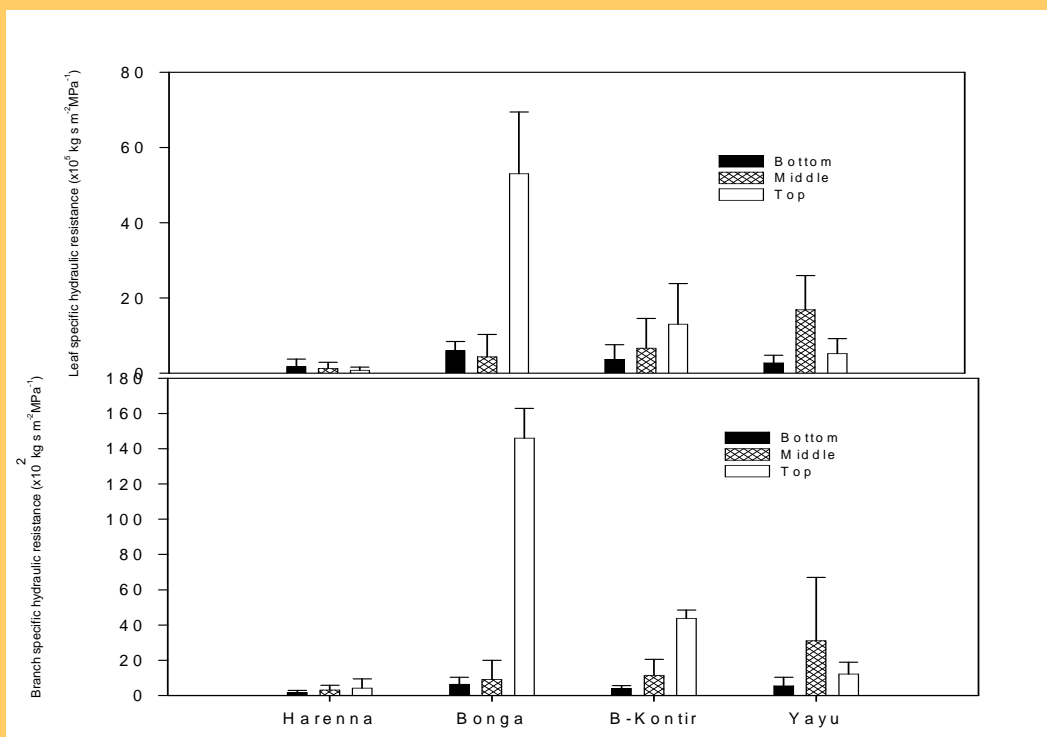


Figure 8 Branch- and leaf- specific hydraulic resistance as influenced by branch position in the crown of wild coffee trees at the four montane rainforests of Ethiopia

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