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Ecophysiological diversity of wild Arabica coffee populations in Ethiopia: Growth, water relations and hydraulic characteristics along a climatic gradient

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I would like to dedicate this dissertation to my late family members:
Mom **Ayelech Belihu**, sister **Guchi Kufa** and brother **Gebe Kufa,** who can not share
my fulfilled dreams and joy today. May God give them peace and serenity.

ABSTRACT

Coffee (*Coffea arabica* L.) is a shade-adapted plant occurring in the undergrowth of humid montane rainforests of southwestern Ethiopia, where it has its center of origin and diversity. However, the remnant rainforests with the occurrence of wild coffee populations are under continuous threat largely due to a high deforestation rate and recurrent drought, and demand urgent actions for their conservation. This study was conducted with the aim to investigate the ecophysiological diversity in growth architecture, hydraulic characteristics and water relations of wild coffee populations in southeastern and southwestern Ethiopia. *In-situ*-investigations were made within four rainforests along a rainfall gradient between 2,100 and 950 mm per year, following the order of Berhane-Kontir>Yayu>Bonga>Harenna, with the driest site, Harenna, situated in the southeast. Moreover, coffee accessions from these wild coffee populations were established at the Jimma Research Center. In an *ex-situ* experiment, the one-year-old coffee seedlings were evaluated under contrasting daylight and drought stress regimes over a period of 16 days. For this period and during the following weeks, diurnal soil and leaf water potentials, root and shoot hydraulic conductance and saturated hydraulic resistance components were recorded along with root and shoot parameters, extent of drought damage and recovery rates. In addition, foliar chlorophyll, leaf composition and stomatal characteristics were determined. A high-pressure flow meter was employed to measure hydraulic flows in root and shoot segments of mature trees and coffee seedlings.

The Harenna and Berhane-Kontir populations had open crowns, while Yayu and Bonga showed intermediate to compact canopies. The wild coffee trees displayed highly significant variations in the diameter and length of coarse lateral roots, but not in the proportion of root classes. Hydraulic conductances of stems and branches differed highly significantly between populations (Harenna>Berhane-Kontir>Yayu>Bonga), both for whole branches as well as length specific. The juvenile primary branches showed the lowest hydraulic conductance within the crowns. The removal of growth parts significantly reduced hydraulic resistance components in the primary branches of the coffee trees and shoot of the coffee seedlings.

The *ex-situ* results show highly significant differences among the coffee accessions in seedling emergence and subsequent growth stages. In addition, the relationships between growth and hydraulic characteristics, and soil and plant composition were different for shade and irrigation levels. The analysis of variance also depicts significantly ($P<0.01$) higher total biomass for unshaded and drought-stressed seedlings as compared to those in shaded and well-watered plots. Again, significantly lowest and highest total biomass were obtained from the Berhane-Kontir and Harenna coffee accessions, respectively. Moreover, the Harenna accessions were also noted to have higher values for such variables as average leaf area, main stem diameter, leaf chlorophyll, leaf nitrogen and stomatal density. The Berhane-Kontir accessions had highly significant lowest root partitioning compared with Harenna, which had the highest root share. In consistence with the *in-situ* results, the Harenna accessions exhibited higher root and shoot hydraulic conductances as compared to the other sites. However, they failed to withstand persisting drought-stress situations, while the accessions from the moist southwestern regions were still performing well. The Harenna accessions, however, were better adjusted to drought stress through such features as high root to shoot ratio, deep root system, thick leaves, and their leaves showed greater changes in leaf water potentials and a high accumulation of potassium ions. In contrast, the Berhane-Kontir and Bonga accessions had shallow roots and maintained a better water storage in the dehydrated potting medium. As a whole, moderate shading was noted to extend the occurrence of drought stress effects by a two-fold time period over those seedlings subjected to soil drying rapidly in full sun.

This work outlines very different strategies for coping with drought stress in seedlings of wild coffee accessions, whereby accessions from the southeastern and southwestern areas followed opportunistic and conservative ways of water use in drought stress conditions,

respectively. The results provide the first detailed ecophysiological analysis and demonstrate inter- and intra-regional variability among wild coffee populations in morpho-physiological characteristics, water relations and hydraulic conditions. This variability underlines the importance of the four studied natural coffee forests as gene pools for future breeding programs, and the need for multi-site *in-situ* conservation strategy. The study provides research recommendations on the management and use of coffee forests and wild coffee populations in Ethiopia.

Ökophysiologische Diversität von Wildkaffee-Populationen in Äthiopien: Wachstum, Wasserhaushalt und hydraulische Eigenschaften entlang eines Klimagradienten

KURZFASSUNG

Der Ursprung und das genetische Zentrum von Kaffee (*Coffea arabica* L.) liegen in Südwest-Äthiopien, wo die Art im schattigen Unterwuchs der Bergregenwälder vorkommt. Starker Nutzungsdruck und zunehmende Trockenheit gefährden die noch verbliebenen Bergregenwälder und machen Maßnahmen zu deren Schutz erforderlich. Die vorliegende Studie untersucht die ökophysiologische Diversität von Wildkaffee-Populationen im Südosten und Südwesten Äthiopiens mit Blick auf die Wuchsform, die hydraulische Konstruktion und den Wasserhaushalt der Bäume. Die *in-situ*-Untersuchungen konzentrierten sich auf vier Bergregenwälder mit Niederschlägen zwischen 2.100 und 950 mm/Jahr (Berhane-Kontir>Yayu>Bonga>Harenna), wobei die drei feuchteren Standorte im Südwesten Äthiopiens liegen, Harenna dagegen im Südosten. Die von allen vier Standorten gewonnenen Samen (Akzessionen) wuchsen in der Forschungsstation Jimma zu einjährigen Setzlingen und wurden dann unterschiedlichen Licht- und Wasserverhältnissen ausgesetzt (*ex-situ*-Experiment).Während und nach einer 16-tägigen Trockenperiode wurden täglich die Boden- und Blattwasserpotenziale, die hydraulische Leitfähigkeit von Wurzel und Spross, sowie Schäden und anschließende Regeneration der Pflanzen ermittelt. Weiterhin wurden Blattchlorophyll, Blattzusammensetzung und stomatäre Charakteristik bestimmt. Zur Bestimmung der hydraulischen Widerstände und Leitfähigkeiten in Spross und Wurzeln der Kaffeepflanzen wurden der druckabhängige Durchfluss durch die entsprechenden Segmente mittels eines Hochdruckflussmessgeräts (HPFM) ermittelt.

Die Populationen in Harenna und Berhane-Kontir hatten einen offenen Kronenaufbau, die Bäume in Yayu und Bonga dagegen hatten eher kompakte Kronen. Deutliche Schwankungen traten bei Durchmesser und Länge der lateralen Wurzeln auf, nicht aber in der Zusammensetzung der Wurzelklassen. Die hydraulischen Leitfähigkeiten von Stamm und Ästen unterschieden sich hochsignifikant zwischen den einzelnen Standorten (Harenna>Berhane-Kontir>Yayu>Bonga), sowohl bezogen auf die Gesamtlänge als auch längenspezifisch. Gleiches galt für die hydraulische Leitfähigkeit der Äste. Innerhalb einzelner Baumkronen zeigten die jüngsten Äste jeweils die niedrigste hydraulische Leitfähigkeit. Ein Abschneiden der Wachstumszonen reduzierte die Widerstandskomponenten in primären Ästen ausgewachsener Bäume und im Spross von Setzlingen jeweils signifikant.

Die Ergebnisse des *ex-situ*-Experiments zeigten bei Austrieb und Wachstumsentwicklung hochsignifikante Unterschiede zwischen den einzelnen Kaffee-Akzessionen. Die Licht- und Beregnungsvarianten wiesen Unterschiede bei Wachstum und hydraulischen Eigenschaften, sowie der chemischen Zusammensetzung von Boden und Pflanzen auf. Die unbeschattete Variante hatte gegenüber der beschatteten eine höhere Gesamtbiomasse, ebenso die schlecht wasserversorgte gegenüber der gut wasserversorgten Variante (jeweils P<0,01). Die signifikant niedrigste Gesamtbiomasse trat bei den Berhane-Kontir-Akzessionen, die höchste bei den Harenna-Akzessionen auf. Darüber hinaus hatten die Harenna-Akzessionen höhere Werte von Blattfläche, Stammdurchmesser, Blatt-Chlorophyll, Blatt-Stickstoff und Stomatadichte. Im Vergleich zwischen Berhane-Kontir und Harenna-Akzessionen zeigten letztere einen signifikant höheren Wurzelanteil und hatten auch insgesamt den höchsten Wurzelanteil. In Übereinstimmung mit den *in-situ*-Ergebnissen zeigten die Harenna-Akzessionen die höchsten hydraulischen Leitfähigkeiten von Wurzel und Spross, allerdings auch die stärksten Schäden bei anhaltender Trockenheit, jeweils verglichen mit den Akzessionen der drei übrigen Standorte. Die Harenna-Akzessionen zeigten andererseits die stärkste Tendenz zur Stressvermeidung, etwa durch hohes Wurzel/Sproß-Verhältnis, tiefes Wurzelsystem, dickere Blätter; in ihren Blättern traten stärkere Schwankungen des

Wasserpotenzials und hohe Akkumulation von Kalium-Ionen auf. Dagegen hatten speziell die Akzessionen aus Berhane-Kontir und Bonga ein flaches Wurzelsystem und der Boden blieb bei Trockenheit feuchter. Trockenstress-Symptome traten bei Setzlingen der Beschattungsvariante etwa zwei Wochen nach der unbeschatteten Variante auf.

Die Ergebnisse dieser Arbeit zeigen sehr unterschiedliche Strategien der Kaffee-Wildpopulationen im Umgang mit Trockenstress. Die Akzessionen aus dem Südwesten Äthiopiens zeigten einen wesentlich konservativeren Umgang mit Wasser verglichen mit dem opportunistischen Umgang der Akzessionen aus Harenna. Die dargestellten Ergebnisse bilden die erste detaillierte ökophysiologische Analyse von Wildkaffee-Populationen und zeigen inter- und intraregionale Unterschiede der Morpho-Physiologie, des Wasserhaushalts und der hydraulischen Bedingungen auf. Diese Unterschiede belegen die Bedeutung der untersuchten vier Kaffeewälder als Genpools für zukünftige Züchtungsprogramme und die Notwendigkeit einer Strategie zur *in situ*-Erhaltung. Die Studie schließt mit der Ableitung von Empfehlungen für die entsprechende Nutzung der Waldressourcen in Äthiopien.

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LIST OF ABBREVIATIONS AND UNITS

Abbreviation	Description	Unit
BA	Basal area	cm^2
BD	Bulk density	$g\ cm^{-3}$
CA	Crown area	cm^2
CV	Coefficient of variation	%
FC	Field capacity	PMa/bar
K_h	Hydraulic conductance	$kg\ s^{-1}\ m^{-2}MPa^{-1}$
k_h	Hydraulic conductivity	$kg\ s^{-1}m^{-1}MPa^{-1}$
LA	Leaf area	cm^2
LAI	Leaf area index	$cm^2\ cm^{-2}$
LAR	Leaf area ratio	cm^2g^{-1}
LARMR	Leaf area root mass ratio	cm^2g^{-1}
LMR	Leaf mass ratio	$g\ g^{-1}$
LWP	Leaf water potential	MPa
OM	Organic matter	%
PWP	Permanent wilting point	MPa/bar
RD	Root density	$g\ cm^{-3}$
RGR	Relative growth rate	$cm\ time^{-1}$
R_h	Hydraulic resistance	$MPa\ m^2\ s\ kg^{-1}$
RH	Relative humidity	%
RLWC	Relative leaf water content	%
RMR	Root mass ratio	$g\ g^{-1}$
SD	Standard deviations	%
SLA	Specific leaf area	cm^2g^{-1}
SSL	Specific stem length	$cm\ g^{-1}$
SLM	Specific leaf mass	$g\ cm^{-2}$
SMC	Soil moisture content	% vol
SMR	Stem mass ratio	$g\ g^{-1}$
TN	Total nitrogen	%
WHC	Water holding capacity	% (dry wt)

1 GENERAL INTRODUCTION

1.1 Background and problem statement

The genus *Coffea* belongs to the family Rubiaceae and includes approximately 100 species (Stoffelen, 1998). The two main species of coffee cultivated on a world scale are Arabica coffee (*Coffea arabica* L.) and robusta coffee (*Coffea canephora*), which account for about 98-99% of the world coffee production. Out of this, 90% of the world coffee market is based on Arabica coffee (Cambrony, 1992; Coste, 1992; Wintgens, 2004). The center of origin and diversity for *C. arabica* is the Ethiopian high plateaus between 1,300 and 2,000 meters above sea level (m a.s.l). Since time immemorial, it has been grown in the humid montane rainforests of southwestern Ethiopia, specifically in the massive highlands of the Kaffa and Buno districts. Coffee is a perennial woody tree crop occupying the lower to middle canopy strata of the forest ecosystem. Natively, as an understorey species, Arabica coffee is a shadow-adapted plant (Coste, 1992; Demel, 1999). The cultivation of coffee is distributed throughout the world within the limits of tropical to sub-tropical regions. Hence, coffee is a tropical plant, which thrives best between the latitudes of 25°N and 25°S, but different species require very specific environmental conditions for commercial cultivation (Coste, 1992; Wrigley, 1988).

Coffee is one of the most important commodities in the international agricultural trade, representing a significant source of income to several coffee producing countries including Ethiopia. Ethiopia's economy is based on agriculture, and about 90% of the population earns its living from the land, mainly as subsistence farmers. It accounts for 50% of the gross domestic product, 60% of the exports and 80% of the total employment. In other words, agriculture is the backbone of the national economy and coffee is by far Ethiopia's most important export crop in the national economy, contributing decisively to the country's foreign currency income. It accounts for 60-70% of the total agricultural export earnings and 10-20% of the total government revenue (EEA, 2001). The livelihood of 25% of the total population directly or indirectly depends on its production, processing and marketing. Thus, as well as being an important export crop, coffee plays a vital role both in the cultural and the socio-economic life of the country. In Ethiopia, the estimated area devoted to coffee is about 400,000 ha with the average annual production amounting to about 250,000 t. Coffee is

produced in four main production systems: forest, semi-forest, cottage and plantation, which account for 10, 35, 50 and 5%, respectively (Taye and Tesfaye, 2002; Workafes and Kassu, 2000). Because of the diverse agro-ecological zones, immense genetic diversity, predominant subsistence and traditional production systems and other socio-economic aspects, Ethiopian coffee is de facto wild and organic and known for its unique quality. However, it has not yet been fully accredited, certified and offered at fair and premium prices on the world market (Taye and Tesfaye, 2002), though some attempts are being undertaken by coffee farmers' cooperative unions in Oromia and Southern Nations Nationalities and Peoples' Regional States.

Ethiopia is Africa's third largest coffee producer after Uganda and Ivory Coast, and it is currently the seventh largest coffee producer worldwide and ranked ninth in coffee export. About 50% of the total volume of coffee production is sold abroad, of which almost 30% is exported to Germany. The forest ecology and farmers' traditional production systems, which have conserved the Arabica gene pool in its center of origin, are now seriously threatened by several factors. These include, among others, increasing population pressure, expansion of farmlands, forest land-use conflicts, priority for other food and cash crops and other socio-economic factors (Demel et al., 1998; Francis et al., 2000; Paulos and Demel, 2000; Tadesse, 2003). In this regard, the importance of rainforest conservation can be viewed against the background of man-made destruction or change in about 60% of the Ethiopian forests during the last thirty years. This is a serious challenge to the remaining and fragmented forest areas (2.6%, about 2,000 km^2) with wild coffee populations (Tadesse et al., 2003). Much of the remaining forested area is located in less accessible and/or relatively less populated areas of the south and southwest parts of the country (Paulos and Demel, 2000).

The volatizing coffee price in the international market has also aggravated the reduction of the area devoted to cultivation of the adapted coffee landraces. 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. Moreover, no or little management practices have been applied to boost coffee productivity mainly because of slumped prices and coffee crises in recent years. In other words, growth conditions for coffee plants are far from optimal and suitable environments are lacking, resulting in either severe competition or inefficient utilization of the available above-

and below-ground resources. Proper growth and development of coffee plants cannot be expected on abandoned, mismanaged fields or with little consideration regarding matching suitable coffee types and environmental factors.

Besides the escalating deforestation rates primarily due to settlement projects, agricultural land-use pressures and fluctuating coffee prices, the regional climatic result of deforestation is becoming one of the major problems for the coffee industry and the existence of wild coffee in the montane rainforests of 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 enormous variations among Arabica coffee populations, demonstrating the long lasting environment-plant relationships. This calls for special attention to growth and hydraulic characteristics in order to tailor site-specific conservation options. The resource-use efficiency of coffee trees remains little studied, and detailed ecophysiological information is missing. Hence, investigations on responses of diverse coffee accessions under specific environments with a special emphasis on soil drought stress and determination of coffee water requirements for the different production systems are amongst the high priority research areas identified and documented in the strategy and priority of the national coffee research (EARO, 2002).

The ever increasing demands for forest products and forestland together with the growing human population is putting intolerable pressure on the remaining forest fragments (Paulos and Demel, 2000). The increasingly threatened genetic resources of Arabica coffee urgently call for actions before the status is irreversible. For this, understanding plant-environment interactions is crucial to design site-specific corrective management options and sustain utilization of the immense Arabica coffee gene pools. It is, therefore, imperative to investigate the ecophysiological diversity of wild coffee populations in the remnant forests of the country with the view to contribute to concepts of the project: conservation and use of the wild populations of *Coffea arabica* in the montane rainforests of Ethiopia (CoCE)1. The concepts should be based on the conservation of the montane rainforests as the natural habitat of the wild coffee populations and the forest coffee systems as the traditional use of the wild coffee

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[1] The main objective of the CoCE project is to assess the genetic diversity and the economic value of the Ethiopian coffee gene pool and to develop concepts of model character for conservation and use of the genetic resources of *Coffea arabica* in its center of origin and diversity in Ethiopia.

populations. The CoCE project has six sub-projects, of which subproject 3 addresses the ecophysiological amplitude of wild coffee populations to drought stress along a rainfall gradient in the region. This study is part of subproject 3.

1.2   Hypothesis of the study

It was hypothesized that a climatic gradient would promote regional differentiation 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 drought stress. The hydraulic conductivity of the roots and shoots are among the key ecophysiological factors 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.

1.3   Scope and objective of the study

As mentioned earlier, wild coffee populations colonize most potential and marginal sites along the climatic gradients of the major coffee growing areas with immense ecophysiological diversity in terms of adaptation to biotic and abiotic stresses. However, information on the mechanisms underlying the adaptation of coffee plants to specific environmental stress, including drought stress, is lacking in the country. In this study, four Afromontane rainforests with the occurrence of wild coffee populations spanning a broad climatic gradient were selected. The aim of this study was to characterize the growth and hydraulic properties of Arabica coffee to provide the first detailed ecophysiological analysis for conservation and use of wild coffee populations in Ethiopia. The results could support the design of forest resource management concept or transfer ecophysiologically desired plant traits through breeding programs. If coffee populations or accessions with outstanding drought adaptability in terms of growth architecture and hydraulic conditions could be identified, this would be an important argument to preserve and use the wild Arabica coffee populations by the protection of the respective montane rainforests in Ethiopia. Within the framework of the overall objectives of the CoCE project and the aims of subproject 3, the specific objectives of this study were therefore:

1. To describe the prevailing climatic gradients and soil conditions both under field and nursery conditions;

2. To analyze and compare the variability in morphological and physiological growth characteristics of wild Arabica coffee trees and seedlings;

3. To assess seasonal and diurnal changes in plant water relations in mature and young wild coffee trees;

4. To examine the responses of seedlings of wild coffee accessions to contrasting light and drought stress conditions;

5. To analyze the relationships between growth architecture and hydraulic characteristics of wild Arabica coffee populations and suggest future research areas for coffee forest management and use of wild coffee in Ethiopia.

1.4   Thesis structure

The study was conducted both under field (*in-situ*) and nursery (*ex-situ*) conditions. The thesis is organized into nine chapters. It starts with a general introduction, which includes background and problem statement, and scope and aims of the study. Chapter 2 elaborates the state-of-the-art of morphological and physiological aspects of Arabica coffee, its ecological requirements and plant-water relations. The study areas and the general methodology are described in Chapter 3. The *in-situ* experiment is described in Chapters 4 and 5 and the *ex-situ* experiment is presented in Chapters 6 and 7. Accordingly, in Chapter 4, the growth architecture of wild coffee trees is discussed. Water relations and hydraulic characteristics of wild coffee trees are dealt with in Chapter 5. Seedling germination and early growth vigor, morphological and physiological characteristics like dry matter production and partitioning patterns, growth rates and response to light regimes are addressed in Chapter 6. In Chapter 7, the water relations and hydraulic characteristics of coffee seedlings including sensitivity to drought stress, loss of hydraulic conductance, and rate of recovery from drought stress upon rewatering, influence of environmental stress (irradiance and soil moisture) on soil-plant chemical composition, hydraulic properties and leaf stomatal characteristics of coffee seedlings are described. Details on methods and data analysis are presented in the respective chapters. Chapter 8 focuses on the overall summary of the findings. The final Chapter 9 provides general conclusions and recommendations for further research.

2   STATE-OF-THE-ART

2.1   Morphological and physiological features of Arabica coffee[2]

2.1.1   Morphology of Arabica coffee

Arabica coffee (*Coffea arabica* L.) is the only self-fertile species of the genus *Coffea* (Coste, 1992; Wrigley, 1988). It is isolated from other species and naturally only occurs on the montane rainforests of Ethiopian. Its shoot and root morphological growth characters have been described by several authors (Cambrony, 1992; Masaba, 1998; Wintgens, 2004; Wrigley, 1988). Schematic representations of shoot (Figure 2.1) and root (Figure 2.2) systems are presented below. A well known feature of Arabica coffee is the existence of two types of branches: orthogeotropric, commonly called suckers, which grow vertically, and plagiogeotropic branches, commonly called primaries, which have different orientation angles in relation to the main stem. Primary branches give rise to secondary branches, which in turn split to tertiary branches and that also branch to form quaternary branches (Wintgens, 2004). The typical root system of a mature Arabica coffee tree consists of a taproot, axial vertical roots; lateral roots, some of which are more or less parallel to the soil surface (surface plate roots) and other deeper roots that ramify evenly in the soil and sometimes become vertical, feeder bearers evenly distributed, and feeder-borne roots at all depths. The horizontal and vertical growth of coffee roots can be influenced by plant, environmental and soil factors. Soil conditions include soil texture, depth, reaction and soil moisture (Wrigley, 1988). In this study, the morphology of shoot and root growths of young and mature wild Arabica coffee trees were studied and discussed in relation to hydraulic conditions in nursery and field conditions.

Arabica coffee is primarily reproduced and distributed by seeds. Buds that will develop into flowers are usually induced 4 to 5 months before anthesis. Depending on temperature and atmospheric humidity, the time between breaking of the dormancy and anthesis may vary from 4 to 10 days. Flower buds start to wither after 2 days and its all parts drop except the ovaries. It takes 7 to 9 months for coffee fruits to mature, depending on the climatic conditions and coffee cultivars. The seed consists of a horny

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[2] Unless and otherwise stated, coffee refers to Arabica coffee of Ethiopian origin, specifically the wild Arabica coffee populations in the studied montane rainforests (Harenna, Bonga, Berhane-Kontir and Yayu) of Ethiopia.

endosperm containing an embryo, which is wrapped in two husks: the outer parchment and the silver skin just underneath. Depending on the climatic conditions in the area, the coffee plant takes approximately 3 years to develop from germination to first flowering and fruit production (Coste, 1992; Wintgens, 2004; Wrigley, 1988).
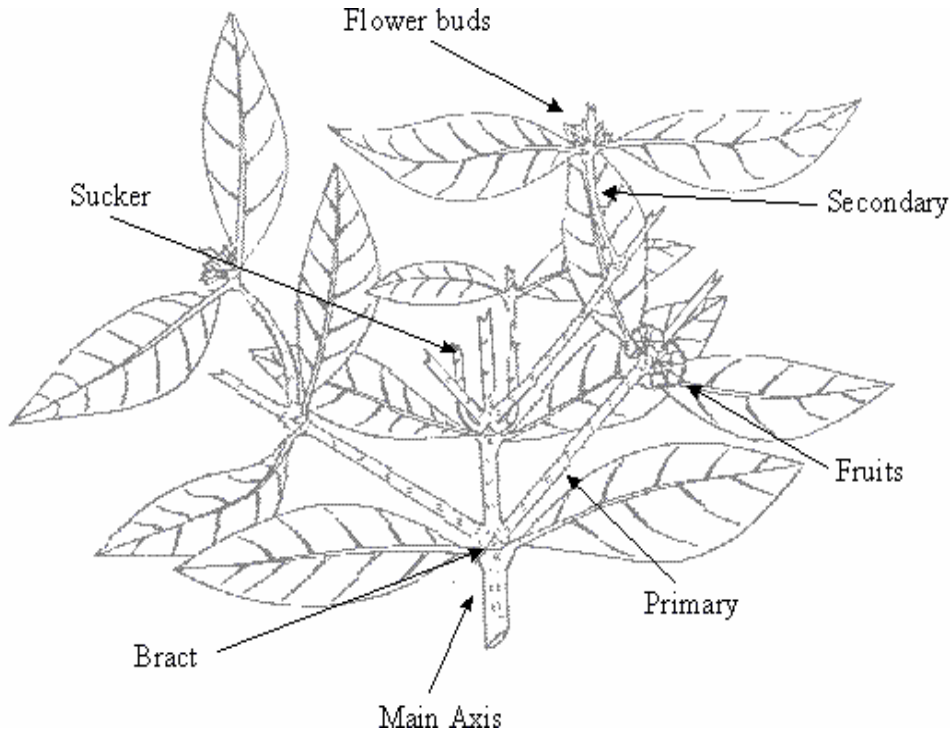
Figure 2.1   Shoot morphology of mature Arabica coffee tree
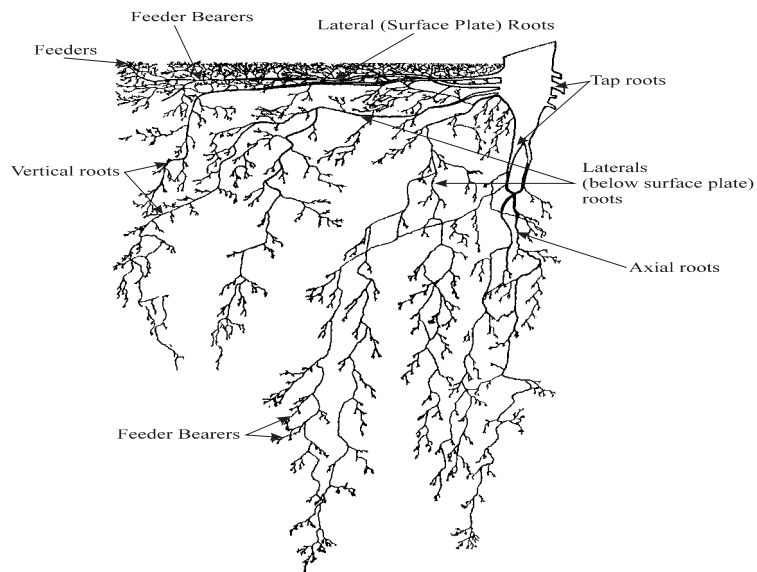
Figure 2.2   Root system of mature Arabica coffee tree

2.1.2   Physiology of Arabica coffee

In its country of origin, Arabica coffee materials have been grouped into three broad canopy classes of open, intermediate and compact types having different shoot and root growths (Yacob et al., 1996). The specific morphological differences of coffee reflect the hydraulic architecture of the plants, through their influence of the boundary layer resistance as well as by the determination of the hydraulic resistance for the soil-root-shoot-leaf system (Meinzer et al., 1990b; Tausend et al., 2000b). Shade trees (Tesfaye et al., 2002) and spacing patterns (Taye et al., 2001) are known to influence the productivity of coffee plants. However, information on the water economy of these practices is insufficient.

The internal water balance of plants is guided by the relative rates of water absorption and water loss (Lambers et al., 1998). Leaf water potential was found to be the most suitable technique for assessing the internal water balance. When soil moisture is depleted, root resistance decreases. Plants attempt to maintain a water balance at decreasing soil moisture by stomatal closure, by increasing permeability to water in the root zone, or both. The leaf petiole was found to have the highest resistance to water followed by the root. Stomatal resistance was found to follow the pattern of leaf water potential. Applications of nitrogen and potassium fertilizers have been found to improve drought resistance (Coste, 1992; Wrigley, 1988). The reasons given were that potassium participates in many enzyme synthesis processes, which enhance drought resistance, and that potassium normally works in conjunction with nitrogen in most processes. When water is plentiful, stomatal resistance is low in plants that are high in nitrogen (Lambers et al., 1998).

In coffee, the internal water balance is influenced by soil moisture, soil type and root resistance. This balance has been shown to serve as a useful index in monitoring the irrigation requirements of the coffee crop (Kumar, 1979). Coffee trees do not appear to suffer in respect of absorption of major elements and carbon assimilation when soil moisture level is at 55% of field capacity. At around 45% of field capacity, growth is minimal, although the processes mentioned above proceed almost normally (Kumar, 1979). It is also known that when water potentials fall below -2.0 MPa, photosynthetic rates are severely reduced; therefore, when the water potential lower than this value, the crop should be irrigated.

In Kenya, wilting was observed in coffee when relative turgidity was about 87% or lower (Kumar, 1979). Stomatal aperture has been closely related to soil moisture. Stomatal aperture was also reduced at high radiation levels and during the dry season even when the plots were irrigated, confirming the dependency of stomatal aperture on temperature as well as soil moisture. Stomatal movement is controlled by internal factors, for example, the presence of monovalent ions such as sodium and potassium increased the pore size, kinetin and ATP induced opening and 2 pyridyl-hydroxy methane sulphuric acid induced stomatal closure. Nitrogen fertilizer was found to increase stomatal opening under low soil moisture (Coste, 1992; Wrigley, 1988).

The influence of drought stress on flushing and blossoming of mature Arabica coffee has been demonstrated by introducing irrigation after a few months of drought (Gibramu and Taye, 1994). Irrigation stimulated flushing, increased the growth rates and stomatal aperture opening and also broke bud dormancy, which resulted in blossoming. Flushing and flowering were also induced by a rapid reduction in temperature provided there was enough moisture in the soil. It was observed that dormancy could be broken without the plants being in direct contact with water. Flower-bud development was observed to be more rapid in trees maintained at field moisture capacity using irrigation. Presence of old leaves was found to inhibit internode extension. Nutrient levels also affected apical dormancy and regeneration. For example, nitrogen was observed to play an important role in the emergence of primaries, while phosphate and potassium did not have significant effects (Wrigley, 1988).

2.2   Ecological requirements of coffee

Coffea arabica, one of the economically most important crops worldwide, occurs naturally in the undergrowth of montane rainforests of Ethiopia. In natural environments, limitation of single resource is uncommon and plants must simultaneously cope with a range of suboptimal resources. Understanding the response of coffee plants to the environment is imperative to circumvent environmental stresses and to target future corrective management alternatives, because coffee trees cannot grow if certain limits of these conditions are not met or if the coffee trees are more sensitive to the prevailing limiting climatic conditions. The growth of coffee is affected by several factors including drought, temperature, photoperiod, water logging and

leaching of nitrates by high rainfall. In Ruiru, Kenya, leaf growth occurs most rapidly during the wet season, with larger leaves produced than during the dry season. In Brazil, more leaves are produced on lateral branches in the hot, rainy season than in the dry, cool season. The rate of leaf expansion, as well as final size of leaves follows a similar trend, indicating the plant's inherent growth characteristics (Coste, 1992; Wrigley, 1988). As to the ecological requirements, climate and soil are ecological factors affecting coffee cultivation. The major climatic factors include temperature, water, light and wind (Coste, 1992) and thus are reviewed in the following.

2.2.1   Temperature

Arabica coffee can withstand fluctuations in temperature, provided that they are not too extreme. The ideal average temperature ranges between 15 and 24°C though it can tolerate temperatures much below or above these limits for short periods (Wrigley, 1988). Physiological processes can be influenced by increases in temperature above 30°C, especially if the air is dry. Coffee growth and fruiting can also be easily affected by physiological problems due to temperature drops, particularly with increased altitudes. In general, Arabica coffee does best at higher altitudes and is often grown in hilly mountain areas (Cambrony, 1992; Coste, 1992; Wrigley, 1988). As altitude relates to temperature, *C. arabica* can be grown at lower levels further from the equator, until limited by frost.

2.2.2   Water

Growth and development of coffee plants are dependent on internal, ecophysiological and climatic factors like moisture, temperature and soil factors (Cambrony, 1992; Wrigley, 1988). In terms of importance, rainfall is the second most limiting climatic factor, after the ambient temperature. Water is required for the manufacture of carbohydrates, to maintain hydration of protoplasm, and as a vehicle for the translocation of carbohydrates and nutrients. Soil moisture level also influences plant growth indirectly by its effects on the behavior of soil micro-organisms. At extremely low or high moisture levels, the activity of organisms responsible for the transformation of nutrients into plant-available forms is inhibited (Brady and Weil, 2002).

Coffee plants cannot tolerate water logging and extended drought conditions. Growth is suspended during drought stress and resumed upon its elimination. Drought also has profound effects on growth, yield and quality. The first effect of the stress can be a loss of turgor that affects the rate of cell expansion and ultimate cell size, i.e., loss of turgor is probably the process most sensitive to drought stress. The result is a decrease in growth rate, stem elongation, leaf expansion, and stomatal aperture (Hale and Orcutt, 1987). Extreme lack of water also affects cell division and reproductive development (Williams, 1971). The effect ranges from flower bud initiation and development to fruit or seed maturation and germination (Kramer, 1983). The work done by Mulualem (1997) showed that cell and organ enlargements were inhibited in indigenous tree species due to water deficits. In seedlings subjected to severe drought stress, shoot growth is much slower, shoot elongation often ceases (reduces) at midday, and shrinkage occurs in the lower parts of the stem. Furthermore, leaf area is reduced following water deficits, thus decreasing the amount of photosynthate available for growth. Coffee roots cannot tolerate water-logging conditions and will not grow near permanent water tables. Roots in water-logged soils have no root hairs and are swollen and abnormal in appearance (Wrigley, 1988). Optimum moisture levels and low to medium soil bulk densities are necessary to enhance healthy root and shoot growth of coffee seedlings (Taye et al., 2002b).

Arabica coffee needs an optimum total annual rainfall of 1,500 to 1,800 mm that is evenly distributed over the growing period of 8 to 9 months. The suitable coffee growing agro-ecological zones of Ethiopia have different ranges of altitude (800-3,200 m a.s.l.), temperature (11-26°C), rainfall (500-2,200 mm) and length of growing period (181-300 days) in terms of soil moisture availability (EARO, 2002; Paulos and Tesfaye, 2000). Coffee can also be grown in warm lowland areas with enough moisture, but may not be potentially productive. Generally, the minimum requirement of annual precipitation is about 1,000 mm distributed over the length of the growing period. Otherwise, supplementary irrigation is required for the cultivation of coffee. Hence, it is important to consider both the amount and the distribution pattern of rainfall in relation to the requirement and critical growth stages of a coffee plant.

Coffee shows substantial drought resistance and requires a period of reduced water availability to trigger phenological events such as floral bud break (Alvim, 1960).

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This has led to efforts to identify water deficit thresholds required to synchronize flowering (Crisosto et al., 1992). A dry period of 3-4 months is also physiologically important to break bud dormancy and trigger the reproductive growth processes (Alvim, 1960; Wrigley, 1988). Flowering remarkably coincides with the onset of the rainy season. For this, an about 20 mm rain shower is enough to flush flowering, but the subsequent availability of soil moisture is crucially important for the normal development of flowers and fruits. Flowering may occur once or twice a year depending on the rainfall patterns (uni-modal or bi-modal). However, the water requirement of a coffee plant also depends on climatic variables (atmospheric humidity, light, wind and cloud cover), soil properties, cropping patterns and management regimes. In Ethiopia, coffee is mostly grown under shade trees and in association with other economical crops in different cropping patterns and agro-forestry systems, mimicking the natural habitat of coffee (Taye and Alemseged, 2004; Wetsphal, 1975; Wrigley, 1988).

Where the rainfall distribution is uni-modal, there is one major flowering and thus one period, usually lasting from three to four months, during which the crop matures and can be harvested. With a bi-modal rainfall pattern, there are two flowering and two major harvest periods. The rainfall periods, which are in different months north and south of the equator, approach and overlap in equatorial regions, in which there are typically two flowerings (Coste, 1992; Clifford 1985; Wintgens, 2004). Atmospheric humidity has a pronounced effect on the vegetation of the coffee tree, as the intensity of transpiration depends upon the atmospheric vapor pressure deficit and the temperature. *Coffea arabica* prefers a less humid atmosphere, comparable to that of the sub-temperate Ethiopian high plateaux. The humidity level during the dry season is important and the highly suitable areas have average values of 40-50%, as high humidity reduces the stress on the plants and extends the rainless period through which the plants will survive without damage. The amount of water supplied by the morning dew represents a significant contribution to the amount of water present in the foliage, particularly in the dry season (Cambrony, 1992; Clifford, 1985; Wrigley, 1988).

2.2.3   Light and wind

In its natural habitat, coffee is found in shaded or semi-shaded situations. Its response to light has caused it to be traditionally considered a heliophobic plant requiring high,

somewhat dense cover in a plantation. Today, the cultivation of coffee in open sun is not uncommon in most coffee producing countries. It is known that coffee trees with high productivity potential are capable of high yields when they are cultivated intensively without shade (Coste, 1992). Although coffee is said to be a shade-loving plant with greater quantum utilization efficiency for photosynthesis, excessive shading or light interception by the upper two to three canopy strata of various tree species would decrease growth and productivity of the crop, as the plant spends much of its photosynthetic activities for maintenance (Yacob, 1993). On the other hand, if the light intensity is too high, there will be inadequate reaction centers in the leaves of the crop to accommodate the light energy and convert it into biochemical energy. As a result, the coffee trees excessively photorespires and eventually most of the stored carbohydrates become depleted. Consequently, the trees may suffer from a serious die-back. Besides, excessive evapotranspiration and severe drought stress, death of actively growing shoot parts, seasonal crinkling of leaves, frost damage and subsequent yield reduction are common problems observed in unshaded coffee orchards (Wrigley, 1988).

Excessively strong winds can cause physical damage to the trees. Wind increases water loss by evapotranspiration and therefore drought stress of the trees. The effect is much more pronounced when the soil-water reserves have been seasonally lessened or exhausted as in light, very permeable soils with little retentive capacity. Provision of good windbreaks is essential in exposed situations (Clifford, 1985).

2.2.4   Soil factors

Coffee does not appear to have very specific soil requirements. In fact, it performs just as well in the clay-silcaceous soils of granite as it does on soils of volcanic origin with diverse characteristics or even on alluvial soils. Water-logging will reduce yield by a substantial amount and kill trees if it is prolonged. Texture and depth of the soil are, therefore, extremely important factors. Coffee tree is capable of extending its root system considerably. It requires an effective depth of greater than 150 cm. This characteristic enables it to exploit a considerable volume of land and to thus offset a relative lack of fertility. Highly suitable areas had high soil organic matter (>3%) content. With regard to soil pH, a slightly acid soil is preferred. The best conditions are between pH 5.3 and 6.5. However, there are also highly productive coffee plantations

on soils that are nearly neutral (pH 7.0) (Clifford, 1985; Coste, 1992; Paulos, 1994). Nitrogen is the most important single element affecting the growth of roots. However, shoots lack nitrate reductase and thus cannot utilize nitrate. Phosphorus is an important element in shoot growth and leaf initiation. Thus, when shoot growth is more needed than root growth, phosphatic fertilizers should be applied to encourage faster growth of suckers.

2.3   Plant-water relations

It is axiomatic that water is essential for plant growth. Without copious quantities of water, plants will cease growing and ultimately die. Water constitutes more than 80% of the fresh weight of actively growing shoots of woody plants forming a continous liquid phase from the root hairs to the leaf mesophyll cells (Joly, 1985). Living cells require a high degree of internal water saturation to function efficiently, and tissue water content can fluctuate only within narrow limits if growth and development are to continue unimpaired. Life cannot exist without water, and in plants water is necessary for the maintenance of turgor, for the conduct of normal metabolic functions, and as a medium for the transportation of nutrients and assimilates (Hopkins, 1995; Salisbury and Ross, 1992). It is important to a plant because it forms the milieu in which vital biological reactions occur, and its hydraulic properties drive cell expansion and provide structural support (Hopkins, 1995). Water acts as a solvent in most physiological processes that take place in protoplasm. In addition to this, water molecules themselves participate in many chemical reactions such as the processes involved in photosynthesis or fat break down (Hopkins, 1995; Salisbury and Ross, 1992). Furthermore, the macromolecules of protoplasm, including the nucleic acids, starch and pectin, form a unique structure by being associated with water molecules (Salisbury and Ross, 1992).

Shoot systems of terrestrial plants steadily lose water to the surrounding air and this water has to be replaced from the soil. Transpiration, water uptake and conduction of water from the root to the transpiring surfaces are inseparably linked processes in the water balance. The water vapor deficit of the air is the driving force for evaporation and the water in the soil is the crucial source of water supply. The water balance is maintained by a continuous flow of water and is thus in the state of dynamic equilibrium (Hopkins, 1995; Larcher, 2003; Salisbury and Ross, 1992). Soil water is

necessary to keep plant nutrients in solution, maintain the important soil micro-organisms in an active state and allow normal root growth, development and functions. The rate and direction of root growth are determined, principally, by soil water gradients; roots grow from areas of low water concentration to areas of high water concentration and they are unable to grow through zones of dry soil. Soil moisture level also has a pronounced effect on the uptake of plant nutrients. Low levels of extractable water in the root zone retard nutrients availability by impairing each of the three major processes, i.e., (1) diffusion, (2) mass flow and (3) root interception. There is an increase in nutrient uptake when extractable water is high rather than low (Brady and Weil, 2002).

Water infiltrates the soil following precipitation and gradually percolates to the groundwater table. The rate of percolation depends on the nature of the soil and the distribution of pore sizes within it. The soil water content at saturation is higher in fine-grained soils and in soils with high colloid contents and those rich in organic substances compared to soils with coarse texture, low in colloids and soil organic matter. The values increase in the following order: sand, loam, clay, and raw humus (Larcher, 2003). The transfer of water from the soil through plants to the atmosphere is considered in terms of water potential gradients. It is the thermodynamic state of the water rather than the total quantity that influences the biochemical activity of the protoplasm. The water potential is therefore the work necessary to raise the bound water to the potential level of pure water (Larcher, 2003). Movement of water depends on the existence of gradients of decreasing water potential from higher to lower water potential (Hopkins, 1995; Russel, 1977). Water potential in the atmosphere is much lower than water potential in the leaf, causing the atmosphere to be the sink for water lost by plant transpiration. The water-conducting tissue of the leaves (xylem) is connected to the xylem of the stem and the xylem of the stem is again connected to the xylem of the root; a water potential gradient develops between leaves and stems, and between stems and roots due to loss of water by transpiration. The gradient established between the roots of transpiring plants and the soil causes water to move from the soil into the roots (Foth, 1990; Larcher, 2003). The water potential in a plant is the sum of turgor potential, osmotic potential, and matric potential. The turgor potential is created by water molecules bombarding the surfaces of membranes and cell wall, retaining water in a

closed system such as a vacuole; osmotic potential is created by dissolved particles, and matric potential is the water adhering to surfaces and interfaces. Turgor potential is the first component of water potential to be affected by drought stress (Hale and Orcutt, 1987). Hence, soil water helps to facilitate the absorption of minerals by plants while plant water content helps in maintaining the right type of turgidity for growth. Kumar (1979) reviewed various aspects of soil-plant-water relations in coffee. The movement of water from the soil into the roots is mainly affected by the extent to which the roots spread (Coste, 1992; Wrigley, 1988). The coffee tree has a limited surface area but widely spreading surface roots, and therefore has generally low rates of water uptake. The uptake of water and thus the optimal soil temperature for Arabica coffee was found to be between 20° and 28°C. This temperature range can be extended where mulching, irrigation and shading are practiced, because they can reduce temperature variations (Kumar, 1979).

Roots form an intimate and dynamic association with the soil in which they grow and from which they extract nutrients and water (Hale and Orcutt, 1987; Hopkins, 1995). The process of transpiration is controlled partly by physiological factors such as leaf area and the size, density and orientation of stomata. It is also to a great extent influenced by climatic conditions (wind spread, temperature, humidity and turbulence) and solar radiation (Salisbury and Ross, 1992). It may also be controlled by the hydraulic system of roots and shoots. Most of the active roots are found to be close to the trunk (within a radius of 83-120 cm) and at a depth of 45-75 cm. Studies on the seasonal distribution of functional roots of coffee indicate that regrown roots were healthy and consisted of feeders, feeder-bearers and laterals. Root growth was observed to occur in fruiting and non-fruiting, irrigated and non-irrigated trees from the long rains to the beginning of the short rains, after which extension growth was at a slow rate. Tips of functional roots on trees with a crop had a higher uptake than those on trees without a crop, suggesting that fruiting load may stimulate the activity of roots (Wrigley, 1988).

2.3.1 Plant response to drought stress

The definition of plant drought stress depends on the objectives of the observer. For farmers, foresters and horticulturists, for instance, stress is viewed as reduction in quantity and sometimes quality of economic yield. For physiologists, however, drought

stress is evaluated in terms of loss of turgor, reduction in growth, closure of stomata, inhibition of processes such as photosynthesis and disturbance of the normal course of other processes like nitrogen and carbohydrate metabolism (Salisbury and Ross, 1992). Drought results in sustained plant moisture stress as a result of decreasing water potential difference between roots and soils, and increasing resistance to water movement toward roots through drying soil (Kramer, 1983), while transient drought stress often develops on hot sunny days in the absence of drought. Internal plant water deficits develop whenever evaporative demand is higher and transpiration losses are greater than the water supply available to the leaf (absorption). It should also be long enough to cause a decrease in plant water content and sufficient loss of turgor to cause a decrease in cell enlargement and perpetuation of various essential physiological processes (Hopkins, 1995; Williams, 1971).

Stress of the shoot is a measure of the gradient of water between the root and the leaf (Williams, 1971). In hot and sunny weather as transpiration increases rapidly in the morning, water usually is removed from the leaves and adjacent sap wood, since the resistance to removal of water from cells of those tissues is lower than the resistance to intake through the roots. With increasing stress, resistance to movement through the xylem may be increased by cavitation. Consequently, water absorption of plants often lags behind transpiration during the morning and early afternoon. The resulting midday water deficits are often severe enough to cause temporary wilting, stomatal closure, reduction in photosynthesis and even shrinkage of stems and fruits. The severity and duration of midday drought stress, therefore, vary in different parts of plants. The exposed leaves are subjected to significant water deficit on almost every hot and sunny day. Therefore, exposed leaves are expected to transpire more than shaded leaves (Hale and Orcutt, 1987). Later, as the soil gets drier, the soil water potential progressively decreases until it approaches the plant water potential. As a result, absorption becomes too slow to replace the water loss of the previous day and permanent wilting develops.

Plants are often subject to periods of soil and atmospheric water deficit during their life cycle. Plant responses to water scarcity are complex, involving deleterious and/or adaptive changes, and under field conditions these responses can be synergistically or antagonistically modified by the super imposition of other stresses (Chaves et al., 2002). Moreover, both physiological and growth response to drought

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stress varies with the species, the stage of the life cycle of the plant and also with the physiological mechanism through which it is mediated. According to the literature (Hale and Orcutt, 1987; Salisbury and Ross, 1992), responses of plants to drought stress can be reduction of leaf and shoot growth, photosynthetic rate, water potential and cell turgor pressures; alteration of spatial relations in the plasmalema, tonoplast and organelle membrane; change in structure or configuration of macromolecules, closing of stomata and differences in the distribution of roots. Furthermore, stress responses are typically complex, are exhibited by various parts of the plant, and may involve such stress hormones as abscisic acid (ABA) and ethylene, which are distributed throughout the plant (Hopkins, 1995). It is also pointed out that plant responses are classified as drought escapers, water spenders, water collectors, water savers and dehydration tolerance (Hale and Orcutt, 1987; Salisbury and Ross, 1992). A study on woody and herbaceous species indicated that changes in root:shoot ratio or the temporary accumulation of reserves in the stem is accompanied by alterations in the nitrogen and carbon metabolism (Chaves et al., 2002).

Similar to all other plants, growth of coffee is driven by moisture supply. In several coffee growing countries, drought is considered to be the major environmental stress affecting coffee production. The physiology of plant responses to drought stress is complex, showing different modifications following soil drying. Furthermore, particularly in the tropics, drought episodes are aggravated by both high solar radiation and temperature, so drought should be accounted for as a multidimensional stress (DaMatta, 2003 cited by DaMatta, 2004b). Change in leaf color, shape, texture and specific leaf area, rate of photosynthesis, development of buds (both vegetative and flower buds), and closing of stomata are the responses of coffee plants to drought stress. As pointed out by Yacob et al. (1996), specific leaf area, leaf dry weight and leaf moisture content are indirect indicators of drought resistance in coffee.

2.3.2   Soil moisture and transpiration

Soil is a very complex medium, consisting of a solid phase comprised of inorganic rock particles and organic materials, a soil solution containing dissolved solutes and a gas phase generally in equilibrium with the atmosphere (Brady, 1990; Brady and Weil, 2002). The inorganic solid phase of soils is derived from a parent rock that is degraded

by weathering processes to produce particles (sand, silt and clay) of varying size. Soil moisture content at permanent wilting point varies between soil types, and is relatively low for sand and high for clay. Loam soils fall between these two extremes, depending on the relative proportion of sand and clay. Regardless of soil type, however, the water potential of the soil at the permanent wilting point is relatively uniform at about -1.5 MPa. Although there are some exceptions to the rule, most plants are unable to extract significant amounts of water when the soil water potential is below this. In a sense, field capacity may be considered a property of the soil, while the permanent wilting point is a property of the plant (Brady and Weil, 2002; Hopkins, 1995). Several authors (Brady and Weil, 2002; Hopkins, 1995; Larcher, 2003; Prasad, 1997; Salisbury and Ross, 1992) showed that the water content of the soil between field capacity and the permanent wilting point is considered as available water, i.e., water that is available for uptake by plants. The volume of available water is high in silty loam soils, somewhat less in clay and relatively low in sand. In a dry soil, plants will begin to show signs of drought stress and reduced growth long before the soil water potential reaches the permanent wilting point.

From all the factors influencing stomatal conductance and transpiration of the coffee plants, soil moisture is the one that has been most intensively studied. Well-watered, one-year-old *C. arabica* cv. Typica plants had increased transpiration with increasing light intensity under cloudy conditions, while there was no significant increase in transpiration under sunny conditions if the plant was dried (Kanechi et al., 1995). The same authors found reduced net photosynthesis due to drought stress under controlled environmental conditions. In a field study, the coffee crop was able to maintain relatively high levels of gas-exchange activity during periods of severe drought stress (Gutierrez and Meinzer, 1994). The work done by Tausend et al. (2000a) shows that the reaction to drought stress was different for different coffee cultivars, which could be due to differences in water uptake and hydraulic conductance by the leaves causing different responses to drought stress. There are also indications for osmotic adjustments involved in drought resistance (Venkataramanan and Ramaiah, 1988). In another field study, stomatal conductance in three cultivars was found to be similar when well-watered, but decreased more in Typica and Yellow Caturra than in San Ramon (the smallest of the cultivars, with a dense crown and higher boundary layer

resistance) when irrigation was withheld (Tausend et al., 2000b). Both environmental variables and plant hormones (ABA and cytokinins) control stomatal movements (Hopkins, 1995; Salisbury and Ross, 1992).

In coffee, stomata occur only in the lower epidermis of the coffee leaf. As with most plant species, coffee stomata are usually open during the day and closed at night. Under conditions of moisture tension in the plant, widening of the stomata cannot take place because the guard cells cannot absorb water. Light, temperature, water availability, atmospheric humidity, CO_2 concentration and wind movements directly affect stomatal movements (Coste, 1992; Wrigley, 1988). The first discernable response of the stomata to the onset of drought stress is to open slightly. Consequently, water will be withdrawn from the epidermis into the mesophyll tissues, resulting in a relatively temporary flaccidity, which allows a turgor advantage for the guard cells and hence, stomatal opening. This opening phase, however, is only transient and as drought stress continues, water passes out of the guard cells. Therefore, the stomata close progressively with increasing drought stress (Martin et al., 1983) and stomatal closure occurs when the coffee leaves start to wilt (Kanechi et al., 1995). Furthermore, under normal conditions, a temporary decrease in stomatal aperture could be encountered, as midday stomatal closure is common in plants growing under tropical conditions. Coffee leaves show a decrease in stomatal opening with a deficit of only 20 or 30 mg of water per dm^2 of leaf surface and complete closure with a deficit of about 80 mg per dm^2. The quantity of water evaporated per day by a non-shaded coffee tree is approximately 6 g dm^2. Moreover, high irradiance and temperature can cause a rapid increase in transpiration, which in turn causes enough moisture deficiency to reduce stomatal aperture. In contrast, Kanechi et al. (1995) reported that both turgid and wilted coffee leaves had higher transpiration rates on cloudy than on sunny days, which means greater stomatal opening on cloudy days. However, sun-exposed leaves showed no significant increase in transpiration as light intensity increased under drought conditions. This might be explained by the stomatal regulation in response to the vapor pressure deficit, which increased due to rising leaf temperature when the leaves were exposed to direct sunlight.

According to Coste (1992), the stomata of coffee leaves were closed when the leaf water deficit reached between 18 and 30%, but the leaf dehydrated slowly and

steadily, and gradually lost turgidity until it reached the wilting point. Moreover, it is stated that very different drought-resistant capabilities in two cultivated varieties of *C. canephora* have manifested in the ability of the leaf tissues to withstand and resist a high degree of dehydration. The most resistant variety demonstrated swift stomatal closure and less active use of the water supply. Stomatal closure cuts off gaseous exchange. Therefore, photosynthesis and respiration are affected and hence, there is less dry matter production under conditions of drought stress (Williams, 1971). Transpiration and stomatal conductances are sometimes used almost synonymously. This, however, may be problematic: low wind speed, large leaves, and compact tree crowns lead to the formation of boundary layers around each leaf and around the whole crown (Grace et al., 1980). The resistances of these boundary layers to water vapor diffusion decouples transpiration from stomatal control (Jarvis and McNaughton, 1986). Relatively high air humidity within the canopy reflects the low coupling between the inner part of the crown and the atmosphere. The importance of the boundary layer decreases with increasing wind speed. When stomatal regulation of transpiration was studied in hedgerow coffee, transpiration at the crown scale increased linearly with net radiation and tended to increase with increasing wind speed. The apparent stomatal responses to wind were partially a reflection of the stomatal response to humidity (Gutierrez et al., 1994).

Additionally, the stomatal aperture of coffee leaves seems to be an adaptation of *C. arabica* to the conditions in the understorey vegetation of montane rainforests with little light and wind and well buffered against temperature change by the enveloping trees (Cambrony, 1992; Coste, 1992; Wrigley, 1988). Coffee has several times been reported to keep stomata closed at high temperatures even under conditions of sufficient water supply from the soil, thus not taking advantage of the cooling effect of transpiration. A negative correlation between leaf temperature and stomatal conductance was also found in pot experiments (Goldberg et al., 1984). According to the investigations made in Costa Rica concerning water-use efficiency and water-use strategies of *C. arabica*, $\delta^{13}C$ values provide valuable information concerning drought stress. It was shown that complete elimination of shadow during a period of dry and sunny weather led to continuous stomatal closure of *C. arabica* leaves for a period of 10 days. Leaf temperatures thus reached 35-41°C, as much as 10-15°C above the ambient

air temperature (Weidner et al., 2000). Stomata started to open only during a period of increased cloudiness and rainy weather.

2.3.3   Photosynthesis and water-use efficiency

Photosynthesis is sensitive to drought stress and can be affected in two ways. First, closure of the stomata normally cuts off access of the chloroplasts to the atmospheric supply of carbon dioxide. Second, there are direct effects of low cellular water potential on the structural integrity of the photosynthetic machinery (Hopkins, 1995). Dry matter production in any crop depends upon leaf area index, structure of the canopy, photosynthetic rate per unit of leaf area, and strength of the metabolic sinks in attracting assimilates, which is particularly important in coffee, where the fruits have been shown to be the dominant sinks. Photosynthesis in coffee exhibits all the characteristics of plants with predominantly C_3 or Calvin cycle pathways, as coffee leaves placed in darkness after a period of light produce a burst of CO_2 following photorespiration, i.e., a type of respiration activated by light (Wrigley, 1988). There are four notable features concerning the photosynthetic rate of leaves of Arabica coffee, all of which seem to reflect its recent evolution as a shade-adapted species. These include: 1) the maximum net photosynthetic rate of sun leaves are low, 2) the saturating irradiances for coffee leaf photosynthesis are low, 3) the net photosynthetic rates of coffee leaves decrease markedly with increase in leaf temperature above 20-25°C, and 4) even with the light-adapted sun leaves of coffee, the photosynthetic apparatus seems to be physically damaged by continuous exposure to high irradiance, perhaps by the disruption of photosystem II. Because there is increased mesophyll resistance, high temperature will be associated with low leaf water potentials, which cause midday stomatal closure and increase in internal CO_2 concentration.

Stomatal conductance decreases logarithmically with increasing leaf temperature and vapor pressure deficit (Kanechi et al., 1995). Parallel to this, stomatal and mesophyll conductances are decreased sensitively with decreasing water potential, indicating that both conductances contribute to decline in the leaf photosynthetic rate (Kanechi et al., 1995). Maestri and Barros (1977) reported that the maximum rate of net photosynthesis in coffee was 4.5 mg CO_2 dm^{-2} h^{-1} and that there was a midday decrease in photosynthesis. They associated this to stomatal closure induced by direct action of

sunlight, but not by leaf water relations. The complete inhibition of photosynthesis of dehydrated leaves occurred at about -3.0 to -3.5 MPa for *C. canephora* and *C. liberica*, respectively. On the other hand, *C. arabica* had still positive photosynthetic rate at about -4.0 MPa water potential and was thus more tolerant to leaf dehydration (Kanechi et al., 1995). The recent work by Tesfaye (2006) also shows considerable differences among coffee cultivars and the compact ones were significantly more tolerant to drought stress.

Even if net photosynthesis is sometimes more related to mesophyll conductance than to stomatal conductance (Kumar and Tieszen, 1980), transpiration and CO_2 assimilation are strongly coupled by stomatal aperture. The photosynthesis of sun leaves is very low compared to other C_3 species and is also lower than the photosynthesis of shade leaves (Kumar and Tieszen, 1980). There are reports of damage to the photosystem II even of sun-adapted leaves (Cannell, 1985; Nunes et al., 1993). Despite this, commercial coffee cultivars are increasingly grown in full sun and are able to out-yield shade-grown plants (Kumar and Tieszen, 1980). This leads to an inequality, as fruit production in the sun is higher and photosynthesis of leaves in full sun is reduced. About 20 cm^2 of leaf is needed to support each fruit without severely checking vegetative growth (Cannell, 1974). However, net photosynthesis of coffee leaves decreases in full sun, leading to critical imbalances within the distribution of assimilates. This may lead to early dieback of entire coffee plantations and the overbearing syndrome (Coste, 1992; Wrigley, 1988). Closely related coffee cultivars growing under identical conditions exhibited large differences in water relation characteristics, including a 30% variation in intrinsic water-use efficiency (Meinzer et al., 1990a, 1992), indicating the genetic basis for the variations.

2.3.4   Biomass assimilation and partitioning

In some cases, drought resistance is intimately connected with stomatal functioning and leaf area development. In this regard, the stomata along with cuticle thickness, protection of the stomatal aperture and leaf folding are associated with drought resistance. These qualities, however, reduce CO_2 diffusion and potential net assimilation rate (Williams and Joseph, 1970). Moreover, under drought stress in addition to the alteration of CO_2 exchange of the light-exposed leaves by changes in stomatal aperture

and by differences in resistance to diffusion of CO_2 in mesophyll cells, rates of photorespiration in C_3 plants like coffee remain high and do not decrease as rapidly as gross photosynthesis. The leaves under these conditions use carbon sources within the leaf instead of synthesizing them; the result is death from starvation if the severe stress endures (Hale and Orcutt, 1987).

In Kenya, Maestri and Barros (1977) reported that the net assimilation rate of deblossomed trees was very low during the hot and dry season and then increased in the rainy season. During the cool and dry season, net assimilation rate was as high as during the rainy season. The low values in the hot dry season were attributed to high day temperatures as well as to drought stress. Net assimilation rate of seedlings of young coffee plants has also been determined under different climatic conditions. In brief, as a result of low leaf area development, alteration of CO_2 exchange and stomatal aperture, high photorespiration and resistance to CO_2 diffusion in the mesophyll cells in C_3 plants can lead to reduced net assimilation under drought stress (Hopkins, 1995; Salisbury and Ross, 1992). The rate of net assimilation of coffee plants in the hot dry season is thus very low compared to other seasons.

Plants must have regulatory mechanisms to ensure that photosynthetic and nitrogen assimilates are allocated to various parts of the plant in ratios that provide well-balanced, whole-plant functions. For example, during the vegetative growth stage, assimilates should be distributed to leaf production and production of new roots in ratios that provide a balance between the capacity for photosynthesis and the capacity for acquisition of mineral nutrients and water. During the reproductive stage, the total number of reproductive parts should be balanced with photosynthetic capacity. Such balance points differ depending on the particular plant and environmental situations (Setter, 1992). Water deficit and other environmental factors that alter plant water relations such as high temperature might be expected to exert a substantial influence on biomass allocation. However, compared with the dramatic inhibition of photosynthesis in plants subjected to water deficit, many studies (Salisbury and Ross, 1992; Setter, 1990, 1992) indicated that the effects on photosynthate allocation are much less severe. This difference in sensitivity may be an adaptive response that allows plants to conserve water by closing stomata, while translocation of the available photosynthetic products takes out assimilates from the leaves so that sinks will continue to grow. Also temporary

reserves of photosynthate in stems, taproots or senescing leaves may be mobilized and exported into the sinks to provide a buffer of photosynthate during water deficit. As far as the competition between vegetative and sink parts is concerned, drought stress has been observed to promote flowering in coffee trees (Alvim, 1960; Wrigley, 1988).

Moreover, shoot and root growths compete for assimilates. It is often the practice to subject coffee seedlings to slight drought stress (hardening off) to increase root-shoot ratio. Drought stress often first affects leaf growth. Consequently, the arresting of this should promote root development under sufficient light conditions (Williams and Joseph, 1970). As a result, photosynthate allocation is altered to increase root:shoot ratio (Hopkins, 1995; Setter, 1992), partly due to organ-specific response to abscisic acid. Increase in ABA stimulates root elongation, whereas shoot growth is inhibited. Generally, plants have a mechanism to allocate assimilates to different parts of the plant to provide balanced whole plant functions. Water deficit stress is one of the environmental factors that alter allocation of assimilates (dry matter partitioning). Under drought-stress, the available photosynthate stored in leaves, stems, taproots and senescing leaves may be mobilized and exported to the various sink organs to supplement the limited supply of photosynthate and ensure subsequent growth and development.

2.3.5   Hydraulic characteristics

The coordination between photosynthetic capacity and plant hydraulic properties is expected in an evergreen and perennial coffee plant. In this case, xylem tissues serve several biological functions including mechanical support and vascular transport. Because the relative importance of these functions varies according to branch location, there may be some measure of order in the structure of the internal water transport system and its relationship to the morphology of a tree crown. Long distance transport of water and nutrients is a vital function of the xylem. A practical measure of the xylem's hydraulic supply capacity is leaf-specific conductivity (Zimmermann, 1978). For example, the leaf-specific conductivity of a stem segment can be used to relate the average transpiration water loss from leaves supported by the segment to the decline in water potential per unit path length within the segment. Thus, the distribution of leaf-specific conductivity within a tree influences patterns of water potential throughout the

crown and can impose constraints on such physiological processes as transpiration and photosynthesis (Shumway et al., 1993; Yang and Tyree, 1993). It is becoming increasingly evident that whole-plant hydraulic resistance or conductance can limit whole-tree performance measured in terms of the rates of transpiration, carbon gain and growth. Plant hydraulic resistance is the proportionality constant between evaporative flux density (transpiration) from leaves and the water potential difference between the soil and leaf needed to maintain the evaporative flux density. The relationship is based on a hydraulic model called the soil-plant-atmosphere continuum model and the cohesion-tension theory (Tyree and Zimmermann, 2002).

Large differences among five coffee cultivars were found when measuring the rates at which leaf water potential and gas exchange activity declined when irrigation was discontinued (Meinzer et al., 1990b). Such apparent differences between regulations of transpiration among cultivars are possibly governed by divergent hydraulic architecture rather than stomatal physiology (Tausend et al., 2000a). During a drying experiment, 50% of the leaves were lost, but nearly constant photosynthetic characteristics on a unit leaf area basis were maintained (Meinzer et al., 1992). This suggests that maintenance of overall photosynthesis based on a smaller total leaf area might constitute a major mode of adjustment to reduced soil moisture availability in coffee. Stomatal conductance and transpiration have often been found to positively correlate with the hydraulic conductance of the soil-root-leaf pathway (Küppers, 1984; Sperry and Pockman, 1993). Electrical conductance of the leaf surface was found to correlate with stomatal aperture (Burkhardt et al., 1999). Possibly, there are also cultivar-specific water-potential set points, which trigger rapid stomatal closure (Tausend et al., 2000b). This indicates the usefulness of the search for genetically based properties controlling hydraulic conductance and the adaptation to drought stress.

While the xylem has been regarded for a long time as a system of inert pipes, very recently evidence was provided that plants may regulate their internal flow regime with the xylem. Increasing concentrations of ions were found to produce rapid, substantial, and reversible increases of hydraulic resistance (Zwieniecki et al., 2001). The water-reducing effect of potassium nutrition has been known for a long time (Acunda et al., 1990). Apart from affecting the osmotic potential of the cells and root pressure, it can also influence the hydraulic conductance of xylem and will be explained

in this work. Maherali and DeLucia (2000a) stated that high transpiration rates could be associated with increased specific hydraulic conductivity and increased resistance to xylem caviatation. The authors examined the effects of increased transportation demand on xylem hydraulic conductivity and vulnerability to cavitation of mature *Ponderosa pine* by comparing trees growing in contrasting climates. They also found that desert trees had higher specific hydraulic conductivity than montane trees, primarily because of larger tracheid lumen diameters.

The Hydraulic Pressure Flow Meter (HPFM) is designed to perform quantitative root and stem analysis. The hydraulic architecture of a whole shoot or of a single leaf can be represented by a resistance component. The values of the individual hydraulic resistances can be measured and the pattern of water flow and water potentials in the resistance network computed. With the HPFM method, the resistance of the root and shoot are measured separately by pressure perfusion and the results added. These help plant physiologists and agronomists to predict root and shoot progression, water potential, or soil treatment effects. The first analysis is an *in-situ* transient analysis of hydraulic conductance. The HPFM measures the flow as the water pressure increases while flowing into the root or shoot. The software then calculates the slope of the increased flow and pressure and the slope is the hydraulic conductance. The second analysis is a quasi-steady state, with constant water pressure and flow into the sample, which derives the flow pressure and conductance in a steady state environment (Tyree et al., 1994, 1995). Hydraulic conductivity of roots and shoots are highly heritable and are amongst the key functional traits to be investigated to identify drought tolerant wild Arabica coffee populations.

3   THE STUDY AREA AND METHODOLOGY

Ethiopia is located in the horn of Africa between latitudes 3 and 15°N and longitudes 33 and 48°E (Figure 3.1). There are four seasons in a year: spring (September-November), autumn (December-February), winter (March-May) and summer (June-August). The dry season is from October to May; and the wet season from June to September. According to MoA (1998), the country is divided into 18 major- and 49 sub-agro ecological zones3 providing ample opportunities and varying potentials for different crop and livestock species. High plateaus with central mountain ranges are divided by the Great African Rift Valley that runs through the heart of the country. Hence, the physical conditions and variations in altitudes have resulted in a great diversity of climates, soils and vegetation, making the country one with the richest in biodiversity in Africa in particular and in the world in general (Vavilov, 1951; Westphal, 1975). In Ethiopia, coffee grows in a wide range of climates and soil types with varying suitability ranges (EARO, 2002; Paulos, 1994). This study focuses on wild coffee populations in four minimally disturbed montane rainforests in southwest and southeast Ethiopia.

3.1   Study area

3.1.1   Field study

A total of 8 natural forests with wild coffee populations have been identified and designated (Paulos and Demel, 2000) as potential forest coffee units (FCUs) with the primary objective of *in-situ* conservation of the genetic diversity of forest coffee plants in particular and the associated flora and fauna in general. The FCUs include Berhane–Kontir, Geba-Dogi, Amora-Gedel, Boginda-Yeba, Harrena, Maji, Dawa-Tobi and Mankira (Demel et al., 1998; Paulos and Demel, 2000). Four of these forests, namely, Harenna, Bonga, Berhane-Kontir and Yayu are the focus of this study. They are geographically distant and represent the climate gradients of the remaining fragmented and undisturbed high mountain rainforests of the country with wild coffee populations.

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3 The classification of agro-ecological zones is based on the FAO classification, which defines agro-ecological zones based on rainfall, soil moisture availability and in terms of the length of the growing period derived using a water balance model and temperature conditions during the length of the growing period.

In this study, these populations are abbreviated as follows: Harenna (PI), Bonga (PII), Berhane-Kontir (PIII) and Yayu (PIV). Except Harenna in the southeast, the other forests are located in the southwest Ethiopia (Figure 3.1). They are separated by the Great East African Rift Valley, which dissects the country into southeast and northwest highlands. The study areas differ in the area of agro-ecological zones: highland (*Deiga*), medium altitude (*Weina-Dega*) and lowland (*Kolla*) (Figure 3.2a). According to Paulos and Demel (2000), these forests differ in area coverage (Harenna 15,000 ha, Bonga 5,000 ha, B-Kontir 1,000 ha and Yayu 1,000 ha), physical characteristics and forest vegetation. The rainfall gradients follow the decreasing order of Berhane-Kontir>Yayu>Bonga>Harenna with the respective long-term average yearly total precipitation values of 2,200, 1,800, 1,700 and 1,000 mm and average temperatures of 18, 18, 22 and 21°C (EMSA, 2002; Paulos and Demel, 2000).

Harenna forest

The Harenna (DoloMena) forest is located in the Mena-Angetu district (*wereda*) of the Bale zone in Oromia Regional State (Figure 3.1; Table 3.1). It is the most eastern Afromontane rainforest lying between 1,300 and 3,000 m a.s.l. The district is classified into three agro-ecological zones: highland (*Deiga* = 15.4%), medium altitude (*Woina-Deiga* = 21%) and lowland (Kolla = 63.6%) (Figure 3.2a). The forest coffee, however, occurs in lower altitudes. The soil is reddish-brown silty clay, rich in exchangeable cations. Its pH is acidic to slightly acidic. The rainfall pattern is bi-modal with short (March-April) and long (August-October) peak rainy seasons (DoA, 2004 unpublished). The rainfall distribution decreases from North to South of the district. The short rain season (*Meher*) is between September and November, the long rainy season (*Belg*) between February and June. The driest months are from December to February and June to August. The lowest (1.3%) and highest (21.8%) contributions to the annual mean total rainfall were calculated for the months of July and October, respectively. Moreover, the distribution of rainfall over the last 17 years (1984-2002) indicates that it varies from year to year, the maximum being in 1995 and 1997. Annual rainfall is low (950 mm) compared with the other three southwest sites and the average annual temperature is 18°C (Figure 3.2b; Table 3.1). According to the land-use categories,

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25.6% is covered by forest and the share of coffee is 2.1%, of which 82.3% is forest coffee (DoA, 2004 unpublished).

Bonga forest

The Bonga forest is situated in the Ghimbo district (*wereda)* of the Kaffa zone of Southern Nations Nationalities Peoples' Regional State (SNNPRS). It is located in the southwestern part of the Ethiopian high lands (Figure 3.1; Table 3.1).The area has two distinct agro-ecological zones: the highland (1,500-3,350 m a.s.l) and the lowland (500-1,500 m a.s.l) with 70 and 28% of the area, respectively (Figure 3.2a). The remaining 1.5% is below 500 m a.s.l. The area is known for high rainfall and high relative humidity and thus long growing period (almost 10 months). According to the climate data at the WushWush station (1988-1997), annual rainfall is about 1,820 mm; May and September being the wettest months, while the driest months are between December and February (Figure 3.2b). The annual mean minimum and maximum temperatures are 12 and 25°C, respectively, with an average of 19°C.

The area is characterised by rolling hills and steep slopes. The dominant soil groups (FAO/UNESCO) are Nitisols, Acrisols and Vertisols, the most common being Nitisols. This is clayey and reddish brown in color with moderate CEC, high soil organic matter and total nitrogen content (Francis et al., 2000; Murphy, 1968; Paulos, 1994), limited available phosphorus (Murphy, 1968) with medium to strong soil acidity. The forest-based farming system has an abundant forest cover with semi-domesticated coffee and spices. There are different scales of deforestation and land degradation in the area (Francis et al., 2000; Mekuria, 2005). According to Francis et al. (2000), the main problems of the farmers in the coffee-based farming systems are damage to crops by the wildlife and the coffee berry disease. The livelihood of the local community depends directly or indirectly on coffee production and forest resources.

Berhane-Kontir forest

The Berhane-Kontir (Sheko) forest is located in Sheko district in the Bench-Maji zone, SNNPRS (Figure 3.1; Table 3.1). The area is categorized into lowland (*Kolla* = 60%) and mid-land (*Weina-Dega* = 40%) in the altitude ranges of 1,500-1,800 and 1,800-2,200 m a.s.l, respectively (Figure 3.2a). The agro-ecological zone of the area represents

the hot to warm humid low to high altitude, which is transition between the highland rainforests and the lowland forests. It is humid and wet almost throughout the year, except between October and February (Paulos and Demel, 2000). The maximum rainfall is between April and September with an annual contribution of about 10%. The topography is undulating to steep. The soils are moderately acidic with high CEC (Murphy, 1968). About 82.1% of the area is forestland. This consists of natural forest, secondary vegetation and plantation forest covering 98.27, 1.62, 0.12%, respectively. This area receives the highest amount of rainfall, which can be as high as 2,100 mm per annum. The mean annual temperature is also high (22°C) with short drought period (Beining, 2006). The livelihood of the local people (indigenous) is closely linked to forest resources, i.e., timber and non-timber products (coffee, honey, spices, hunting).

Yayu forest

The Yayu (Geba-Dogi) forest is located in the Yayu-Hurumu *wereda* of the Illubabor zone, Oromia Regional State (Figure 3.1; Table 3.1). According to the department of agriculture (DoA, 2004 unpublished), the *wereda* is situated within altitude range of 1,139 to 2,582 m.a.s.l, mainly between 1,300 and 2,100 m.a.s.l, representing medium altitude (*Weina-Dega* = 85.2%). Lowland (*Kolla*) and highland (*Dega*) agro-ecologies cover of 11.1 and 3.7%, respectively (Figure 3.2a). Slopes range from 0 to >50%, mainly (40%) between 8 and 15%. About 30% of the area has a slope range from 15 to 30%, indicating the undulating nature of the land .

According to the long-term data, the *wereda* experiences mean annual maximum and minimum temperatures of 28°C and 19°C, respectively. The daily mean temperature is 23°C. The rainfall follows a uni-modal pattern with an average yearly precipitation of 1,900 mm. The long rainy season lasts from June to October, while the short rainy season is between March and April. The rain starts in May reaching a peak between June and September (Figure 3.2b). The remaining months (November-March) are relatively dry with a contribution of only 5% to the annual total. In other words, nearly 75% of the annual rainfall is concentrated between May and September and the remaining 20% falls in March, April and October. The monthly contribution to the total annual rainfall varied from 1.0 to 16.1% in February and September, respectively. About 55.8% of the *wereda* is covered by forestland. Coffee land is about 9.6%, of

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which 6.3% is wild coffee (DoA, 2004 unpublished). The forest and semi-forest coffee consists of 25 and 75%, respectively (Demel et al., 1998; Paulos and Demel, 2000).
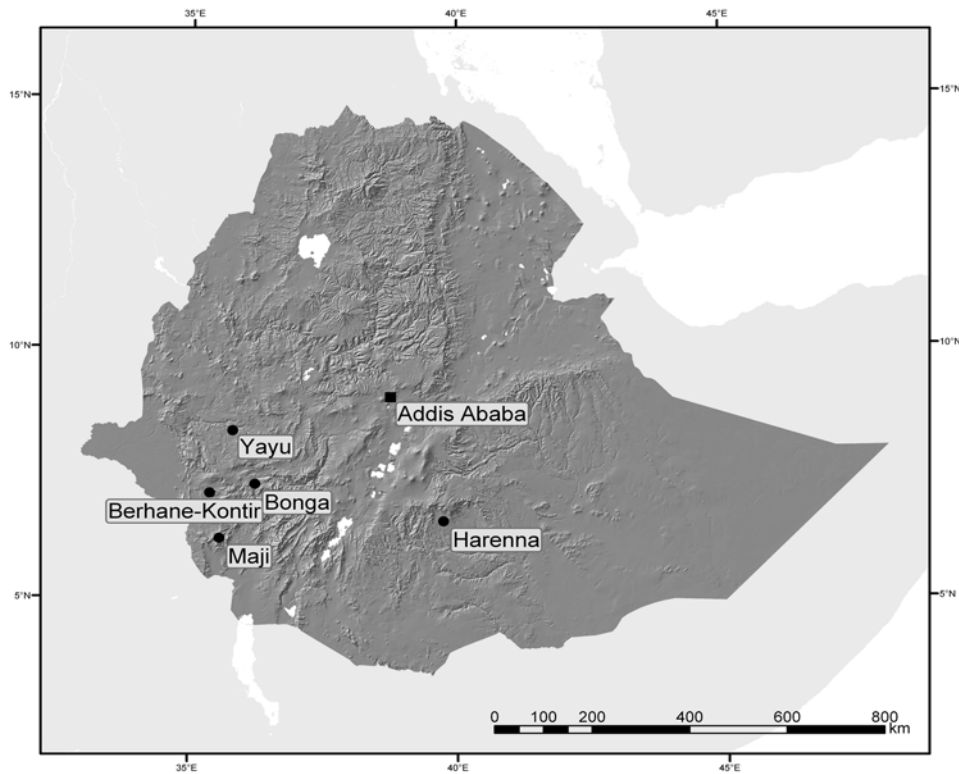
Figure 3.1   Map of Ethiopia and location of the studied montane rainforests (Harenna, Bonga, Berhane-Kontir and Yayu)
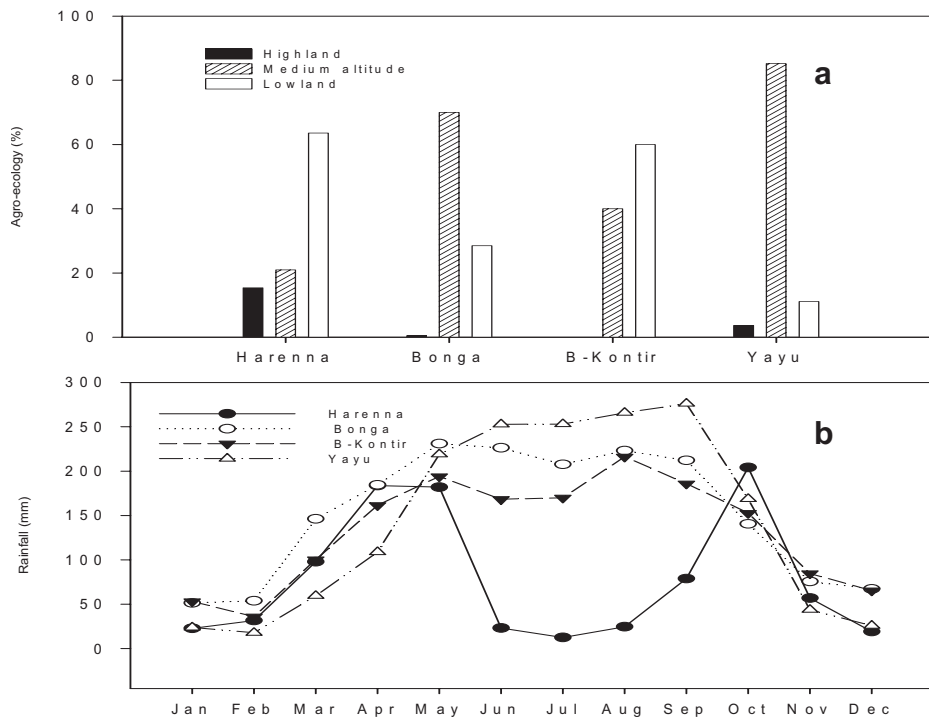
Figure 3.2   (a) Agro-ecological area coverage and (b) long-term rainfall patterns at the study montane rainforests of Ethiopia

3.1.2   Nursery study

The *ex-situ* experiment was conducted in southwest Ethiopia, at the Jimma Agricultural Research Center (JARC) (7°46'N and 36° E), 8 km west of Jimma and 343 km southwest of Addis Ababa, the capital city. The center coordinates the coffee research in the country. Here, several national and international coffee collections are maintained with which various breeding, agronomy-soil-related studies are undertaken. JARC is situated within the sub-humid tepid to cool mid highland agro-ecological zone at an altitude of 1,753 m a.s.l (EARO, 2002). According to the meteorological data of the center for a long- term (1968-2003) and the study period (2004-2005), the area receives a high amount of rainfall with a mean total of 1,556.88 mm per annum, which is distributed over 168 days, the peak being between June and September, while the driest months usually last from November to February (Figure 3.3). Analysis of the weather station for the long- term data indicated a 2% reduction in rainfall, while the minimum and maximum temperatures increased by 18 and 3%, respectively. The long- and short-term average maximum and minimum temperatures had reduced ranges during the rainy months as compared to the dry hot and cold months. The dry months usually coincide

with the cool months, December to January being the coldest months of the year (Figure 3.3). The average maximum and minimum temperatures are 26.7 and 12.8°C, respectively.
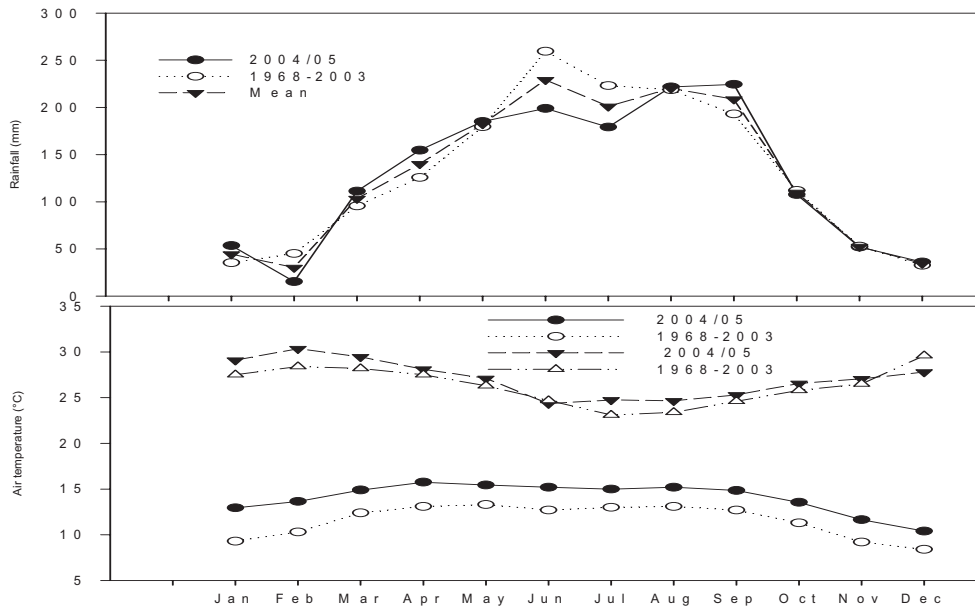
Figure 3.3   Average monthly rainfall and temperatures at Jimma Research Center for long term (1968-2003) and study period (2004/05). Minimum temperature (short-term ● and long-term ○; maximum temperature short-term ▼ and long-term Δ)

3.2   Methodology

3.2.1   Field experiment

Site selection and climate data

Three specific study sub-sites: site 1 (S1), site 2 (S2) and site3 (S3) were selected in each forest coffee unit/population4. The criteria taken into account for the sub-site selection were (a) the degree of disturbance of the forest, (b) the age of the coffee trees and (c) the accessibility of the sites. The physical characteristics of the sites are described in Tables 3.1 and 3.2. A Garmin GPS-72 was used to measure geo-coordinates and elevation. Altitude was measured using a pocket altimeter. Besides a visual observation, silva compass was used to display the aspect (exposition) of the sites. Degrees of slope were measured using a clinometer.

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[4] Forest coffee units (FCUs) and wild coffee populations refer to the four montane rainforests with the occurrence of wild Arabica coffee trees, while sub-sites are specific fields within each FCU. These are interchangeably used in this thesis.

Four automated weather stations were installed to collect climatic data, one at each study forest. Precipitation, air temperature, relative humidity, solar radiation and wind speed were measured at a height of 2 m. Readings from the sensors were stored in a data logger at interval of 10 minutes. One additional sensor (Hobo) rain gauge sensor was installed to measure rainfall. The climate data were summarized to provide information on the prevailing weather situation of the study period (2003-2005). The long-term climate data were obtained from the respective districts and Ethiopian Meteorological Service Authority (EMSA, 2002). These were computed and presented as short- and long-term climate data of the study areas (Figure 3.2b).

Experimental coffee trees

Nine to twelve coffee trees were systematically selected at each sub-site, from which again two primary branches were selected per tree. The coffee trees were chosen based on uniformity in age (5-7 years-old) and general growth performance. Based on the prevailing field features (slope, aspect, shade gradients), the trees were grouped in three blocks of a randomized complete block design. Seasonal soil-plant moisture dynamics and plant growth response were recorded and analyzed.

Coffee-associated plants

The total number of dominant plant species was recorded in a quadrant of 40 m x 40 m for large trees and 20 m x 20 m for small trees and shrubs. The trees include the remnant indigenous large trees of different species, mostly broadleaved, evergreen and deciduous types. The total number of plants per plot were counted and grouped into three classes: upper canopy large trees (>10 m height), coffee trees (lower to middle canopy strata) and small shrubs (<2 m height, lower strata). The major spices were also recorded and abundance or percent coverage of each group was computed. The spacing between coffee trees was measured and simple descriptive analysis performed. The canopy cover (shade level) of the multi-storey forest habitat was described as deep, medium and light shading. The distribution, description and economic importance of the useful plant species in the study forests have been reported by Tadesse (2003) and Feyera (2006). The purpose of this study was, therefore, to describe the pattern and

density of major plant types and examine the growth response of wild coffee trees under a specific micro-environmental condition.

3.2.2   Nursery experiment

Pre-sowing operations

Fully ripe red cherries were collected from selected experimental coffee trees at the three sub-sites of the four wild Arabica coffee populations, namely, at Harenna, Bonga, Berhane-Kontir and Yayu. Consequently, a total of 12 coffee accessions (I-1, I-2, I-3, II-1, II-2, II-3, III-1, III-2, III-3, IV-1, IV-2 and IV-3) were established and examined under controlled nursery settings at JARC. Depending on climatic and field conditions, the time of fruit maturity was different among the forest coffee units and thus, the coffee seeds were harvested between October and December 2003. The prepared seeds were stored between 3 and 5 months in a conventional well-ventilated coffee seed storage room at JARC with average minimum and maximum daily temperatures of 10 and 20°C, respectively.

At the same time, an ideal nursery site was selected and all pre-sowing activities including site clearing, digging, levelling, transporting soil and coffee compost to the nursery site, crashing and sieving were accomplished in January 2004. The so prepared ingredients were blended at the recommended ratio of 3:1 topsoil and decomposed coffee husk compost, respectively (Taye et al., 2002a). The black plastic pots were perforated at the bottom, firmly filled with the soil medium and arranged on a nursery seedbed.

Post-sowing operations

To ensure maximum germination, two coffee seeds were sown (March 29 and 30, 2004) in each plant plastic pot (volume = 5.8 cm^3) filled with the prepared blends of potting medium. All conventional post-sowing nursery operations (mulching, watering, shading, weeding, disease and insect control) were uniformly and timely applied according to the recommendations of the center (IAR, 1996; Tesfaye, 1995; Yacob et al., 1996). These practices were adhered to until the seedlings had reached the desired growth stage to start the treatments. They were uniformly managed under partial shade

conditions and irrigation was applied at a 4-day interval during the dry months. In addition, weeding and insects were monitored and controlled. Frequent hand weeding and hoeing were applied to loosen the potting soil and allow the penetration of water. Because of the climatic situation of the study period (low humidity and long summer rain), there was a high occurrence of insects, which were often controlled by hand picking at the early stages. Furthermore, Malathion (1ml 10^{-3} ml of H_2O) was used once to control the major insects such as semi-luper, hak moth (*Caphonodes hylas*), giant luper (*Ascotis selenaria reciprocaria*) and bloch leaf miner (*Leucoptera* sp.).

A split-split plot design with three replications was used to arrange the shade, irrigation and accessions as main-, sub- and sub sub-plot treatments, respectively. This was accomplished according to the procedures described by Gomez and Gomez (1984). The blocks (terraces) and the shade treatment were oriented in east to west direction. The treatments included two shade levels (moderate shade and full sun), two irrigation regimes (well-watered and drought-stressed) and 12 coffee accessions. Each accession consisted of 25 seedlings per plot. Moderate (50% light interception) overhead shade (2 m height) and side shades were constructed from bamboo slants. Care was taken to avoid side-shading effects between the treatments. In this case, the shade plots were far apart from each other (12 m), while the spacing between irrigation and accession plots were 2 m and 1 m, respectively. The spacing between coffee seedlings was also changed with increased extension growth of the seedlings. At the beginning, it was 10 cm x 10 cm and later increased to 20 cm x 20 cm. Drought-stressed seedlings were covered with white plastic sheet whenever there is rain and during the night time. The detailed methods and data analysis are presented independently in the respective chapters.

3.2.3 Soil analysis

Soil samples were collected from the three sub-sites within each forest population. About 500 g soil samples were collected from two soil depths: surface (0-20 cm) and sub-surface (20-40 cm) for laboratory analyses on physico-chemical properties. This was accomplished between June and July 2004, the main rain season in the southwest, but the dry season in the southeast Harenna forest. The soil-physical analysis included bulk density, soil texture and soil water status at field capacity (FC), permanent wilting point (PWP), water storage (WS), available water holding capacity (AWHC), saturated

water holding capacity (WHC), percolation rate (PR) and saturated hydraulic conductivity (SHC). The soil samples were air-dried and ground to pass through a 2 mm sieve for determination of soil reaction (pH), cation exchange capacity (CEC), exchangeable bases (K, Ca, Mg), organic carbon (OC), total nitrogen (TN) and available phosphorus (AP). Except for some soil physical parameters, the analyses were undertaken at the laboratory of International Livestock Research Institute, Ethiopia, using the procedures described by Okalebo et al. (1993) and Tekalign et al. (1991).

3.2.4   Data analysis

Analysis of variance (ANOVA) and multivariate analyses of the relevant variables were seperately performed for each chapter using the SAS system for Windows-v8 (SAS Institute Inc. Cary NC, USA).

3.3   Ecology of the study montane rainforests

3.3.1   Climate

The physical characteristics of the study area and the short-term climate data are presented in Table 3.1 and the specific study sites within each forest unit are described in Table 3.2. The forest coffee units differ in elevation ranging between 1,040 and 1,780 m a.s.l at Berhane-Kontir and Bonga forests, respectively. The slopes ranged from almost flat at Harenna to undulating/rolling at the Berhane-Kontir sites. The total annual precipitation varied from 950 mm at Harenna to 2,100 mm at Berhane-Kontir. The air temperature was relatively lower at Bonga as compared to the other sites. The average temperatures were 18.2, 19.7, 20.3 and 22.2°C at Bonga, Yayu, Berhane-Kontir and Harenna, respectively. Harenna had the lowest relative air humidity (37.9%) with a high wind speed as compared to the other sites, relative humidity was high at Bonga and Yayu. The velocity of the wind was low, ranging from calm (Berhane-Kontir and Yayu) to light wind (Harenna and Bonga). Wind speed may be much lower in the actual forest sites due to the wind breaking effect of the vegetation. Beining (2006) calculated a maximum drought period in the descending order Harenna>Yayu>Bonga>Berhane-Kontir. As a whole, the short-term meteorological data of the study period revealed a clear climatic gradient among the selected montane rainforests, particularly between the southeast Harenna and the southwest sites. This is in line with the long-term

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meteorological data (ESMA, 1998, 2002). The study plots differed in topography from flat to steep slope landforms with varied directions of exposure (aspect) to solar radiation (Table 3.2).

Table 3.1   Characteristics of the study montane rainforests (2003-2005)

Variable	Harenna	Bonga	Berhane-Kontir	Yayu
Wereda/district	Mena-Angetu	Ghimbo	Sheko	Yayu-Hurumu
Site code/symbol	PI	PII	PIII	PIV
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 (°C)	34.4	29.9	31.4	34.7
Min temperature (°C)	10.4	8.7	13.8	7.6
Mean temperature (°C)	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 3.2   Description of the study sub-sites in montane rainforests of Ethiopia

FCU (P)	Sub-site (S)	Code	Latitude (N)	Longitude (E)	Altitude (m a.s.l)	Slope (%)	Aspect[§]
Harenna (PI)	Magnete (S1)	PIS1	6°23′	39°45′	1420	2-3	EW
	Magnete (S2)	PIS2	6°29′	39°45′	1420	3	SN
	Magnete (S3)	PIS3	6°29′	39°44′	1490	3	WE
Bonga (PII)	Yabito (S1)	PIIS1	7°18′	36°03′	1780	4-6	NW
	Arabcasha (S2)	PIIS2	7°17′	36°12′	1520	3-6	NS
	Alemgono (S3)	PIIS3	7°19′	36°13′	1660	4-5	NE
Berhane-Kontir (PIII)	Beko-1 (S1)	PIIIS1	7°07′	35°26′	1040	4-18	NE
	Beko-2 (S2)	PIIIS2	7°07′	35°26′	1080	5-10	WE
	Shimi (S3)	PIIIS3	7°04′	35°25′	1180	9-17	NE
Yayu (PIV)	Yayu (S1)	PIVS1	8°23′	35°47′	1400	1-8	WE
	Yayu (S2)	PIVS2	8°23′	35°47′	1400	2-3	SE
	Yayu (S3)	PIVS3	8°23′	35°47′	1400	5-7	EW

§ refers to exposition

3.3.2   Plant association

The study sites varied in land nature and plant composition, among others. At all sites, the forests strata consisted of large trees, coffee trees and shrubs. The quadrant count and coffee spacing results show that plant density and coffee spacing varied at the four rainforests. The proportion of the remnant indigenous trees was high in the Berhane-Kontir sites (PIIIS1 and PIIIS2), followed by Bonga (PIIS1) and Yayu (PIVS1) (Table

3.3). It was lowest at the Bonga site (PIIS2) and Berhane-Kontir site (PIIIS3). The density of large trees was significantly higher at the Berhane-Kontir (60.7%) and lowest (12.7%). At most sites, however, the frequency of economically valuable trees (e.g., *Cordia africana*) was lower than that of others (e.g., *Croton macostachyus*).

The number of coffee trees was highest at Harenna (PIS1), Bonga (PIIS1), Berhane-Kontir (PIIIS2) and Yayu (PIVS3) as compared to the other respective sub-sites within each FCU. These were sites with deep shade conditions. Increased coffee tree spacing (reduced coffee population) was measured at Berhane-Kontir (PIIIS3) Harenna (PIS2), Bonga (PIIS2) and Yayu (PIVS1). Hence, the density of coffee trees was found to be significantly lowest (19.3%) at Bonga and highest in Harenna (53.3%) forests. There was a slightly positive correlation (r = 0.11, P>0.05) between the density of large trees and coffee plants, suggesting the shade-adapted features of *Coffea arabica* in its original forest ecology. Nevertheless, the weak association could be attributed to the adverse effects of excessive shading on the regeneration of young coffee seedlings, prevalence of insects and diseases. The coffee leaves were thin (high specific leaf area) and easily attacked by insects. The more humid microenvironment might also favour the occurrence of diseases and insect pests. As a result, there was a high infestation of the coffee berry disease (*Colletotrichum kahawae* Waller). Moreover, the coffee trees were also highly affected by the coffee wilt disease (*Gibberella zylariodes*), particularly at the Yayu sites, where about 23-27% of the experimental coffee trees had dried. Armillaria root rot (*Armillaria mellea*) was found to attack the coffee trees at the Berhane-Kontir sites. As a result, the vegetative and reproductive growth of coffee trees under such heterogeneous stand structures, environmental and biotic stresses suggest the need to reduce shade covers and wetting periods.

On the other hand, the population of shrubs was lowest in Berhane-Kontir and Harenna as opposed to the Bonga and Yayu forests (Figure 3.4). Wild spices (e.g., *Aframonium angustifolia, Piper capense, Capsicum* sp.) were found to co-exist with the wild coffee trees, mainly in the Bonga and Berhane-Kontir forests. As a whole, the relative proportions of the major plant growth forms differed from site to site. There was a significantly negative relationship between coffee trees and shrubs (r = -0.68*) in the minimally disturbed natural forest ecosystem, particularly at Harenna and Berhane-Kontir (Figure 3.5). The results mainly indicate the level of human intereference and

livelihood dependence on forest resources as reported in detail by Tadesse (2003) and Feyera (2006).

Table 3.3   Abundance and frequency of large trees, coffee trees and shrubs and spacing between coffee trees at each study montane rainforest of Ethiopia

Site	Abundance plot^{-1}				Frequency (%)			Coffee spacing (cm)		
	Trees	Coffee	Shrubs	Total	Trees	Coffee	Shrubs	Min	Max	Mode
PIS1	10	19	2	31	32	61	7	21	243	83
PIS2	8	7	2	17	47	41	12	27	318	140
PIS3	7	15	4	26	27	58	15	23	390	106
PIIS1	17	18	61	96	18	19	63	18	143	43
PIIS2	5	15	62	82	6	18	76	28	315	87
PIIS3	8	12	36	56	14	21	64	39	266	77
PIIIS1	23	5	7	35	66	14	20	37	214	113
PIIIS2	23	15	0	38	61	39	0	19	247	152
PIIIS3	6	5	0	11	55	45	0	65	272	197
PIVS1	14	13	31	58	24	22	54	27	202	77
PIVS2	11	26	38	75	15	35	50	26	150	74
PIVS3	13	39	27	79	17	49	34	22	170	54
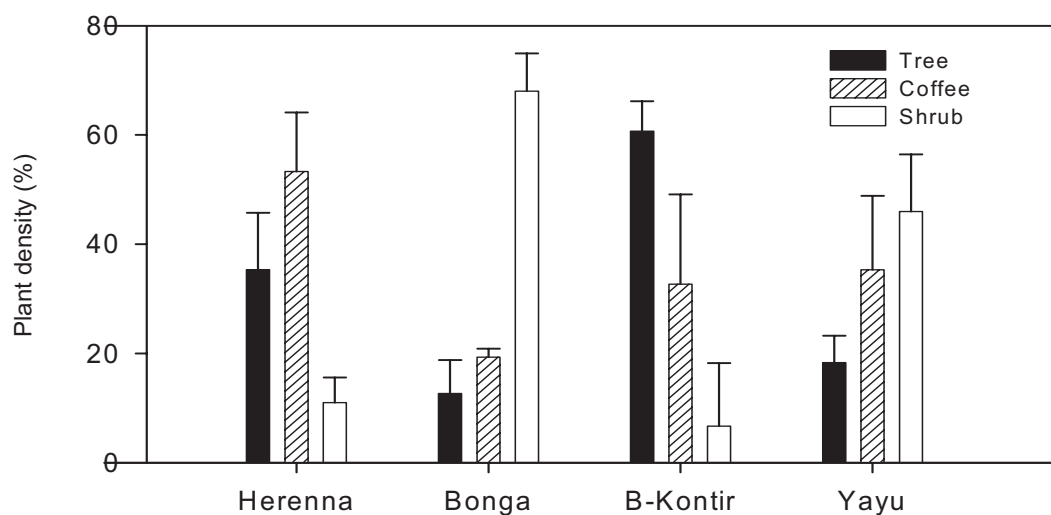
Figure 3.4   Relative plant density for the dominant plants in the four montane rainforests of Ethiopia

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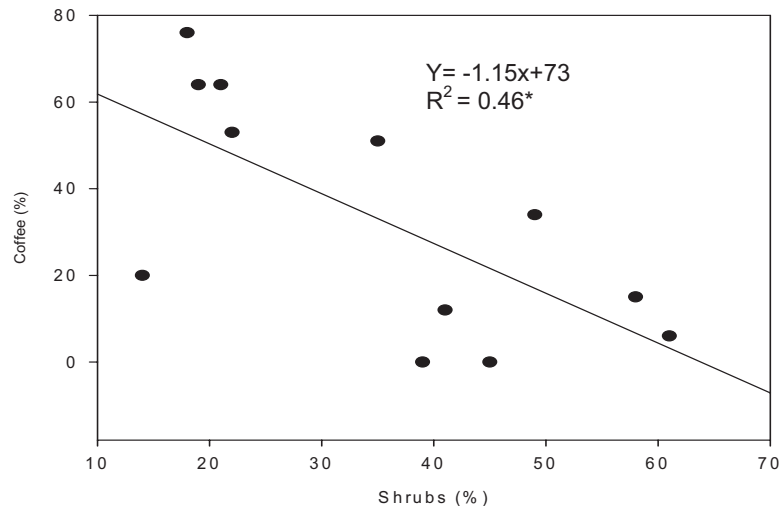
Figure 3.5   Relationship between coffee trees and small shrubs in montane rainforests of Ethiopia

3.3.3   Soil

Physical properties

Highly significant differences were noted among the four wild coffee populations in soil bulk density, silt and sand particles. The lowest (1.01 g cm^{-3}) and highest (1.42 g cm^{-3}) soil bulk density were recorded for the Bonga and Harenna soils, respectively (Table 3.4). Yayu soils had significantly the highest sand (38.6%) content compared to the other sites, particularly the Berhane-Kontir soils with the lowest proportion of sand (15.4%). In addition, highly significant differences in silt content were recorded; the mean values ranged from 16.3 to 29.6% for the Yayu and Berhane-Kontir soils, respectively. In contrast, the clay contents did not show significant differences, though the average values decreased in the order of Harenna>Berhane-Kontir>Bonga>Yayu (Figure 3.6). This could be the reason for the significant differences in water holding capacity with the highest (61.5%) and lowest (51.9%) values measured for the Harenna and Yayu soils (Figure 3.6), respectively. There were highly significant variations in the available water holding capacity of the soils. Accordingly, the respectively highest (5.73 cm) and lowest values (4.46 cm) were obtained from Yayu and Bonga soils, which was quite similar to the patterns noted for soil bulk density. The soil water contents (field capacity and permanent wilting point), percolation rate and hydraulic conductivity were comparable among the forest soils. This could be related to the similarity of the soils in soil organic matter content and textural class, among others. All soil samples were

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determined to have a clay texture, though Yayu soils had a high proportion of sand. On the other hand, the highly significant lowest field soil water content at Harenna showed seasonal variations according to the rainfall patterns between the southeast and southwest parts of the Great Rift Valley in Ethiopia.

The correlations between the soil parameters were different among forest sites (Appendix 1). At Harenna, silt particle was negatively and significantly (r = -0.87*) correlated with clay content. However, positively and significantly (r = 0.89**) improved the soil moisture content. This was in contrast to the negative, but insignificant relationships between clay and water contents of the soil. Field capacity was significantly and directly correlated with profile soil water holding capacity and field capacity (r = 0.89*), water holding capacity (dry weight basis, r = 0.95**), rate of percolation and hydraulic conductivity (r = 0.83*). In the Bonga forest, the clay content of the soil was negatively and significantly correlated with the sand (r = -0.94**) and silt (r = -0.92**) content. There were indirect relations between sand content and soil water retention, and this was significant for the water holding capacity on a dry weight basis (r = -0.84*). At Bonga, the amount of soil water (% dry weight) was directly and significantly correlated with the soil moisture content at field capacity (r = 0.83*) and permanent wilting point (r = 0.96**). Similarly, maximum water holding capacity, percolation rate and saturated conductivity were correlated with soil bulk density, though not significantly.

In the soil samples from the Berhane-Kontir forest, clay and silt correlated negatively and and significantly (r = -0.89*). Unlike silt, sand and clay particles were negatively correlated with most soil physical characteristics. Field soil moisture content and saturated percolation rate and conductivity showed indirect relationships with soil bulk density, indicating the influence of the high clay contents. This was evident from the positive significant correlation between bulk density and saturated water holding capacity (r = 0.94**) of the soil. Further, soil water content (% dry weight) was significantly and directly correlated with the water contents at field capacity (r = 0.89*) and permanent wilting point (r = 0.92**). In the Yayu soils, clay was significantly and inversely correlated with sand (r = -0.96**) and silt (r = -0.91*). As a consequence, the level of sand was indirectly and significantly correlated with soil water at field capacity (r = -0.94**) and permanent wilting point (r = -0.93**). In addition, the influence of

clay was positive and significant on soil water content at field capacity (r = 0.86*). In this case, soil bulk density was slightly and directly associated with saturated water holding capacity, percolation rate and conductivity of the soil, which indicates the predominant effect of sand in Yayu soils.

The results of the soil physical properties along depths are inconsistent among the four forests. Soil bulk density was significantly influenced by profile depth at Harenna and Yayu, but not at Bonga and Berhane-Kontir. However, lower bulk densities were obtained for the surface (0-20) than for the deeper (20-40 cm) soil samples, with the highest (21.0%) and lowest (13.2%) reductions at Berhane-Kontir and Harenna, respectively. However, minimum (0.92-1.10 g cm^{-3}) and maximum (1.32-1.52 g cm^{-3}) average soil bulk densities were determined for the Bonga and Harenna soils, respectively (Table 3.5).

Likewise, at Harenna, profile depth had significant influence on soil water contents at field capacity, available soil water depth and field water contents. Hence, significantly lower soil available water (3.12 cm), higher field capacity (39.75) and water holding capacity were measured in the surface and deeper soils, respectively. Similarly, soil water conditions (permanent wilting point, field soil water content, percolation rate and hydraulic conductivity) were higher for upper than for sub-surface soil, although the differences were statistically not significant. Similarly, unlike clay, sand and silt were higher in the topsoil. At Bonga, soil depth had a significant effect on silt particle and soil water contents. The results reveal a lower proportion of silt (17.3%) and increased soil water content at permanent wilting point (28.6%) and available soil water (6.03 cm) in the deeper soil than that of surface soil (Table 3.5). In contrast, the field soil moisture status was significantly higher (53.06±4.45% dry wt) in the surface soil, indicating the role of increased silt content in reducing soil bulk density and thus enhancing soil water holding capacity. On the other hand, there were no significant variations between profile depths in soil physical conditions, with the exception of a significantly higher available soil water in deeper (7.75 cm) than in shallow soils (2.95 cm). This is in line with the highly significantly higher silt (19.3%) and significantly lower clay (40.2%) contents in the surface soils than in the subsurface soils. Similarly, highly significantly more available soil water (8.21 cm) was calculated for deeper soils (Table 3.5).

Table 3.4   Physical properties (means±SD) of forest soils at study montane rainforests

Property	Harenna	Bonga	B-Kontir	Yayu	Pr>F
BD (g cm^{-3})	1.42±0.06a	1.01± 0.06b	1.07±0.05b	1.23±0.11ab	**
Sand (%)	21.61±2.52b	23.95±7.37ab	15.35±3.02b	38.56±5.57a	**
Silt (%)	14.95±1.15b	22.28±4.36ab	29.61±6.11a	16.28±2.00b	**
Clay (%)	63.44±1.73	53.77±11.02	55.04±5.50	45.16±7.55	Ns
SMC (% dry wt)	33.06±1.10	48.36±5.49	37.76±9.21	34.54±4.45	Ns
SMC (% vol.)	14.01±1.40b	31.88±1.84a	27.94±5.48a	28.09±3.65a	**
WHC (% dry wt.)	61.47±3.37a	60.38±5.53ab	53.65±0.87ab	51.86±1.91b	*
PR (cm^3 min^{-1})	8.75±1.81	9.63±6.64	5.87±3.94	5.43±4.76	Ns
SHC (cm min^{-1})	1.44±0.30	1.59±1.10	0.97±0.65	0.90±0.79	Ns
FC (0.33 bar)	37.98±1.95	42.54±4.76	39.31±3.84	33.70±3.45	Ns
PWP (15 bar)	26.73±0.70ab	27.79±3.43a	23.34±4.12bc	18.72±2.84c	*
AWHC (cm)	4.81±0.59bc	4.46±0.59c	5.35±0.55ab	5.73±0.45a	*

Ns = Not significant; *, ** significant at P≤0.05 and P≤ 0.01, respectively. Means with the same letter within a row are not significantly different (Tukey test at P = 0.05 probability level). Abbreviations: BD = Bulk density, SMC = soil moisture content, WHC = water holding capacity, PR = percolation rate, SHC = saturated hydraulic conductance, FC = field capacity, AWHC = available water holding capacity.
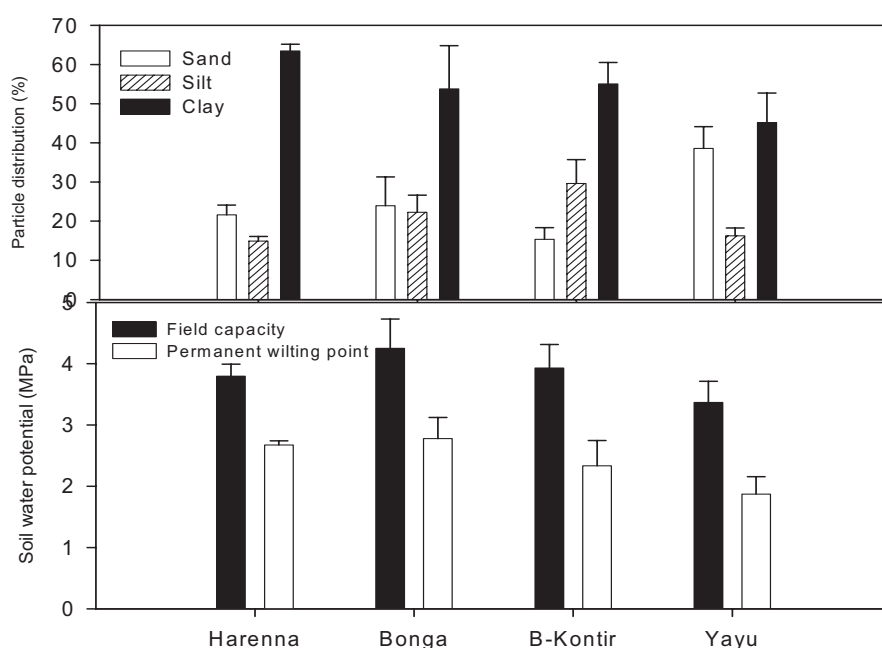
Figure 3.6   Particle distribution and water potential (field capacity and permanent wilting point) of soils from the four montane rainforests

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Table 3.5   Soil physical properties (means±SD) for surface and deep profile depths at the study montane rainforests of Ethiopia

Site/depth (cm)	BD (g cm⁻³)	Sand (%)	Silt (%)	Clay (%)	FC (0.33 bar)	PWP (15 bar)	AWC (cm)	FMC (% dry wt)	WHC (% dry wt)	PR (ml/min)	Ksat (cm/ml)
Harenna	*	Ns	Ns	Ns	**	Ns	**	Ns	*	Ns	Ns
0-20	1.32±0.04b	24.61±1.15	17.95±7.57	57.44±7.21	39.75±2.14a	27.94±1.20	3.12±0.37b	33.55±3.67	65.99±2.87a	10.67±0.71	1.76±0.12
20-40	1.52±0.08a	18.61±4.16	11.95±7.02	69.44±5.29	36.19±1.77b	25.52±0.20	6.48±0.82a	32.57±1.58	56.95±4.30b	6.83±3.18	1.12±0.52
Bonga	Ns	Ns	*	Ns	Ns	*	*	*	Ns	Ns	Ns
0-20	0.92±0.14	26.61±5.03	27.28±5.29a	46.11±9.87	42.72±4.37	26.97±3.53b	2.88±0.41b	53.06±4.45a	57.81±5.18	8.60±5.58	1.42±0.92
20-40	1.10±0.03	21.28±10.39	17.28±4.00b	61.44±14.00	42.36±5.23	28.60±3.35a	6.03±1.02a	43.65±6.56b	62.95±6.07	10.65±7.80	1.75±1.29
B-Kontir	Ns	Ns	Ns	Ns	Ns	Ns	*	Ns	Ns	Ns	Ns
0-20	0.94±0.06	16.80±2.04	27.28±9.17	55.92±8.36	39.57±4.27	23.90±4.92	2.95±0.16b	42.04±12.00	52.36±4.61	8.10±5.57	1.34±0.92
20-40	1.19±0.13	13.89±4.16	31.95±5.03	54.16±6.93	39.06±3.44	22.77±3.39	7.75±1.07a	33.47±6.44	54.93±2.87	3.63±2.36	0.60±0.39
Yayu	*	Ns	***	*	Ns	Ns	**	Ns	Ns	Ns	Ns
0-20	1.10±0.13b	40.56±4.00	19.28±2.00a	40.16±6.00b	33.23±3.36	18.57±2.44	3.23±0.31b	39.29±6.78	51.95±2.41	3.13±1.66	0.52±0.28
20-40	1.34±0.10a	36.56±7.21	13.28±2.00b	50.16±9.17a	34.16±3.71	18.86±3.38	8.21±0.63a	29.79±3.53	51.76±1.71	7.73±7.92	1.27±1.31

Ns =Not significant, *, ** and *** = significant at P≤0.05, P≤ 0.01 and P≤0.001, respectively. Means with the same letter within a column are not significantly different according to Tukey test at P =0.05 probability level. Abbreviations: BD = bulk density, FC = field capacity, PWP = permanent wilting point, AWC = available water content, FMC =field moisture content, WHC =water holding capacity, PR = percolation rate, Ksat = saturated hydraulic conductivity.

Chemical properties

Correlations between soil chemical properties were found to be different among the forests (Appendix 1). Nonetheless, at all sites, total nitrogen (TN) of the soil was strongly correlated with soil organic matter ($P<0.001$). In addition, there were direct relationships between soil organic matter (SOM) and inorganic ions (K, Ca, Mg) at all sites, and available K and Ca in the Harenna soils correlated significantly. The concentration of these soluble ions in the soil varied slightly with soil reaction. Soils did not reveal significant variations for most chemical properties, except for Mg, CEC and C:N. However, the Berhane-Kontir soils had the highest pH (6.23±0.42), available K (1.71±1.48 meq/100g), exchangeable Ca (18.14±8.07 meq/100g), electrical conductivity (0.12±0.02) and available P (12.84 ppm) as compared to others. On the other hand, the Yayu soils had the lowest pH (5.39), available K (0.49 meq/100g) and TN (0.18%) contents. The average Ca content varied from 9.00 to 18.14 meq/100g in the Bonga and Berhane-Kontir soils, respectively. Berhane-Kontir and Harenna soils contained almost the same amount of exchangeable Ca. The Berhane-Kontir soils had the significantly highest Mg (7.54 meq/100g) as compared to the other soils, which did not significantly differ between each other (Table 3.6).

The significantly lowest CEC (20.29 meq/100g) was determined for the Yayu soils in contrast to the highest values (30.16 meq/100g) in the Berhane-Kontir and Harenna (29.15) soils. Similarly, the Berhane-Kontir soils had higher electrical conductivity (EC) values as compared to the other sites, with values ranging between 0.09 and 0.12. Available P ranged from 0.35 to 12.84 ppm for the Bonga and Berhane-Kontir soils, respectively, followed by Yayu (4.65 ppm) and Harenna (0.90±0.52 ppm). According to Hofner and Schmitz (1984), the level of P at the Berhane-Kontir and other forests is medium to low, respectively. This indicates the specific ability of each soil type in fixing P. The highest SOM was found in the Harenna (4.9%) and Bonga (3.7%) soils, the lowest at Berhane-Kontir (2.2%) and Yayu (2.6%). At all sites, SOM was higher than the range reported in forest soils (Brady, 1990). As a result, highly significant differences in C:N were determined and the highest (12.41) and lowest (6.63) values were obtained for the Harenna and Berhane-Kontir soils, respectively (Table 3.6). This shows the relatively higher mineralization rate at the low altitude hot-humid Berhane–Kontir sites. This was almost equal for the Bonga and Yayu soils.

With regard to the influence of soil depth, the Harenna soils showed significant differences in TN and SOM and thus, C:N between the upper and lower layers. In the upper layers, TN (0.34%) and SOM (6.42%) were higher, while C:N (10.78) was lower than in the lower soil layer. On the other hand, soil pH and EC were slightly increased at the deeper profile. Accordingly, pH values ranged between 6.04 and 6.35, which represents a slightly acidic soil. Exchangeable bases, CEC and available P, however, declined down the profile. The decline in available P was significant at the Harenna and Yayu sites. On the other hand, soils collected from the two depths at Bonga were not statistically different for all the soil chemical parameters analysed. However, surface soil had relatively higher mean values for all the variables, except CEC, which increased from 28 to 32 meq/100g. Similar to Bonga, the Berhane-Kontir soils did not vary due to depths and with the exception of pH and EC, the values were slightly lower for deeper soils. At Yayu, TN and SOM were significantly ($P<0.01$) reduced from surface to sub-surface soils. C:N was also significantly ($P<0.05$) higher in the surface (9.24) than in the deeper soil layer (7.83) (Table 3.7).

Table 3.6   Soil chemical properties (means±SD) of the studied montane rainforests

Property	Harenna	Bonga	Berhane-Kontir	Yayu	Pr>F
pH(H_2O,1:2.5)	6.19±0.43	5.64±0.72	6.23±0.42	5.39±0.41	Ns
K (meq/100 g)	0.51±0.53	1.04±0.07	1.71±1.48	0.49±0.31	Ns
Ca (meq/100 g)	18.10±7.78	9.00±0.95	18.14±8.07	11.43±1.44	Ns
Mg (meq/100 g)	3.21±0.30b	3.35±0.22b	7.54±1.80a	3.21±0.45b	**
CEC (meq/100 g)	29.15±5.85a	30.16±4.81a	26.01±1.53ab	20.29±1.04b	*
EC (1:2.5)	0.09±0.05	0.09±0.03	0.12±0.02	0.09±0.03	Ns
AP (ppm)	0.90±0.52	0.35±0.12	12.84±8.35	4.65±7.09	Ns
TN (%)	0.24±0.03	0.25±0.04	0.19±0.07	0.18±0.03	Ns
OC (%)	2.83±0.83	2.14±0.61	1.27±0.48	1.51±0.25	Ns
SOM (%)	4.87±1.43	3.69±1.05	2.18±0.82	2.61±0.44	Ns
C:N	12.41±1.85a	8.55±1.15b	6.63±0.24b	8.54± 0.40b	**

*Ns =Not significant; *, ** = significant at P≤0.05 and P≤ 0.01, respectively. Means with the same letter within a row are not significantly different according to Tukey test at P = 0.05 probability level.*

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Table 3.7   Soil chemical properties (means ± SD) as influenced by profile depth at the four montane rainforests of Ethiopia

Site /depth (cm)	TN (%)	SOM (%)	pH (H_2O, 1:2.5)	EC (1:2.5)	Exchangeable base (meq/100 g)			CEC (meq/100 g)	Available P (ppm)	C:N
					K	Ca	Mg			
Harenna	*	*	Ns	Ns	Ns	Ns	Ns	Ns	***	*
0-20	0.34±0.06a	6.42±1.99a	6.04±0.42	0.07±0.05	0.84±0.87	22.24±9.58	3.29±0.58	33.53±8.35	1.50±1.14a	10.78±1.58b
20-40	0.17±0.03b	3.32±0.92b	6.35±0.46	0.11±0.06	0.18±0.19	13.97±6.13	3.12±0.05	24.76±3.32	0.30±0.13b	14.05±2.16a
Bonga	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns
0-20	0.30±0.07	4.53±1.47	5.77±0.81	0.10±0.03	1.11±0.21	10.14±2.50	3.47±0.73	28.10±5.45	0.50±0.28	8.73±0.81
20-40	0.20±0.02	2.85±0.65	5.51±0.64	0.08±0.05	0.96±0.34	7.85±3.28	3.22±0.55	32.21±6.92	0.20±0.05	8.36±1.49
B-Kontir	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns
0-20	0.24±0.10	2.88±1.07	6.17±0.56	0.12±0.02	2.11±2.07	22.60±9.91	8.14±2.34	24.09±4.50	14.77±7.38	7.05±0.45
20-40	0.14±0.05	1.48±0.61	6.28±0.40	0.12±0.03	1.30±0.92	14.03±9.06	6.94±2.31	27.93±5.56	10.91±9.37	6.20±0.31
Yayu	**	***	Ns	Ns	Ns	*	Ns	Ns	***	*
0-20	0.21±0.02a	3.36±0.47a	5.54±0.20	0.08±0.02	0.70±0.45	13.04±2.06a	3.50±0.30	23.25±2.28	8.90±14.13a	9.24±0.50a
20-40	0.14±0.03b	1.85±0.41b	5.23±0.62	0.09±0.03	0.27±0.17	9.82±0.81b	2.91±0.60	17.41±1.97	0.40±0.23b	7.83±0.31b

Ns =Not significant, *P≤0.05, **P≤ 0.01, ***P≤0.001. Means with the same letter within a column are not significantly different according to Tukey grouping at P = 0.05-probability level. Abbreviations: TN = total nitrogen, SOM = organic matter, EC = electrical conductivity, CEC = cation exchange capacity, C:N = carbon to nitrogen ratio.

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3.3.4   Discussion

Coffee and associated plants

The geographical position and the altitude ranges lead to different climatic gradients and thus vegetation covers of the study sites. The forests differed in the pattern of vegetation cover and plant population density. In addition, the correlation between the most abundant plant forms was significantly different in the forests where the frequency of coffee was negatively correlated with that of shrubs, and thus not compatible. Such differences in the regeneration and adaptation capacities might be explained by the competition effects between coffee trees and shrubs with similar growth characteristics. The high proportion of shrubs at Bonga and Berhane-Kontir could be due to the suitability of the sites for the growth of shrubs or intensity of human impact on plant composition. The sites were characterized by broad-leaved forest with a dominant upper story of tall tree species. Nontheless, yield and quality aspects of coffee trees under the dominant shade trees and soil conditions remain to be investigated. Spices such as *Aframonium corrorima, Curcuma domestica, Zingiber offocinale, Piper capense and Piper guineense* were found to co-exist with wild coffee trees in the southwest forests, especially in Bonga and Berhane-Kontir. It was also not uncommon to find *Gesho* (*Rhamnus prinoides*), a major ingredient of local drinks (*tela and tej-honey wine*), in the studied forests. The priorities of the farmers and the intensity of management practices could be the possible reasons for the changes in the dominance of different plant species and stand structure as has been described in detail by Tadesse (2003) and Feyera (2006). Feyera (2006) also reported an indirect correlation between the abundance of wild coffee and species richness in the Afromontane rainforests.

According to the primary information, the vegetation cover has declined primarily due to population pressure and expansion of commercial farms (tea and coffee) around the Bonga and Berhane-Kontir forests. Furthermore, most farmers are also interested in opening up the forests for cultivation of food crops, indicating the limited awareness of climate change and loss of genetic resources. Nonetheless, the present study on the analysis of the long- and short-term meteorological records clearly indicates a decreasing trend in rainfall amount and distribution as well as increasing air temperature at the four study areas. This will undoubtedly continue unless sustainable conservation options are put in place. In this regard, Tadesse (2003) and Feyera (2006)

reported in detail on the impacts of human use and ecological factors in changing the biodiversity in the Afromontane rainforests. Seasonal assessment on the functioning of the forest ecosystem, however, calls for further research.

Soil physical properties

The studied forest soils were comparable in most physical and chemical properties. All soil samples had clayey texture and, despite the highly sloping topography, the soils had ideal physical and chemical properties. This could be attributed to the high soil organic matter due to decomposition of litter fall. The high vegetation cover could also reduce the run-off. Since both the volume of pore spaces and soil solids determine the bulk density of a given soil medium, the soil media with a high proportion of pore space to solids have lower bulk densities as compared to more compact soil with less pore spaces. Further, soils with high organic matter constituents markedly improve soil structures with an ultimate reduction in soil bulk density. Soils with high organic matter status were found to promote hydraulic conductivity. These can be categories in moderate to moderately rapid flow classes according to Brady (1990) and Foth (1984). Reduced bulk density of soils with increased humus status has been long recognized (Brady, 1990). However, in this study soil bulk density was significantly and indirectly related to saturated water-holding capacity and percolation rates and hydraulic conductivity of the soil. This indicates the compactness of the soil with reduced pore spaces and decreased soil water content at field capacity. According to Brady and Weil (2002), in compacted soils, plant water use may be restricted by poor aeration at high water contents and by soil strength at low water contents.

The field soil water content and soil permeability were not statistically different between soil depths, mostly due to reduced rainfall during the measurements. The friable structure of the coffee soils and high SOM content could also be among the possible reasons for the absence of significant differences in soil moisture contents under field conditions. This supports the works of Taye et al. (2002a), who showed enhanced soil water contents with increased proportion of decomposed organic resources in potting media blends. They associated this with the beneficial direct or indirect effects of the organic matter to form a stable structure that can facilitate the movement of water.

Unlike other the sites, at Berhane-Kontir, surface soils had slightly lower silt and higher clay contents than deeper soils, reflecting the influence of run-off with increased slope and soil exposure at the two sites (PIIIS1 and PIIIS3). Consequently, the relatively higher percolation rate and hydraulic conductivity of the surface soil could partly be associated to the reduced bulk density and increased sand contents. In general, the soils were characterized by good physical properties: friable, well-drained, high moisture storage capacity and deep rooting depth. This could primarily be related to the high soil organic matter content rather than to the proportion of particle size distribution. This has to be therefore maintained for sustainable functioning of the forest ecosystem.

Soil chemical properties

The results do not differ in most of the soil chemical properties studied, with the exception of significant differences in CEC, Mg and C:N ratio (Table 3.6). This could be related to the similarity in forest vegetation and availability of sufficient soil moisture during the different seasons. According to the general guidelines on the interpretation of soil analysis results (Tekalign, 1991), the soils of the four study sites had moderate TN. Soil organic carbon was ranked as moderate for the Harenna and Bonga soils, but low in Yayu and Berhane-Kontir. This could be attributed mainly to the differences in the rate of decomposition and carbon sequestration capacity of the soils. Similarly, the soils contained exchangeable bases, ranging from medium to very high. Nonetheless, the Ca content of the Bonga soils was found to be low, while magnesium was very high at all the study forests, possibly demonstrating the similar soil-forming processes in the forest ecosystems (Mesfin, 1998; Murphy, 1968).

The relatively high total nitrogen contents at Harenna and Bonga could be related to the release of mineralized nitrogen upon decomposition unlike the relatively high organic sources, which bind nitrogen in the organic form. The least C:N ratio at Berhane-Kontir suggests the influence of high temperature and higher microbial activity. In general, the narrow C:N ratio indicates that the soils contained low organic matter with ultimately increased total nitrogen. This could minimize the competition for the inorganic nitrogen between coffee trees and soil microorganisms, as opposed to the undecomposed materials, and indicates decreased decomposition of organic materials

with an increased C:N ratio, which caused a shortage of nitrogen in the soil. Other authors have reported similar findings (Brady and Weil, 2002; Franco and Mannus, 1982; Myers et al., 1994). The low C:N value could also be associated with the contribution of leguminous shade trees to increase nitrogen. The high rate of decomposition of organic material and the concentrations of acid-forming ions, production of weak acids and basic cations could also be amongst the possible reasons for this low C:N ratio. Similar findings were reported elsewhere (Brady, 1990).

There were also remarkable differences in the CEC of the soils, the highest and lowest being from the Bonga and Yayu soils, respectively. This is in line with the particle distribution of the two soil types, i.e., higher sand content in Yayu than in Bonga soils. Moreover, such differences in CEC could also be attributed to differences in the humification and generation of pH-dependent adsorptive sites on the organic exchange complex. Several studies (Murphy, 1968; Mesfin, 1998; TewoldeBerhane, 1986; Paulos, 1994) reported similar findings in coffee soils of Ethiopia. These authors have associated soil fertility status with rainfall and temperature gradients, and soil biochemical processes. Consequently, soils of high rainfall areas are highly leached and weathered with low pH, poor saturation of cation exchange complex, low total exchangeable bases, low concentrations of available phosphorus and total nitrogen. The present results for soil CEC and available phosphorus were not consistent with the rainfall gradient, as the soil samples were taken under moist forest covers at shallow soil depths. The high soil available phosphorus in the Berkane-Kontir soil as compared to the others might come mainly from decomposition of organic sources. The relatively low available P in the Bonga soils could be related to the capacity of the soil for fixing P due to the high concentration of Aluminium (Al) and iron (Fe) in the soil. Mesfin (1998) and Paulos (1994) have shown the limited availability of P in most coffee soils, underlining the adaptation and low requirement of coffee plants to P as reported by Paulos and Moorby (1995) .

The higher TN and exchangeable bases in the upper soils could partly illustrate the contribution of shading and soil cover to reduce leaching and improve the nutrient retention capacity of forest soils. According to Wintgens (2004), the C:N ratio provides an indication of the type of organic matter present in the soil and, in particular, the degree of humification. The C:N values of 12 and less than 10 indicate good and

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impoverished (low organic matter content) soils, respectively. However, the low C:N values obtained at all forest sites except Harenna, demonstrate the high concentration of TN in the soil, possibly from decomposition of organic matter and/ or nitrogen fixation. This again could be associated to the climatic gradients between the southeast and southwest montane rainforests. Other authors (Franco and Munns, 1982; Hsieh and Hsieh, 1990) reported that the potential nutrient carrying capacity of the soil is determined by the nature and the amounts of organic colloids present in the soil.

According to Tekalign (1991), the more humid the environment, the greater the proportion of recalcitrant organic matter. Moreover, clay particles physically protect recent organic addition to soils and form stable organo-mineral complexes with the humus fraction. In soils low in clay and receiving small amount of annual precipitation, less soil organic carbon is lost, because the capacity of the original soil system to sequester carbon is reduced due to ready soil aeration and the reduced physical protection of organic matter by clay. The maximum available phosphorus at Berhane-Kontir indicates its high fixation capacity. The significant decline down the soil depth at Berhane-Kontir and Yayu suggests that SOM and and exchangeable bases mitigate the fixation problem. The same findings on soil P have been reported for the other coffee soils (Coste, 1992; Paulos, 1994; Paulos and Moorby, 1995). Despite the physical characteristics of the land and the high rainfall patterns of the study sites, the inherent fertility of the soil and thus quality of the land is maintained primarily due to the vegetation cover. The analysis indicates that some soil attributes were noted to decline with soil depth, suggesting the risks associated with soil degradation. Therefore, assessment and management of SOM is important based on the recognition that organic matter plays a role in the supply of major and minor plant nutrients, improvement of physical and chemical constraint, through reduced leaching, and fixation losses, as a storage for plant nutrients and a buffering against adverse conditions (Mesfin, 1998). As a whole, forests play a pivotal role in maintaining ideal soil properties and hence fauna and flora of the forest ecosystem.

4 GROWTH ARCHICTURE OF THE WILD ARABICA COFFEE TREES

4.1 Introduction

Knowledge of the growth architecture of Arabica coffee is important for characterizing coffee types and targeting specific management options, e.g., spacing and irrigation levels. Coffee is a woody perennial evergreen dicotyledonous plant. It has a main vertical trunk (orthotropic) and primary, secondary, and tertiary horizontal branches (plagiotropic) with varying crown and growth habits. Coffee trees can grow to heights of 10 m if not pruned, but producing countries will maintain the coffee at a height reasonable for easy harvesting (Cambrony, 1992; Coste, 1992; Wrigley, 1988). The development of the aerial parts of the plant entails the lengthening of the vertical (orthotropic) main stem and the successive growth of pairs of opposite leaves at each node. Serial buds, headed by one head of serial bud, are located in the leaf axil. The head of the serial buds is the only bud able to generate a primary branch, and the four to six serial buds can generate either new suckers (orthotropic stems) or flowers. Serial buds can remain dormant for a long time. Primary branches grow off the main stem and develop secondary, tertiary and quaternary ramifications (Figure 2.1). Depending on coffee species and environmental conditions, a 1-year-old coffee plant develops approximately 6 to 10 primary branches. After 2 years, it can reach a height of 1.5 to 2.0 m and the first flowers appear. After approximately 3 years, the coffee tree reaches full maturity and begins to yield a normal crop (Wintgens, 2004).

Coffee leaves grow on petioles in opposite pairs on the side of the main stem and branches. They are dark green, shiny and waxed. Leaf shape is elliptical and the veins are conspicuous. The leaves of Arabica coffee are slender and more delicate than the other species (Figure 2.1). The younger leaves are either light green or bronze depending on whether the plant is of Bourbon or Typica origin. The bronze color of the cultivar Arabica Typica fades with age. The leaf surface of an adult coffee tree varies according to species, state of health, light, etc. The life span of coffee leaves is less than a year. The location, shape, size and constitution as well as the absence or presence of hairs around the opening of the leaf domatia and the presence or absence of stomata on the outermost cell layer of the domatia have been used to distinguish *Coffea* species and varieties (Wintgens, 2004; Wrigley, 1988).

The estimation of whole-tree foliage area is an important and critical step in scaling physiological processes measured at the leaf and shoot scales to the tree- and stand-scale dynamics, such as growth, carbon budget and water flux (Ishii et al., 2002). However, direct measurements of foliage area are nearly impossible at the tree and stand levels. In general, allometric relationships offer useful approaches and methods to estimate plant leaf area and spatial patterns of foliage (Kenefic and Seymour, 1999) as already demonstrated for different tree species (Yacob et al., 1993, 1998 for *Coffea arabica*; Porté et al., 2000 for *Maritime pine*; Medhurst and Beadle, 20002 for *Eucalyptus*). Foliage distribution and needle morphology vary considerably within the crown of a tree (Maguire and Bennett, 1996; Yacob et al., 1993).

With regard to root growth, coffee has extensive root systems that can grow deep, depending on coffee type and soil conditions. At full development, the root system of coffee tree consists of five types of roots. These include the central taproot, the axial roots, the lateral roots that run more or less horizontally parallel to the soil surface, the feeder bearers of various lengths distributed on the tap, axial and lateral roots and the root hairs that grow from the feeder roots (Figure 2.2). The root hairs are found at all depths, but are most numerous near the surface of the soil and are the main providers of mineral nutrition to the coffee plant. In humid heavy soils, the surface roots are concentrated mostly in the upper layers, while there are fewer such roots in dry and sun-exposed soils (Coste, 1992; Wintgens, 2004). Coffee trees can root deeply in a normal soil although about 90% of the roots develop in the upper 30 cm layer. These roots are sensitive to climatic variations (temperature, drought and moisture), but can be protected by shade and mulch (Wrigley, 1988).

The prevailing wide ranges of climatic and soil factors in Ethiopia provide immense genetic potentials of *Coffea arabica* populations. According to Yacob et al. (1996), the domesticated coffee landraces are locally identified by specific vernacular names, and farmers can identify them by their inherently unique morphological and agronomic traits (yield, quality, disease resistance and drought tolerance). Yacob et al. (1996) also reported that Arabica coffee materials can be grouped into three broad canopy classes of open, intermediate and compact types with varying shoot and root growth characteristics. Climatic variables and soil moisture gradients were found to influence adaptation of coffee landraces (Taye and Alemseged, 2004).

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Cilas et al. (2006) defined architectural ideotypes, i.e., coffee trees with good production ability. They emphasized the importance of knowing the relation between yield in the early years and yield in later years. Moreover, traits that can be estimated at an early stage can be linked to yield in the early years, with a view to more effectively predicting later tree yields. Plant shapes seem to be merely the result of ongoing adjustments in relation to the environment and appear to structure themselves as they occur. The shape of a plant, therefore, seems to be the result of a morpho-dynamic process that optimizes hydraulic exchanges and gas exchanges depending on environmental conditions for optimum yield (Pearcy et al., 2005).

Therefore, knowledge on growth characteristics would help to explain the strategies involved in adaptation to specific areas and thus target corrective planning in conservation strategy. In other words, characterization of the diverse coffee types would also allow sustainable, wise exploitation and maintenance of the wealth of wild coffee genetic resources in their original habitats. This can be investigated by taking into account the inherent and stable growth parameters of coffee plant. The objective of this study was to characterize and compare the extent of morpho-physiological diversity of wild Arabica coffee populations in the montane rainforests of Ethiopia.

4.2   Material and methods

As mentioned above, 9 to 12 experimental coffee trees per sub-site and 2 primary branches per tree were selected for measurements of morphological and physiological growth parameters of trees and branches. The selected trees and branches were labeled, and vegetative and reproductive parameters were recorded in the dry and wet months of different seasons (summer, autumn, winter, spring) between 2003/2004 and 2004/2005. The characters include plant height, stem diameter, canopy size, number of primary branches, number of nodes, internode length, leaf and fruit growth. The ratio of main stem height to mean length of lateral branches (apical dominance ratio) was determined according to the procedures described by Parent and Messier (1995) as cited by Robakowski et al. (2003). The relative proportions of old, cropping and young growth were determined on the main stem axis of the tree and primary branches. Moreover, the reproductive effort (RE) of the primary branch was calculated as the ratio of

reproductive (R) and vegetative (V), RE (%) = R/Vx100 (Harper and Ogden, 1970 as cited by Larcher, 2003).

In addition, healthy and mature leaf samples were collected from the third to fourth nodes on primary branches. Leaf dimensions (maximum length and width) were measured and the intact leaf area was estimated using a coefficient (K = 0.66) developed for Arabica coffee (Yacob et al., 1993, 1998). The leaves were oven dried at 70°C for 24 h and dry weight was measured using a sensitive balance. Then, estimated leaf area to leaf dry matter ratio, specific leaf area (SLA) and its inverse, and specific leaf mass (SLM) were calculated. According to Larcher (2003), water storage is a mechanism for desiccation avoidance and is most effective, when it is coupled with surface reduction and high transpiration resistance of the epidermis. Such a measure of storage capacity is given by the degree of succulence using the formula: degree of succulence (g cm^{-2}) = water content at saturation per surface area. Moreover, thirty coffee beans of the selected coffee trees were also used to measure seed dimensions (length, width and depth) to characterize the seed according to Alemseged et al. (1997).

The changes in growth patterns over a year period were used to estimate the growth rates. Leaf mortality over this period was used to calculate foliage turnover rates. As leaf longevity in coffee is less than a year, abscission scars were counted to determine mortality of new leaves initiated after the start of study period. Leaf turnover (% year^{-1}) was estimated according to Christopher (2002) as $[(n_i-n_f)+m_n]/n_i \times 100$, where n_i = initial number of leaves, n_f = final number of surviving leaves from n_i and m_n = mortality of new leaves initiated since the first counting. Intact leaf area was calculated from leaf dimensions and a constant (Yacob et al., 1993, 1998).

Subsequent to root hydraulic measurement, the root systems of the coffee trees were carefully uprooted and intact soil removed. Data on root fresh and dry weights, number of lateral roots, root diameter, root length and root volume were recorded for the taproot and lateral roots. Based on root thickness, the lateral roots were broadly grouped into three classes of fine/small (<0.10 cm), medium (0.10-0.30 cm) and coarse/large (>0.30 cm) and their relative proportion was estimated. Root fresh density was calculated from the mass and volume data. Oven-dried root samples (105°C for 24 h) were weighed and root moisture content (%) was determined.

4.3   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. For growth rate analysis, the data were log-transformed and subjected to statistical analysis in order to ameliorate distribution problems. A one-way ANOVA in a randomized complete block design with three replications was used to examine seasonal and diurnal soil-plant moisture status and growth performance of the coffee trees at each site. Comparison between means was carried out according to Tukey test at $P = 0.05$ whenever the F-test declared significant differences. Moreover, the relationship between variables was assessed from Pearson correlations and regressions analyses. Data were also analyzed using the principal component and cluster analyses with the SAS system for Windows-v8 (SAS Institute Inc. Cary NC, USA), and graphs were prepared with SigmaPlot SPW9.0 (SYSTAT Software, Inc.).

4.4   Results

4.4.1   Shoot characteristics

The results of the nested random effect analysis of variance show insignificant variations among and within wild coffee populations for most of the morphological growth characteristics of coffee trees (Table 4.1). The growth proportion of varying age, however, show significant ($P<0.05$) differences among populations, but not within populations. The height of coffee trees in the forest ecosystem was too tall and in most cases unmanageable. The experimental coffee trees were younger (5-7 years-old) than the mother coffee stands at each site. They were regenerated from the self-sown seeds with little or no care at the early-stage in the semi-forest management system. In spite of this, relatively tall and short coffee trees were obtained from the Harenna (335.17 cm) and Berhane-Kontir (275.83 cm) forests. The main stem diameter at 5 cm above ground was high for Berhane-Kontir (3.35 cm) and Harenna (3.22 cm) as compared to Bonga and Yayu coffee trees. In addition, stem diameter at a breast height (DBH) ranged from 1.61 cm to 2.12 cm for Yayu and Harenna populations, respectively. Furthermore, the widest canopy spread (206.33 cm) and longest internode length (8.21 cm) were recorded in Harenna forest as opposed to the compact Yayu coffee trees with a maximum number

of nodes and shortest internodes (Table 4.1). The morphological parameters indicate that Harenna coffee trees were tall with open canopies as opposed to the more compact Yayu coffee types. Coffee trees from Berhane-Kontir and Bonga had intermediate canopy natures.

The results might be due to the effect of dense shading in enhancing single-stemmed, tall to very tall and non-productive coffee trees, particularly in the lower horizontal branches. The apical dominance ratio also shows high values for closely spaced and densely shaded coffee trees at PIS1, PIS2, IVS2 and PIVS3. The average apical dominance ration was higher in Yayu and Harenna than in the Bonga and Berkane-Kontir populations. At all sites, the value was relatively higher in spring /summer seasons (Figure 4.2). The shoots of the coffee and shade trees were covered with epiphytes, indicating the prevailing high rainfall and humidity in the montane rainforests. This could reflect the influence of leaf area index and thus productivity of forest coffee stands under specific climatic variables.

The reproductive performance of the wild coffee trees also depicted substantial differences among the populations. Consequently, the proportion of crop-bearing surfaces was significantly ($P<0.05$) enhanced in Harenna and Berhane-Kontir as compared to Yayu and Bonga forests (Figure 4.3). At Yayu forest, significantly ($P<0.05$) high non-productive and old growth was enhanced, primarily due to the adverse effects of deep canopy cover and high plant populations (Table 4.1). On the other hand, no significant variations were observed in young growth, although it was slightly reduced at the drier Harenna forest.

Similarly, most growth parameters of coffee trees were not significantly different when compared among the three sub-sites within each wild coffee population. However, the Harenna sites significantly ($P<0.05$) vary in the extent of canopy spread. Hence, it was narrow at PIS1 as compared to the other two sites. Although insignificant, tall coffee trees, thick main stems and maximum number of primary branches were found at PIS2. Similarly, coffee trees within Bonga sites displayed significant ($P<0.05$) differences in the number of nodes produced on the main stem axis. Consequently, the greatest and least nodes were obtained from PIIS2 and PIIS1, respectively. At Berhane-Kontir, the growth of coffee trees did not differ for all the parameters studied. Nevertheless, the maximum proportion of old growth was noted at the Berhane-Kontir

sites. In addition, the lowest number of nodes and no current growth were found at PIIIS3. The highest number of lateral branches could be attributed to the low plant density. This was in contrast to the un-topped long and thin stem coffee trees with little or no cropping branches at the other sites. Because farmers at PIIIS3 remove young growing tips to prepare the favorite local drink called *chemo*. It is a home-made drink popular among coffee growing communities in the Bench and Sheko districts. This was noted to modify the inherent growth potentials of coffee trees with short, thick stems, long primary branch and maximum number of crop bearings. Further studies should be made on the influence of topping and other pruning practices on the growth and yield of coffee trees.

Coffee trees at the three Yayu sites had insignificant variations for all the characters considered, except the significant (P<0.05) differences in the proportions of nodes. Moreover, thin-stemmed coffee trees were found there, but the average number of nodes was high. The shortest and the longest main stem intenode lengths were measured on Yayu and Berhane-Kontir coffee trees, indicating their compact and open crown natures, respectively. The average of the three sites within each population also showed similar trends for all the morphological and agronomic parameters considered. At all sites, the growth of old and non-productive branches was higher with increased plant density and canopy cover in the forest ecosystem. Nonetheless, repeated assessment on growth dynamics of coffee trees vis-à-vis seasonal environmental elements with associated biotic and abiotic stresses needs further work.

Growth architecture of the wild Arabica coffee trees

Table 4.1   Morphological growth characteristics (means ± SD) of wild coffee trees at four montane rainforests of Ethiopia

Growth parameter	Harenna	Bonga	B-Kontir	Yayu	Mean	CV (%)	Pr>F
Plant height (cm)	335.17±35.91	284.33±11.36	275.83±28.02	289.83±19.62	296.29	8.56	Ns
Stem diameter, ground (cm)	3.22±0.30	2.79±0.31	3.35±0.28	2.84±0.08	3.05	9.50	Ns
Stem diameter, DBH (cm)	2.12±0.29	1.94±0.38	1.81±0.11	1.61±0.31	1.87	17.48	Ns
Canopy spread (cm)	206.33±25.32	164.50±13.31	158.83±24.96	166.67±25.87	174.08	14.04	Ns
Number of nodes	41.00±3.28	37.83±5.20	41.17±10.12	45.50±9.12	41.38	17.20	Ns
Internode length (cm)	8.21±0.43	7.66±0.89	6.97±1.28	6.50±1.06	7.34	13.59	Ns
Number of primary branches	34.67±3.06	36.17±5.69	27.00±7.55	29.00±4.50	31.71	19.10	Ns
Old nodes (%)	70.35±9.46	71.00±6.20	72.26±1.56	79.61±9.86	73.31	10.12	Ns
Crop nodes (%)	18.63±5.71a	14.03±2.68ab	16.72±8.66a	2.85±4.93b	13.06	51.51	*
Young nodes (%)	11.03±4.14	14.98±3.54	11.02±9.55	17.55±5.09	13.65	35.80	Ns
Old stem length (%)	74.01±3.86 b	74.05±5.83 b	79.69±0.73 ab	87.30±5.70 a	78.76	5.30	*
Crop stem length (%)	18.72±4.81 a	14.33±2.87 ab	12.76±6.36 ab	1.86±3.22 b	11.92	43.76	*
Young stem length (%)	7.28±2.49	11.63±3.15	7.56±6.48	10.84±2.75	9.33	33.85	Ns
Old branches (%)	37.83±18.75 b	41.21±4.42 ab	36.46±5.01 b	66.55±4.72 a	45.51	20.76	*
Crop branches (%)	42.48±11.43 a	33.75±3.66 ab	41.19±16.33 a	3.70±6.41 b	30.28	39.3	*
Young branches (%)	19.69±7.35	25.04±0.81	22.35±19.49	29.76±6.15	24.21	45.36	Ns

Ns = Not significant; * significant at P<0.05 probability level. Figures followed by the same letter within a row are not significantly different from each other according to Tukey grouping at P = 0.05.

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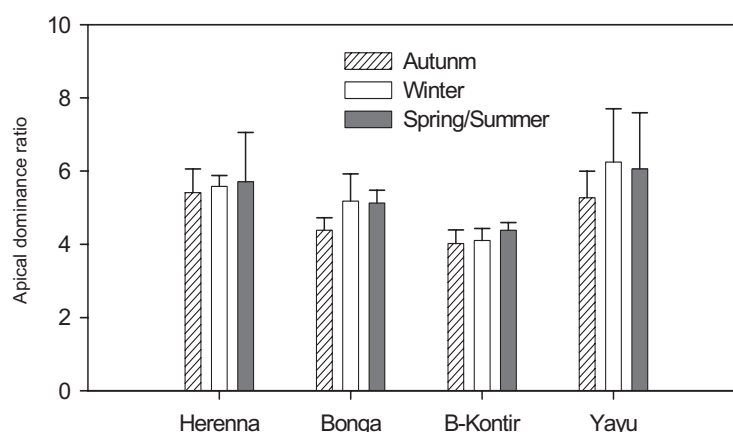
Figure 4.2   Apical dominance ratio of wild coffee trees during the different seasons
of the year 2004/05

On the other hand, there were no significant differences in growth parameters recorded on the main stem cut (30-cm long) of coffee tress in the four montane rainforests. The average stem diameter ranged from 2.73 to 2.18 cm for Harenna and Bonga trees, respectively (Table 4.2). Similarly, the coffee trees at the two corresponding sites exhibited the highest and lowest values for the other stem parameters, Berhane-Kontir and Yayu being intermediate. Dry wood stem density was lightest (0.81 g cm^{-3}) and heaviest (0.93 g cm^{-3}) for the Harenna and Bonga populations, followed by Berhane-Kontir (0.88 g cm^{-3}) and Yayu (0.82 g cm^{-3}). This is in line with the rainfall gradients (Figure 3.2b) and variability in field conditions such as plant density and coffee tree spacing (Table 3.3).

In addition, insignificant differences in the main stem attributes were observed within the sites of each population. Accordingly, at Harenna, slightly thicker stems with high moisture content were obtained at PIS2, compared to the low stem diameters, fresh and dry weights and stem density of the densely populated coffee trees at PIS1. At Bonga, minimum and maximum values were found at PIIS1and PIIS3, respectively. Similarly, increased stem thickness, volume and dry mass were recorded for coffee trees at PIIIS3 and PIVS1 compared to the respective sub-sites within each population. In all cases, the increased stem values suggest improved growth vigor of coffee trees, indicative of reduced plant population and maximum interception of sunlight.

Growth architecture of the wild Arabica coffee trees

Table 4.2   Characteristics of main stem cut (30-cm long) of wild coffee trees at the four montane rainforests of Ethiopia

Stem variable	Harenna	Bonga	B-Kontir	Yayu	Mean	CV (%)	Pr>F
Undebarked girth (cm)	2.73±0.29	2.18±0.19	2.52±0.08	2.34±0.09	2.44	7.91	Ns
Debarked girth (cm)	2.48±0.28	1.95±0.16	2.25±0.10	2.15±0.15	2.21	9.26	Ns
Bark thickness (cm)	0.26±0.01	0.23±0.04	0.27±0.03	0.20±0.07	0.24	18.29	Ns
Basal area (cm^2)	4.87±1.08	3.00±0.48	3.97±0.35	3.66±0.49	3.88	18.66	Ns
Fresh volume (ml)	163.17±20.06	111.67±30.14	145.00±10.00	133.33±10.41	138.29	13.64	Ns
Fresh weight (g)	188.25±25.02	138.28±43.16	166.83±10.72	151.72±17.16	161.27	16.68	Ns
Dry weight (g)	91.161±6.24	70.91±21.65	86.08±5.52	76.36±12.98	81.13	15.12	Ns
Moisture content (%)	51.87±3.50	47.64±2.19	48.40±1.40	47.84±12.01	48.94	12.32	Ns
Fresh density (g cm^{-3})	1.69±0.02	1.85±0.12	1.70±0.07	1.68±0.39	1.73	12.36	Ns
Dry density (g cm^{-3})	0.81±0.06	0.93±0.08	0.88±0.01	0.82±0.04	0.86	6.73	Ns

Ns = Not significantly different from each other (Tukey test at P = 0.05).

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4.4.2   Leaf characteristics

Leaf growth characteristics were quite similar to the other extension growth parameters of the coffee trees. At all sites, leaf production was higher under moderate shading, reduced plant density and during the wet season. In the dry season, the highest leaf number was obtained at PIIS2 in contrast to high leaf defoliation in Yayu (PIVS2 and PIVS3) and Berhane-Kontir (PIIIS2). There was a heavy crop load on the widely spaced coffee trees at Berhane-Kontir (PIIIS3), which could also enhance senescence and foliar defoliation. The average leaf area was highest for Harenna, followed by Berhane-Kontir and Bonga, with a leaf shape varying from ovate to lanceolate. In contrast, the leaf area was smallest for the lanceolate-shaped leaves at the Yayu forest sites (Table 4.3). Generally, leaf shape and size were associated with spatial arrangements of the canopy of the coffee trees and thus different in light and water-use efficiency.

The leaf number was significantly reduced in the winter season and the reduction was highest at PIS1, PIS3 and PIIS3. These were sites with high incidences of coffee leaf rust and coffee leaf skeletonizer. Significant adjustments in leaf area were observed at most sites in Bonga and Berhane-Kontir populations. This was indicated by the inhibited leaf growth in the dry winter season; growth started to increase in spring and summer (Figure 4.1). This suggests the influence of microenvironment variables (moisture, temperature and humidity) and coping mechanisms of the coffee trees. The correlation between leaf number and leaf area was not consistent across sites and over seasons. In general, leaf growth (retention and/or initiation) of varying sizes may also be the reason for the spatial changes in the leaf area of coffee trees.

Statistically significant ($P<0.05$) differences were observed for leaf width, mean leaf area and specific leaf area (SLA). These variables were significantly lowest for Yayu trees compared to the other populations. The destructive leaf parameters did not significantly vary among populations. The coffee trees at the three sites of Bonga, however, significantly varied in leaf dry matter and leaf size. There was also a significant difference in leaf area within the Yayu sites. The results show that leaf area and SLA did not generally follow similar patterns at all sites, except at the Berhane-Kontir sites. As a result, SLA ranged between 124.98 and 151.78 $cm^2\,g^{-1}$ (Table 4.3) for Bonga and Berhane-Kontir, respectively. Further, maximum specific leaf mass (0.008 g cm^{-2}), low leaf water content (72.6%) and low degree of leaf succulence (0.33 g cm^{-2})

were recorded for the Bonga trees. In contrast, Yayu trees exhibited a high degree of leaf succulence (0.46 g cm^{-2}) as compared to the other sites (Table 4.3).

According to the nested design analysis, the crop to leaf ratio on primary branches was statistically (P<0.05) different among forest coffee units (FCUs), but not within each FCU. In this regard, the wild coffee populations had average values that ranged from 2.18 to 0.55 for Bonga and Yayu coffee trees. Similarly, high values were obtained under moderate shadow like at PIS3, PIIS3, PIIIS3 and PIVS1, demonstrating the response to increased daylight conditions. This was noted from the variations in the reproductive effort of the primary branches that varied from 8.2 to 30.5% for the Yayu and Bonga trees, respectively. This could be indicative of constrained fruit and leaf production due to stress as a result of limited light and photo inhibition. This corroborates with the previous findings (Coste, 1992; Tesfaye et al., 2002) on the adverse effects of excessive shading on growth and development of coffee trees. In general, there was a trade-off between crop and leaf growth at most sites. Thus, determination of sink-source relationships, which takes into account plant-environment components, deserves focused attention. It was hypothesized that the higher the number of leaves, the lower the hydraulic conductance (more resistance) in coffee tree and branches (section 5.2).

Table 4.3   Leaf growth parameters of wild coffee trees at the four montane rainforests

Parameter	Harenna	Bonga	B-Kontir	Yayu	Mean	CV (%)	Pr>F
LN	12.00±3.33	11.06±0.34	13.83±2.09	16.28±4.26	13.29	24.84	Ns
LL (cm)	11.97±0.54	10.59±1.71	10.79±0.83	9.97±0.43	10.83	6.57	Ns
LW (cm)	5.30±0.34a	4.40±0.78ab	4.19±0.44b	3.99±0.05b	4.47	8.32	*
MLA (cm^2)	42.42±4.61a	31.90±11.06ab	30.32±5.52ab	26.77±0.73b	32.85	14.66	*
TLA (cm^2)	504.17±298.65	347.73±170.07	424.68±222.76	419.45±215.33	424.01	3.47	Ns
LFW (g)	14.22±2.77	10.09±2.44	11.01±2.83	11.92±3.35	11.81	25.06	Ns
LDW (g)	3.57±0.92	2.80±0.72	2.82±0.72	3.02±0.84	3.05	27.30	Ns
LWC (%)	75.18±2.53	72.55±1.35	74.24±0.79	74.89±0.37	74.21	2.2	Ns
SLA (cm^{2}g^{-1})	150.79±6.55	124.98±9.42	151.78±7.57	140.83±14.30	142.09	7.37	Ns
SLM (g cm^{-2})	0.007±0.001b	0.008±0.001a	0.007±0.01b	0.007±0.001b	0.008	3.85	*
DS (g cm^{-2})	0.35±0.18	0.33±0.11	0.36±0.17	0.46±0.22	0.37	46.54	Ns

*Ns = Not significant; *P<0.05. Means followed by the same letter(s) within a row are not significantly different (Tukey test at P = 0.05). Abbreviations: LN = leaf number; LL = leaf length, LW = leaf width, MLA = mean leaf area, TLA = total leaf area, LFW = leaf fresh weight, LDW = leaf dry weight, LWC = leaf water content, SLA = specific leaf area, SLM = specific leaf mass, DS = degree of succulence.*
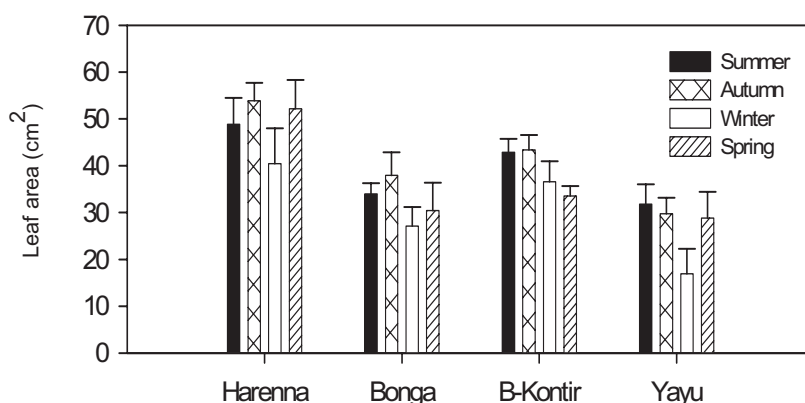
Figure 4.1   Seasonal change in average leaf area of wild coffee populations at the four montane rainforests

4.4.3   Yield and yield components

Fruit and seed growths of coffee trees differed for each forest coffee unit and site. Fruit maturity was fast at Berhane-Kontir, followed by the Harenna and Yayu forests. However, it took a long time at the relatively high altitude Bonga sites as compared with the others. Accordingly, ripe red cherries were collected between November and December 2003. Analysis of the coffee seed characters, revealed considerable variability. Significantly maximum 100-seed weight was measured for Harenna, Yayu, Bonga and Berhane-Kontir coffee trees in descending order. On the other hand, coffee bean length was significantly (P<0.05) shortest in Bonga (0.92 cm), while the highest values were at Harenna (1.12 cm) and Yayu (1.06 cm) (Table 4.4). There were also a slight variation in seed weight and volume within each forest. This may be associated with the high number of fruits per node and thus high competition effect, as fruits are the strongest sink of assimilates.

Table 4.4   Seed characteristics of wild coffee trees at the four montane forests

Bean character	Harenna	Bonga	B-Kontir	Yayu	Mean	CV (%)	Pr>F
Length (cm)	1.12±0.02a	0.92±0.06b	0.99±0.05ab	1.06±0.02a	1.02	4.39	**
Width (cm)	0.66±0.03	0.63±0.04	0.64±0.02	0.68±0.06	0.65	4.70	Ns
Thickness (cm)	0.43±0.01	0.41±0.02	0.41±0.02	0.43±0.02	0.42	3.89	Ns
Volume (cm^3)	0.32±0.02	0.24±0.04	0.26±0.03	0.31±0.04	0.28	11.21	Ns
Weight (g)	0.20±0.01a	0.16±0.02b	0.15±0.01b	0.18±0.02ab	0.17	7.44	*
Density ($g.cm^{-3}$)	0.61±0.03	0.66±0.04	0.56±0.05	0.56±0.03	0.60	5.51	Ns

*Ns = Not significant; * P<0.05; ** P<0.01 significant levels.*

With regard to the reproductive efficiency of coffee trees under forest conditions, the responses differ among populations and sub-sites. Thus, the number of berries on primary branches was notsignificant among the three sites. Nonetheless, the fruit setting capacity increased with decreasing coffee tree density and canopy cover. As a result, relatively high and low fruit counts were found at site PIIIS3 and PIVS2, respectively. This was also evident from the crop to leaf ratio (Table 4.5) and maximum proportions of crop bearing surfaces of 33, 26, 28 and 26% at PIS3, PIIS2, PIIIS2 and PIVS1, respectively. Similarly, a significantly high proportion of young growth on the main stem area was also measured at the sites where minimum coffee tree density was recorded (Table 3.3; Figure 4.3).

However, the smallest crop surfaces were recorded during the spring/summer season at all sites except Bonga (PIIS2 and PIIS3) and Berhane-Kontir (PIIIS3). This could mainly be due to the varying seasonal availability of the natural resources to favor more young vegetative growth across the study sites. In addition, though crop to leaf ratio did not differ within each forest, increased values were recorded with decreasing plant density. Hence, high values were obtained at PIIIS3 (4.13), PIS3 (4.05), PIIS3 (2.75) and PIVS1 (0.98), while the lowest value of 0.75 was found in the most densely spaced site (PIS1), indicating the enhanced reproductive growth with reduced shading.

Table 4.5   Yield and yield components of coffee trees at the study montane rainforests

Variable	Harenna	Bonga	B-Kontir	Yayu	Mean	CV (%)	Pr>F
NPBPT	14.00±6.87	15.65±4.63	15.03±3.52	9.00±2.73	13.42	31.19	Ns
NFPB	26.02±16.54	24.67±10.13	35.61±16.04	7.53±4.86	23.46	43.19	Ns
NNPB	3.95±1.06ab	4.85±1.88ab	6.13±0.70a	2.00±1.24b	4.23	31.54	*
NFPN	5.47±2.83	4.43±0.70	5.46±1.97	2.20±0.95	4.39	37.47	Ns
NFPT	506.80±399.15	453.03±282.34	674.67±413.08	105.53±63.62	435.01	53.81	Ns
FCWPT (g)	602.47±472.76	437.17±285.31	581.17±340.06	106.80±53.37	431.90	54.14	Ns
CCPT (g)	99.84±78.75	72.57±47.36	96.47±56.45	17.73±8.86	71.65	54.29	Ns

*Ns = Not significant (P>0.05), *P<0.05 probability level. Mean figures followed by the same letter(s) within a row are not significantly different according to Tukey test at 0.05% probability level. Abbreviations: NPBPT = No of productive branches per tree; NFPB = No of fruits per branch; NNPB = No of crop nodes per branch, NFPN = No of fruits per node; NFPT = No of fruits per tree, FCWPT = fresh cherry weight per tree; CCPT = clean coffee per tree.*

Moreover, statistically significantly (P<0.05) differences in the number of fruits and cherry yields were obtained within the Bonga sites, though the results do not differ at the other sites. On the other hand, the lowest fruit and highest leaf values were observed in dense shade environments. The highest average clean coffee yield levels

were obtained at PIS3 (161.86 g tree^{-1}) and PIIIS3 (149.27 g tree^{-1}), while PIS1 (11.24 g tree^{-1}) and PIVS3 (11.51 g tree^{-1}) had the lowest yields (Figure 4.3). However, coffee yield levels on a hectare base were low at most sites with increased density of coffee trees and shade, except the relatively high values at PIS3 and PIIS2, which may reflect the extent of human intervention. In general, the low yield results support the work done by Workafes and Kassu (2000). This underlines the potential to improve the environment in a way to prevent damage through insects and fungal diseases and maximize the light-use efficiency of coffee trees. Soil fertility and moisture conditions were found be to sufficient at all sites during the course of the study. In addition, the linear correlation results depict significant associations ($P<0.001$) between all yield and yield variables studied (Table 4.6). This has a practical advantage in the prediction of the yielding potential of a given coffee cultivar or management pratice.

Table 4.6   Correlation values between yield and yield components of the wild coffee trees

Variable	No of crop branches/tree	No of fruits/branch	No of crop nodes/branch	No of fruits/node	No of fruits/tree
No of crop branches/tree	-				
No of fruits/branch	0.91**	-			
No of crop nodes/branch	0.83**	0.87**	-		
No of fruits/node	0.89**	0.94**	0.74**	-	
No of fruits/tree	0.91**	0.99**	0.82**	0.94**	-
Coffee yield (g/tree)	0.93**	0.95**	0.75**	0.96**	0.97**

*** = Correlation is significant at the 0.01% probability level (n = 12; 2-tailed).*
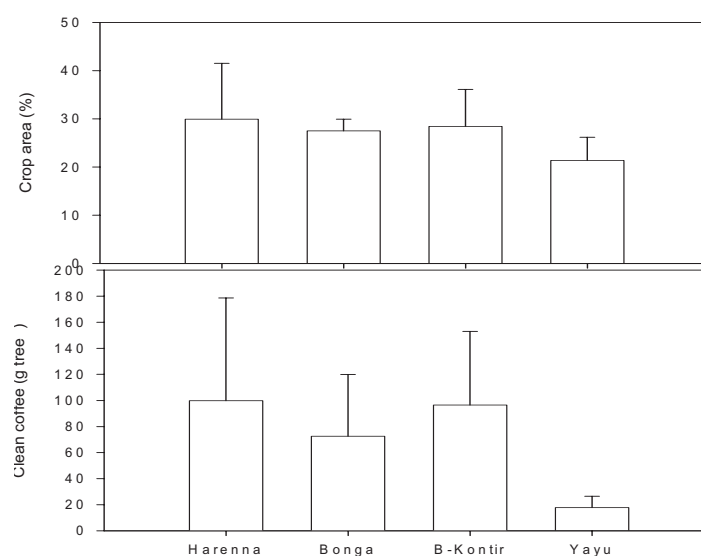
Figure 4.3   Proportion of crop bearing area on main stem and clean coffee yield of the wild coffee trees at the four montane rainforests

From the results of the cluster analysis based on yield and yield components, the different wild coffee populations were classified into 4 broad clusters at about 10 cluster distance (Figure 4.4). Consequently, except for PIS1, PIIS1 and PIVS1, most populations were grouped according to their geographical area. The closest similarity was found between and within the southwestern areas, particularly between the Bonga and Yayu sites (PIIS2-PIIS3, PIVS2- PIVS3 and PIIS1- PIVS1). On the other hand, Bonga (PIIS2) and Harenna (PIS1) populations had the furthest distance (least similarity), reflecting the relatively more humid and drier characteristics of the two forest populations, respectively. The yield components were significantly correlated, indicating the possibility to estimate coffee yield performance of a coffee tree under a given environment.

Rescaled Distance Cluster Combine

```
        0           5          10          15          20          25
        +-----------+-----------+-----------+-----------+-----------+
PIIS2   ┐
PIIS3   ┘
PIIIS1
PIIIS2
PIIIS3
PIS2
PIS3
PIVS2
PIVS3
PIIS1
PIVS1
PIS1
```
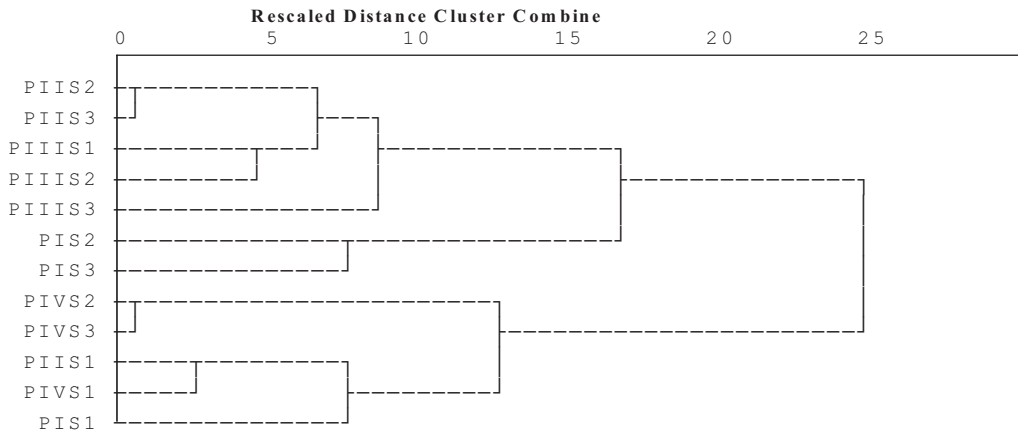
Figure 4.4   Cluster analysis using average linkage between groups of wild coffee populations and yield and yield components of the wild coffee trees

4.4.4   Branch growth

Though Arabica coffee is a shade-tolerant plant, its growth nature and appearance were greatly modified under the heterogeneous forest conditions. Consequently, the selected coffee trees had distinct canopy characteristics and branching habits. Accordingly, the wild coffee populations in Harenna and Berhane-Kontir were dominated by open to intermediate canopy spread with horizontal to semi-horizontal branching. At Yayu forest, the coffee trees were of a more compact type with erect to semi-erect branch orientation, while Bonga forest hosted phenotypically heterogeneous coffee types. According to the analysis of variance, at Harenna, except for branch diameter at the base ($P<0.01$) and number of nodes ($P<0.05$), the other branch variables were not significantly different between the three sites (Appendix 2). Accordingly, significantly maximum of branch sizes (0.52±0.13 cm) and number of nodes (14.33±6.98) were recorded at PIS3. Here, the growth proportions of the node significantly varied due to branch position in the crown. As a result, the values 38.6, 37.0 and 53.4% were determined on old, cropping and young parts of primary branches, respectively.

On the other hand, all branch growth variables were not significantly different within the Berhane-Kontir sites. However, unlike tree growth, maximum branch growth was recorded at PIIIS3, primarily indicating the growth performance of coffee trees with decreased plant populations. This could also be related to the intensity of management practices to modify the potential habit of a coffee plant. Likewise, except

total branch fresh (P<0.05) and dry weights (P<0.05) and number of nodes (P<0.01) on a 20-cm branch cut, the other growth components did not vary within the Yayu sites. Consequently, the highest and lowest total branch fresh and dry weights were obtained at PIVS1 and PIVS3, respectively (Appendix 2). In addition, most branch growth parameters were relatively higher at the Yayu site (PIVS1). Most branch parameters were comparable among the four wild coffee populations. However, statistically significant differences were examined for number of fruits and crop to leaf ratio. These variables were significantly lowest for the Yayu trees as compared to the others. More crop bearing branches were obtained from the Bonga trees. Hence, highest (0.89) and lowest (0.27) crop to leaf ratios were recorded for the Bonga and Yayu trees, respectively (Table 4.7).

In addition, the primary branches revealed slight differences in reproductive effort. The lowest (8.2%) and maximum (30.5%) values were calculated for the Yayu and Bonga trees, indicating the variability in the availability of resources. The water storage capacity of the branches was insignificant and differed from 66.9 to 71.0% on a dry weight basis for the Bonga and Harenna coffee trees, respectively. Generally, branch growth characters exhibited substantial variability and were quite similar to the growth performance of the wild coffee trees. Accordingly, relatively higher values were observed at Harenna and Berhane-Kontir as opposed to Bonga and Yayu. Therefore, it can be expected that branch parameters can affect the patterns of water flow (hydraulic resistance) in the whole coffee plant and its various component parts (section 5.4.5).

Table 4.7   Primary branch characteristics (means±SD) used for the *in-situ* hydraulic measurements at the four montane rainforests of Ethiopia

Parameter	Harenna	Bonga	B-Kontir	Yayu	Mean	CV (%)	Pr>F
BD (cm)	0.48±0.05	0.51±0.08	0.47±0.04	0.49±0.04	0.49	10.68	Ns
BA (cm^2)	0.19±0.04	0.19±0.02	0.17±0.03	0.20±0.03	0.19	16.37	Ns
BL (cm)	66.05±7.71	63.08±4.83	60.89±7.89	57.92±8.04	61.98	12.73	Ns
NNPB	13.05±1.44	12.56±1.00	12.55±1.80	12.67±0.29	12.71	8.92	Ns
INL (cm)	9.56±0.74	8.42±1.32	7.84±0.72	7.63±0.70	8.37	11.34	Ns
NTB	0.50±0.44	1.92±0.78	1.34±1.16	1.72±0.54	1.37	60.92	Ns
NFPB	9.22±5.30ab	10.50±6.06a	10.34±5.48a	3.28±4.96b	8.33	25.85	*
FFW (g)	11.22±5.52	8.87±2.81	9.10±6.31	3.96±5.69	8.29	45.80	Ns
FDW (g)	1.84±0.92	2.18±0.59	1.83±1.27	0.55±0.80	1.60	46.22	Ns
C:L	0.73±0.63ab	0.89±0.51a	0.89±0.37a	0.27±0.32b	0.68	26.81	*
RE (%)	25.81±41.40	30.46±46.89	27.41±48.95	8.15±20.06	22.96	128.85	Ns
BCFW (g)	12.90±2.89	9.01±0.81	9.29±0.84	12.03±2.94	10.81	22.12	Ns
BCDW (g)	4.03±1.35	3.18±0.28	3.05±0.24	3.79±0.79	3.51	24.99	Ns
BCMC (%)	71.00±2.43	66.86±1.24	68.80±1.92	70.06±1.51	69.18	2.76	Ns
VBC (cm^{-3})	4.21±0.34	3.67±0.44	3.89±0.26	4.17±0.44	3.98	10.06	Ns
NNPBC	2.67±0.00	3.05±0.25	2.89±0.42	2.78±0.67	2.85	15.95	Ns

Ns = Not significant; *P<0.05. Means with the same letters within a row are not significantly different from each other according to Tukey test at P = 0.05. Abbreviations: BD = basal diameter; BA = basal area; BL = branch length; NNPB = no of nodes per branch; INL = internode length; NTB = no of tertiary branches; NFPB = no of fruits per branch; FFW = fruit fresh weight; FDW = fruit dry weight; C:L = crop to leaf ratio; RE = reproductive effort; BCFW = branch cut fresh weight; BCDW = branch cut dry weight; BCMC = branch cut moisture content; VBC = volume of branch cut; NNPBC = no of nodes per branch cut (20 cm).

4.4.5   Root growth

Root growth characteristics of the coffee trees of the different populations depicted significant variations in the size and length of large/coarse lateral roots (P<0.01), taproot fresh and dry weights as well as taproot volume (P<0.05). The populations also exhibited significant differences (P<0.05) in total root fresh and dry weights. Again, there were significant site variations in the number of large and fine (small) laterals as well as in the length of medium laterals (Table 4.8; Figure 4.5). The frequency of small laterals varied significantly among sub-sites. In addition, sites significantly differed in the moisture contents of taproot (P<0.05) and total root (P<0.01). However, the other root characteristics did not reveal significant variations among populations and sub-sites. The coffee trees were found to produce few axial roots that grew from the taproot downwards in all directions. These roots were restricted and predominant in the upper 20-cm soil layer and were few in number. Significantly (P<0.05) high proportions of coarse laterals were found in Bonga (49.4%) and Berhane-Kontir (41.3%), whilst the proportions of fine and medium laterals were high in the Yayu and Harenna forests (Figure 4.6), although not significantly different from each other. Hence, the overall average revealed pronounced growth of lateral roots in the same populations. In

addition, these surface plate laterals were significantly (P<0.01) thick (0.80±0.09 cm) and long (116.03±8.52 cm) at Harenna and next longest (87.15±16.19 cm) at Berhane-Kontir. On the other hand, significantly (P<0.05) longest (32.04±2.65 cm) fine lateral roots were measured for Berhane-Kontir as compared to others, particularly Harenna (20.18±6.49 cm).

Furthermore, coffee trees varied in the growth of the taproot system, which grew straight downward and produced many branches in the Berhane-Kontir forest, perhaps reflecting the long-lasting imprints of site-specific stresses during the establishment stages. Accordingly, the average taproot lengths ranged from 68.26±3.64 cm to 104.64±21.41 cm for the Bonga and Yayu coffee trees, respectively. The next longest taproots were obtained from Harenna (94.33±17.49 cm) and Berhane-Kontir (86.24±13.48 cm). Consequently, these coffee trees had significantly (P<0.05) high and low fresh and dry weight taproot, total roots and volume of taproots, respectively. Although statistically insignificant, the density of laterals, taproot and total roots were high in the Harenna and low in the Bonga forest. The results of root moisture content, however, depicted a reverse pattern, illustrating the increased root volume mainly due to more numerous feeder bearers and feeder roots, which are responsible for water absorption. This may also indicate the influence of prevailing rainfall patters, soil conditions and site characteristics.

Within sites, no significant variations were recorded in the diameter of lateral roots (Appendix 3). There were significant site variations in the number of large and small laterals as well as in the length of medium lateral root growth. The results of the large lateral root count show variations among the Berhane-Kontir sites, where more average values were obtained at PIIIS1 (16), compared to PIIIS2 (11). At Harenna, significantly more fine/small roots were recorded at PIS1 (33.00±2.83) as compared to the other sites. Although not significant, these root numbers were higher at PIVS1, where maximum growth of total laterals was also measured. No significant variations were recorded within all sites in the diameter of lateral roots for the three groups (coarse, medium and fine). However, the magnitude of variation varied from location to location. Accordingly, the average values of coarse and fine laterals ranged between 0.90±0.25 and 0.09±0.01, 0.63±0.22 and 0.22±0.04, 0.59±0.04 and 0.21±0.01 and 0.46±0.01 and 0.11±0.02 cm in Harenna, Bonga, Berhane-Kontir and Yayu,

respectively (Figure 4.6). The frequency of small laterals varied significantly within sites. In addition, significant variations in the moisture contents of taproots ($P<0.05$) were detected within the Harenna and Yayu sites (Table 4.9), though the other root parameters were comparable among populations and sub-sites. Accordingly, both lateral root fresh and dry weights were maximum at Berhane-Kontir and lowest at Yayu. Values at Herenna and Bonga were intermediate (Figure 4.7).

Growth architecture of the wild Arabica coffee trees

Table 4.8   Average root growth characteristics (means±sd) of the wild coffee populations at the study montane rainforests of Ethiopia

Character	Harenna	Bonga	B-Kontir	Yayu	Mean	CV (%)	Pr>F
No of laterals							
Large/coarse	7.83±2.08	14.67±3.79	13.50±2.50	11.67±3.25	11.92	28.45	NS
Medium	14.83±4.31	7.83±2.47	8.17±1.76	12.50±2.60	10.83	27.29	NS
Small/fine	26.33±6.29	11.17±10.79	14.17±7.23	30.33±15.78	20.50	45.12	NS
Total	49.00±8.35	33.67±11.09	35.83±4.01	54.67±18.73	43.25	21.21	NS
Girth of lateral root (cm)							
Large	0.80±0.09a	0.48±0.14 b	0.54±0.04 b	0.44±0.02 b	0.57	14.35	**
Medium	0.28±0.05	0.22±0.01	0.23±0.03	0.23±0.03	0.24	13.17	NS
Small	0.10±0.01	0.10±0.03	0.12±0.01	0.11±0.01	0.11	18.20	NS
Root length (cm)							
Large lateral	116.03±8.52a	74.85±9.39 b	87.15±16.19ab	77.35±3.20b	88.85	12.88	**
Medium lateral	55.63±27.96	58.56±15.46	63.87±10.70	52.15±2.38	57.55	27.63	NS
Small lateral	20.18±6.49b	24.04±8.25ab	32.04±2.65a	24.29±3.20ab	25.13	13.20	*
Taproot	94.33±17.49	68.26±3.64	86.24±13.48	104.64±21.41	88.37	19.32	NS
Root weight (g)							
Fresh lateral	130.02±9.75	100.76±37.97	163.02±84.67	81.33±24.76	118.78	43.47	NS
Fresh taproot	396.26±89.84ab	244.50±46.01b	459.44±91.31a	262.25±49.56b	340.61	23.03	*
Total fresh root	526.27±99.60b	345.25±83.30 b	622.46±173.46a	343.57±74.18b	459.39	26.78	*
Dry lateral root	62.03±9.87	41.26±13.19	71.64±38.90	34.58±11.37	52.38	42.83	NS
Dry taproot	223.58±57.85ab	126.91±11.61b	257.57±44.91a	144.25±23.83ab	188.08	21.40	*
Total dry root	285.61±66.40ab	168.17±24.76b	329.21±82.56a	178.83±35.16ab	240.45	24.19	*
Root volume (cm^3)							
Lateral roots	134.67±11.30	105.00±15.00	176.67±88.08	95.00±35.00	127.83	40.95	NS
Taproot	334.17±62.64ab	220.17±50.70	386.67±77.84a	231.67±51.32ab	293.17	22.87	*
Total root	468.88±72.89	325.17±65.54	563.33±163.27	326.67±85.78	421.01	27.03	NS
Root density (g cm^{-3})							
Lateral root	0.97±0.05	0.92±0.29	0.920.03	0.86±0.080	0.92	17.64	NS
Taproot	1.21±0.11	1.13±0.02	1.19±0.01	1.15±0.04	1.17	5.44	NS
Total root	1.13±0.09	1.04±0.08	1.10±0.02	1.06±0.06	1.09	6.22	NS
Moisture content (%)							
Lateral roots	52.42±5.50	58.15±2.69	56.11±0.98	56.90±2.30	55.90	6.04	NS
Taproot	43.88±4.30	46.48±3.69	43.54±1.34	44.70±3.62	44.65	7.72	NS
Total root	46.04±4.83	50.03±4.64	46.67±1.54	47.53±3.12	47.57	8.25	NS

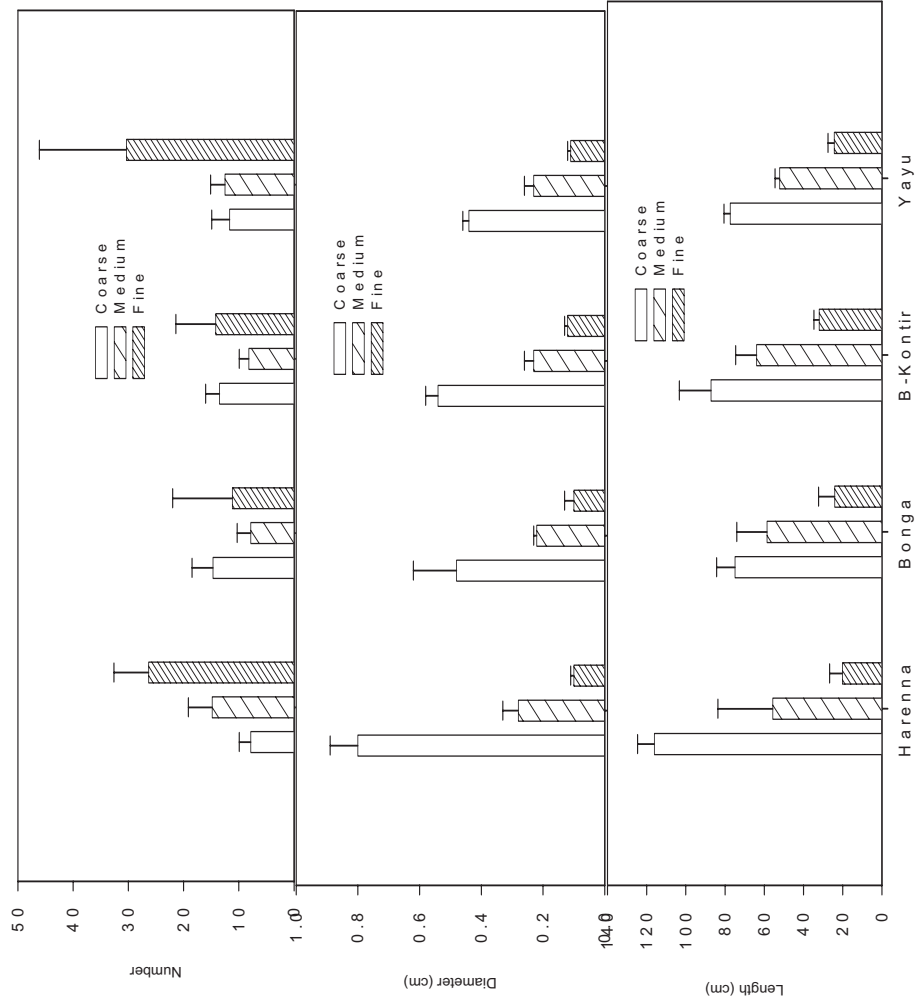Growth architecture of the wild Arabica coffee trees

Figure 4.5   Number, diameter and length of lateral roots of varying size classes in the wild coffee trees at the four montane rainforests

Growth architecture of the wild Arabica coffee trees

Table 4.9 Moisture content (% dry weight), root volume (cm³) and dry mass (g) of lateral roots (means ± SD) for the wild coffee trees at each sub-site within each montane rainforest of Ethiopia

Site	TRV	LRV	LRDW	TRDW	LRD	TRD	LRMC	TRMC
Harenna	Ns	Ns	Ns	Ns	Ns	Ns	Ns	*
PIS1	262.50±88.39	124.00±26.87	54.10±11.26	158.65±57.64	0.96±0.05	1.12±0.01	54.10±2.79	46.19±2.24a
PIS2	361.50±210.01	133.50±9.19	58.92±0.77	242.47±97.15	1.03±0.05	1.33±0.25	56.88±0.35	46.53±0.81a
PIS3	378.50±51.62	146.50±65.76	73.08±33.18	269.63±35.01	0.93±0.04	1.17±0.02	46.28±2.75	38.92±0.72b
Bonga	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns
PIIS1	175.00±91.92	90.00±28.28	27.10±25.80	115.11±64.66	0.61±0.44	1.15±0.08	55.94±0.86	43.03±1.32
PIIS2	275.00±190.92	120.00±42.43	53.20±11.51	138.31±61.86	1.17±0.20	1.12±0.13	61.15±1.01	50.37±8.74
PIIS3	210.50±14.85	105.00±35.36	43.49±9.91	127.31±1.56	0.99±0.03	1.13±0.08	57.37±6.14	46.03±0.54
B-Kontir	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns
PIIIS1	395.00±63.64	150.00±70.71	58.70±24.89	260.42±32.94	0.92±0.00	1.19±0.01	56.95±2.12	44.24±1.34
PIIIS2	305.00±7.07	105.00±35.36	40.85±14.07	211.30±11.99	0.89±0.01	1.20±0.04	56.36±0.28	42.00±0.40
PIIIS3	460.00±183.85	275.00±120.21	115.36±51.31	300.99±118.24	0.94±0.02	1.18±0.02	55.03±0.70	44.39±2.36
Yayu	Ns	Ns	Ns	Ns	Ns	Ns	Ns	**
PIVS1	245.00±21.21	95.00±7.07	36.54±3.18	145.27±15.43	0.93±0.05	1.15±0.01	58.43±4.39	48.63±0.33a
PIVS2	275.00±120.21	130.00±70.71	44.85±23.49	167.55±60.85	0.77±0.08	1.11±0.11	54.25±5.77	43.97±0.74b
PIVS3	175.00±63.64	60.00±14.14	22.36±6.74	119.92±41.34	0.89±0.12	1.18±0.00	58.02±2.84	41.51±1.13c

Ns =Not significant; *P<0.05; **P<0.01significance levels. Means with the same letter(s) within a column are not significantly different according to Tukey grouping at P = 0.05. Abbreviations: TRV= taproot volume, LRV = lateral root volume, LRFW = lateral root fresh weight, TRFW = taptoot fresh weight, LRDW = lateral root dry weight, TRDW = taproot dry weight, LRD = lateral root dry weight, TRD = taproot density, LRMC and TRMC = lateral and taproot moisture content, respectively.

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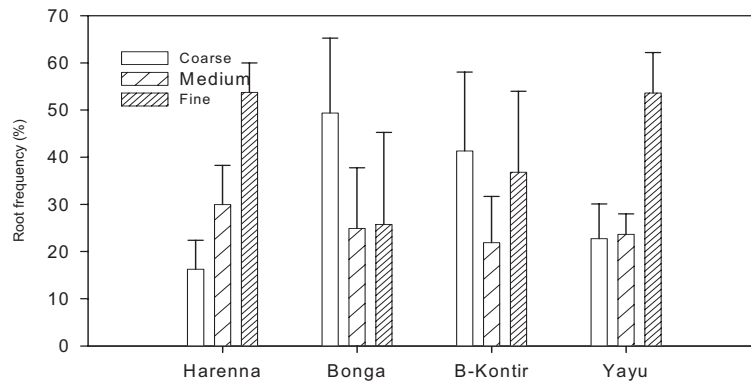
Figure 4.6   Frequency of coarse, medium and fine lateral roots in the wild coffee populations at the study montane rainforests
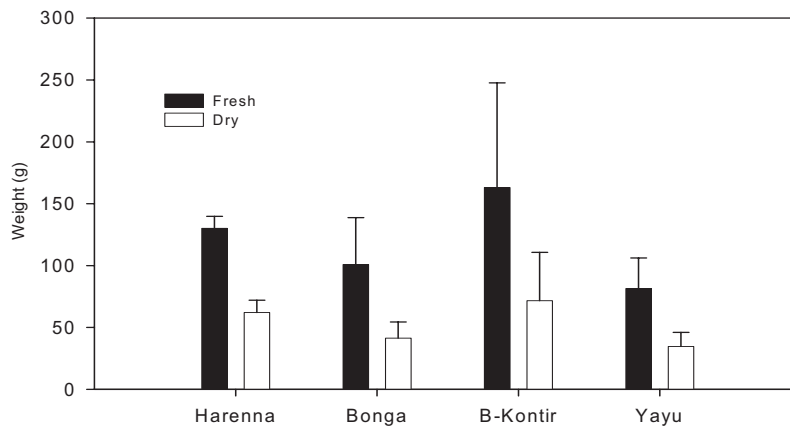
Figure 4.7   Fresh and dry mass of lateral roots for coffee trees of the wild coffee populations in the four montane rainforests of Ethiopia

4.4.6   Growth rate of wild coffee trees

The annual growth rate of coffee trees and primary branches was significantly different among the wild coffee populations (Table 4.10), but not within the sites of each population. Accordingly, the highest growth change for all parameters, except leaf turnover, was recorded in the Yayu forest, while the lowest was for the Harenna population. The fast growth rates in elongation of coffee tree and primary branch was in the order of Yayu>Bonga>Berhane-Kontir>Harenna populations, probably indicating the differences in storage allocation of coffee trees under reduced light regimes. Leaf turnover and leaf area, however, followed opposite patterns and significantly (P<0.0001) high and low annual average leaf turnover rates were determined for the Harenna (6.1%) and Yayu (3.6%) forests, respectively. Bonga and Berhane-Kontir

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exhibited intermediate growth rates. Consequently, significant changes in average leaf size and total leaf area were consistent with the rates of leaf turnover, indicating the variability in leaf production and retention patterns. The estimated leaf turnovers followed the descending order of Harenna>Berhane-Kontir> Bonga>Yayu (Table 4.10).

Table 4.10   Relative growth rate (means±sd) in morphological parameters of the wild coffee trees at the four montane rainforests of Ethiopia

Parameter	Harenna	Bonga	B-Kontir	Yayu	Mean	SEM	Pr>F
PHT	0.07±0.07b	1.49±0.02a	1.44±0.13a	1.51±0.09a	1.12	0.35	***
CD	0.21±0.19b	1.22±0.12a	1.19±0.22a	1.43±0.21a	1.01	0.27	***
BL	0.16±0.09b	1.12±0.13b	1.06±0.28b	1.24±0.08b	0.89	0.25	***
NN	0.28±0.17b	0.77±0.17a	0.68±0.33a	0.82±0.15a	0.64	0.12	**
INL	0.46±0.05b	0.85±0.18a	0.81±0.16a	0.83±0.13a	0.74	0.09	**
NL	0.06±0.35c	0.66±0.34b	0.86±0.29ab	1.22±0.19a	0.70	0.24	**
MLA	-0.22±0.23b	0.94±0.20a	0.81±0.20a	0.84±0.22a	0.59	0.27	***
TLA	-0.15±0.24b	1.59±0.49a	1.68±0.42a	2.02±0.24a	1.29	0.49	***
LTO	6.13±1.02a	3.94±0.18b	4.02±0.35b	3.58±0.16b	4.42	0.58	***
CMLA	3.84±1.05a	2.54±0.31b	2.98±1.05ab	2.43±0.41b	2.95	0.32	*
CTLA	2.53±0.18a	1.83±0.24b	1.78±0.28b	1.73±0.35b	1.97	0.19	**

*$P<0.05$; **$P<0.01$; ***$P<0.0001$. Means followed by the same letter within a row are not significantly different from each other according to Tukey test at $P = 0.05$. Abbreviations: PHT = plant height, CD = canopy diameter, BL = branch length, NN = no of nodes, INL = internode length, NL = no of leaves, MLA = average leaf area, TLA = total leaf area, LTO = leaf turnover, CMLA = change in mean leaf area, CTLA = change in total leaf area, SEM = standard error of mean.*

4.5   Discussion

Although *Coffea arabica* is a shade-tolerant species, canopy openness can influence the efficiency of light and leaf abscission patterns. This demonstrates the influence of dense shading within a forest ecosystem, which can reduce the photosynthetic capacity of the lower leaves, while the upper leaves may experience photo inhibition. Consequently, a significantly high proportion of young growth on the main stem area was measured at the sites where minimum coffee tree density was recorded. The findings could reflect the phenotypic plasticity of coffee plants under low light stress. Tesfaye et al. (2002) reported a similar shade syndrome on the vegetative and reproductive efficiency of Arabica coffee cultivars in Ethiopia. Fruit and seed growths of coffee trees differed among wild coffee populations and fruit maturity was fast in the descending order of Berhane-Kontir>Harenna>Yayu>Bonga. The maximum 100-seed weight was measured for Harenna>Yayu>Bonga>Berhane-Kontir in descending order. Moreover, coffee beans showed variations in length that, beside hereditory factors could be related to the high number of fruits per node and thus increased competition effects. The slight

variation within each forest in some seed parameters could reflect the influence of site-specific microclimatic variables on stand structure and growth performance of the coffee trees. This indicates the influence of climatic conditions on rate of fruit maturity and bean size and thus, coffee quality parameters, which calls for further studies.

The highest leaf dry mass at the Harenna sites could be attributed to the increased carbon assimilation rate due to the relatively limited availability of soil moisture. This corroborates with the findings of Taye et al. (2004a) on dry matter production and distribution in various components of coffee seedlings. The large leaf area, high number of lateral branches and increased fruits on productive nodes may also contribute to the high leaf dry matter yield, reflecting that most assimilates can move to the strongest sinks, i.e, the fruits. This supports the work by Cannell (1971), who reported higher dry matter of fruiting trees than non-fruiting ones due to the high photorespiration in non-bearing trees. The results reveal reduced SLA with reduced shade gradients within the forest sites. Accordingly, relatively higher values were observed at Harenna and Berhane-Kontir as opposed to Bonga and Yayu. This was in line with Hopkins (1995), who showed a positive correlation between SLA and light-use efficiency. Larcher (2003) also reported that shade leaves with high SLA grow better in low light habitats. This was confirmed from the lowest and highest degrees of succulence determined for the Bonga and Yayu coffee trees with the respective low and high leaf water contents. This might demonstrate their high and low sensitivity, respectively to drought stress. Larcher (2003) reported that under certain circumstances succulent plants can survive years of drought; the water reserves after the last rain may be sufficient for several weeks before the stomata remain permanently closed. The water reserves of more succulent plants can protect the plant from too sudden wilting and severe shrinkage of the leaves. In other words, leaves with high specific leaf mass are thick and positively correlated with water-use efficiency under a given radiation load. Yacob et al. (1996) reported similar findings on coffee cultivars.

In addition, the relationships between yield and yield components in wild coffee trees may demonstrate the inherent ties between the attributes. This could underline the possibility to predict potential fruit production of mature coffee trees using the component parameters as shown by Coste (1992) and Wrigley (1988). In this regard, Cilas et al. (2006) identified architectural parameters for predicting the yield

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capacity of *Coffea canephora* using certain architectural parameters. They found that architectural traits are highly heritable and some display strong genetic correlations with cumulated yield. In particular, the proportion of fruiting nodes at the plagiotropic level 15 counting from the top of the tree proved to be a good predictor of yield over two fruiting cycles. Nonetheless, stand structure within each production system and hence the extent of competition during the different growth stages may modify the type of association between the characters. At most sites, crop to leaf ratio and seed weight showed inverse relationships, largely reflecting the influence of environmental stresses on the photosynthetic capacity of coffee trees especially the adverse effects of daylight from high plant density and dense canopy cover. This could result in reduced net photosynthetic rate and constrained reproductive growth of coffee trees (Coste, 1992). The finding is in agreement with the findings of Robakowski et al. (2003) and corroborates with the works of Tesfaye et al. (2002), who reported the same growth responses of coffee cultivars under varying shade regimes. In addition, there was a high indicence of leaf attack by insects, particularly leaf skeletonizers (*Leucoplema* sp.), which were found to cause serious damage and even complete leaf death in deep-shaded coffee trees, particularly at the Harenna sites. There was also damage by coffee leaf rust (*Hemileia vastatrix*), particulary at the Harenna and Berhane-Kontir sites, indicating other causes for the premature leaf defoliation in forest coffee trees. Hence, link between biotic and abiotic stress in the montane rainforests of Ethiopia remains for further investigation.

On the other hand, in maximum light conditions, flowering and crop loads on primary branches were high, indicating the promoted roles of phytohormones. Empty fruits and dried branches primarily due to reduced availability of moisture and nutrients were also not uncommon. This could be explained in terms of unbalanced relationships between demand and supply and relative strength of assimilate sinks among plant components, particularly during the grain filling stage. Under limited availability of soil moisture, this can enhance leaf senescence and shedding as a strategy to reduce the transpirational surface area. The findings, therefore, suggest the need to ameliorate light stress and reduce the competition effect between the vegetative and reproductive parts of the coffee trees through matching coffee types with ideal environmental conditions. Selecting vigorous tree types or improving conditions through wide spacing and pruning

practices could also sustain the productive life span of coffee plants. The present results demonstrate the variability in the interruption of external factors and adjustments involved in coffee plants in stressful forest habitats. Christopher (2002) reported indirect relationships between leaf turnover and availability of light in shade-tolerant and-intolerant trees. Plant growth responses would suggest the successful establishment and adaptation of a plant through maximizing net energy capture and minimizing mortality risks (Christoper, 2002; Kitajima, 1994). Prolonged leaf lifespan requires robustly constructed leaves with low SLA and rendered unattractive to herbivores by toughness, low nutritional value and chemical deterrents (Coley et al., 1985). The findings in the available reports (Christoper, 2002; Lambers et al., 1998; Larcher, 2003) are similar to those of the present study. Therefore, enhancement of energy capture in low light through accumulation of a high leaf area should not jeopardize low light survival. Prolonged leaf retention could be the most cost effective way of enhancing the carbon balance in low light environments. This corroborates with Kitajima (1994), who argued that traits that maximize carbon gain and growth potential are likely to jeopardize survival through increasing vulnerability to herbivores, pathogens and mechanical damage.

The present study provides information on the dynamic availability of resources and growth adjustments of coffee trees in the forest ecosystem. Long leaf retention can be used in the evaluation of coffee types, as it enhances low-light carbon gain, minimize costs of crown maintenance and increases energy through accumulation of a large foliage area, thus avoiding heavy allocation of resources to the production of new leaves. This can be attained through maximum water storage in different plant tissues and organs. The coffee trees at the Yayu and Bonga sites were tall and thin stemmed with small number of nodes and lateral branches. In contrast, the maximum values for most growth variables of the coffee trees in the Harenna and Berhane-Kontir forests indicate facilitation of water flow whenever there is sufficient soil moisture. Hence, the Yayu and Bonga coffee trees have morphological features that could help them to limit hydraulic conductance during drought-stress conditions. Unlike the present findings on the phenotypic diversity, Kassahun (2006) found genetic groupings of Yayu with Berhane-Kontir and Bonga with Harenna, which calls for further studies. The production of high proportions of fine roots at Harenna and Yayu could be due to

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the response to increased water intake when availability is low, whereas, the high proportion of coarse roots at Bonga and Berhane-Kontir may primarily serve as anchorage, as soil moisture is sufficient in these areas. The high mass of lateral roots at Harenna could be an avoidance strategy to cope with drier conditions. When studying the ecology of naturally growing coffee, vegetative parameters of coffee proportional to the actual coffee yields were established by TewoldeBerhan (1986). Previous works (Taye et al., 2004b; Yacob et al., 1996) revealed that compact coffee trees have an extensive but shallow root system that gives access to the upper soil water; these trees were limited to favorable sites. Given the shortage of farmland, coffee farmers have long-standing experience in identifying the right crop types and cropping patterns (Taye and Alemseged, 2004). However, the resource-use efficiency and the magnitude of competition need to be comprehensively examined at the whole-canopy scale.

The fast growth rates in elongation of coffee tree trunk and primary branches was in the order of Yayu>Bonga>Berhane-Kontir>Harenna populations, indicating the differences in storage allocation of the trees under reduced light regimes. According to Kobe (1997), shade-tolerant species allocate proportionally more resources to storage and less to growth than light demanding associates, whereas these differences are not manifested in high light conditions. High allocation to storage while the limiting ability to capitalize on opportunities in resource-rich habitat, provides a buffer against tissue loss in low light, where recovery from such setbacks is difficult (Coley et al., 1985). Highly significant high and low annual average leaf turnover rates were determined for the Harenna and Yayu populations, respectively, while those of Bonga and Berhane-Kontir were intermediate. This is in agreement with leaf size, indicating the variations in carbon assimilation and accumulation patterns. The accelerated foliage turnover at Harenna can also be related to the enhanced leaf photosynthetic capacity and hence, fast leaf ageing and senescence as compared to the other populations. At Harenna, there was a decline in average and total leaf area during the study period, which indicates the importance of leaf area adjustment at the drier sites. The results of leaf growth support the report by Taye (1998) on seasonal leaf growth patterns in improved Arabica coffee cutivars in southwest Ethiopia.

The annual growth rate of the coffee trees and primary branches were significantly different among the coffee populations, but not within the sites of each

population. The fast growth rates in elongation of coffee tree trunk and primary branches was in the order of Yayu>Bonga>Berhane-Kontir>Harenna populations, indicating the differences in storage allocation of the trees under reduced light regimes. The variability in climatic conditions could also be the reason for the differences in growth rates. As a whole, low light stress seems to be the most important limiting factor affecting growth and development of the coffee trees at all sites. Hence, the present findings suggest that light management is amongst the high priority areas that require appropriate adjustments with the view to improve growth architecture and sustain the production of wild and organic coffee while conserving the gene pool in minimally disturbed natural forests. There could be trade-offs between plant population, tree size, water-use efficiency and tolerance to drought-stress conditions, and these are amongst the priority areas that call for further studies. Therefore, hydraulic characteristics in field conditions were examined (Chapter 5). Nonetheless, in-depth studies mainly on the botany of coffee plants is critically important to characterize and maintain the enormous diversity of wild coffee materials. This should take into account, among others, leaf structure and functions with the emphasis on phenological events, biochemical and genetic constituents and nature of trade-offs involved in the underlying shoot and root adaptation strategies. Such knowledge would have great practical implications for the design of *in-situ* conservation of the wild coffee populations in their center of origin.

5 WATER RELATIONS AND HYDRAULIC CHARACTERISTICS OF THE WILD COFFEE TREES

5.1 Introduction

Water availability is one of the most important factors controlling the distribution of plant species at the global scale. Soil water facilitates the absorption of minerals by plants while plant water content helps in maintaining the right type of turgidity for growth. The movement of water from the soil into the roots is mainly affected by the extent to which the roots spread (Coste, 1992). A coffee tree has a limited surface area but widely spreading surface root, and, therefore, has generally low rates of water uptake (Wrigley, 1988). Old coffee trees were found to be highly responsive to improved management inputs such as pruning, soil moisture conservation, rejuvenation practices and population adjustment (Yacob et al., 1996). However, information is lacking on the mechanisms underlying such response.

Plant drought stress requires the understanding of the atmospheric demands on the plant, plant regulation and soil moisture supply. Hence, leaf water potential was found to be the most suitable technique for assessing the internal water balance by integrating soil moisture tension, the resistance to water movement within the plant and the demand for transpiration imposed by the environment. The internal water balance in coffee trees is influenced by soil moisture, soil type and root resistance (Coste, 1992). 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).

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. Cavelier et al. (1996) found no evidence for reduced transpiration rates among cloud forest tree species in Colombia.

There is a lack of knowledge of the water relations of montane forest tree species in relation to their hydraulic architecture. Cavelier et al. (1996) proposed that cloud forest species might differ from lowland species in their hydraulic architecture and that may lead to limitations of transpiration under sunny conditions. They suggested that hydraulic conductance of cloud forest trees may not be high enough to compensate for the high water losses that occur during sunny periods. A water supply limit by the hydraulic conductance of stems would lead to a reduction in leaf size and leaf area index. The well-documented decline in leaf size with increasing altitude in tropical mountains has defied definitive explanation. However, there are no studies providing information to test this and pertinent studies focused exclusively on lowland species (Tyree and Ewers, 1996), although these have not been studied in Ethiopia.

The value of high rainfall in crop production depends on a number of factors affecting availability of water to plants, namely, the evenness of rainfall distribution, the water acceptance and storage properties of the soil, the soil tension and conduction properties and also characteristics of the plant itself (Williams and Joseph, 1970). Plant growth rate is determined by the rate of carbon gain and the rate of cell volume growth. The latter is mostly due to the rate of water uptake by expanding cells and this rate is controlled by cell turgor, which is a function of cell osmotic pressure and leaf water potential. 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.

Leaf water potential is a limiting factor of stomatal conductance. As it decreases with increasing basal diameter (a proxy for tree size), it seems likely that stomatal conductance will be increasingly restricted as trees grow larger. A number of 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. A great deal is known on how drought and frost causes xylem dysfunction and loss of stem and root hydraulic conductivity, and hence loss of plant conductance (Tyree and Zimmermann, 2002). 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 invesigation by Tyree et al. (1998), where five species of tropical seedlings were grown in a common environment. They showed that high plant hydraulic conductance is a necessary condition for high productivity in forest trees. Other necessary conditions might be low leaf area index and high photosynthetic capacity in leaves. These conditions correspond to the structural functional components of a tree that are necessary for good performance. Testing the proper functionality of plant parts can be used as an early predictor of high yield for the selection of trees in a breeding program. 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.

In this regard, studies on the response of Arabica coffee along climatic gradients and in complex production systems are amongst the high priority areas identified in the strategies and priorities of the national coffee research of the country (EARO, 2002). In Ethiopia, drought is one of the reasons for the loss of adapted coffee landraces, particularly in marginally suitable areas. Therefore, within the context of drought-stress adaptation amplitudes of wild Arabica coffee populations, the specific objective of the study was to examine the extent of spatial (seasonal and diurnal) soil-plant water dynamics in the forest coffee trees along climatic and soil moisture gradients. The study also assessed hydraulic conditions such as water relations, hydraulic conductance of the coffee trees, hydraulic resistances of branches as well as leaf- and stem- specific hydraulic conductivity of wild coffee populations in the studied montane rainforests.

5.2   Material and methods

5.2.1   Soil-plant moisture contents

The studied montane rainforests were heterogeneous in terms of canopy structure and other physical characteristics as elaborated in Chapter 3. Seasonal and diurnal soil-plant water dynamics were monitored at predawn and midday using a portable pump-up pressure chamber (PMS Instrument Co., Corvallis, USA) following the method of

Scholander et al. (1965). The tip of a lateral branch with two pairs of healthy leaves was removed from the upper canopy of the selected trees. The leaf sample was carefully cut and immediately enclosed in a steel pressure chamber. The pressure inside was increased gradually until small sap droplets appeared at the position of the xylem vessels on the cut surface. The pressure reading at this point represents the plant water potential in the field.

Simultaneously, soil moisture (% vol.) was determined using a Theta probe type ML2 (Delta-T Devices Ltd., Cambridge, UK). In addition, 500 g soil samples were collected and immediately measured using a sensitive balance (KERN 440-33, Kern and Sohn GmbH, Germany). Then oven-dried dry weight was recorded to calculate volumetric field soil moisture content (% dry wt basis). Moreover, fully expanded and healthy leaves were collected (before sunrise) from the third to fourth nodes on primary branches and leaf fresh weight was immediately measured using a pocket balance (KERN CM 320-1, Kern and Sohn GmbH, Germany). The sample leaves were oven dried at 70°C for 24 h and dry weight was recorded to calculate the osmotic leaf water content (% dry wt basis). In addition, the measurements were made over four seasons: summer (August 2003), autumn (December 2003), winter (March 2004) and spring (September 2004). At Harenna, the last data were collected in the first week of August 2004. The last data on soil-plant moisture contents were determined between August and September 2005. Unlike Harenna of the southeast, this is the main rainy season in the three southwestern rainforests. The summer and winter seasons represent the driest months in southeast and southwest study areas, respectively (Figure 3.2b).

5.2.2   Hydraulic measurements

Two experimental coffee trees per sub-site were used for hydraulic measurements. Three primary branches per tree were sampled from the three positions of a tree crown (bottom, middle and top) thus, representing different age groups. Subsequent to recording all growth parameters, hydraulic measurements were made using a high-pressure flow meter (HPFM). Hydraulic conductances (K_h) in root and shoot parts as well as hydraulic resistance (R_h) in primary branch segments (Dynamax Inc., Houston, TX, USA) were measured following the procedures adopted by several authors (Martinez et al., 2002; Tyree and Dixon, 1986; Tyree et al., 1993). 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 recut under water and connected to the HPFM. Root and shoot hydraulic conductances 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 deionized 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 of the different parts of the coffee trees.

The selected primary branches were labelled, removed and immersed in 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 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). 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 (Chapter 4) and their relationships with hydraulic characteristics were examined.

5.3   Statistical analysis

Analysis of variance was performed with the default SAS procedures. The bivariate Pearson's correlation coefficient was run to assess associations between the variables. Factor analysis was conducted to identify underlying variables that explain the pattern of correlations within a set of observed variables. Moreover, cluster analysis was performed using the stable functional traits like xylem hydraulic measurements. The means were compared using the Tukey test at 0.05% probability level. Graphs of two-way interactions were made with SigmaPlot.

5.4   Results

5.4.1   Soil moisture

The spatial soil moisture dynamics were significantly different at only three of the four studied rainforests. In the southwest sites (Bonga, Berhane-Kontir and Yayu), the average results follow the order spring>winter>autumn. Accordingly, the highest (PIIS2 = 39% vol.) and the lowest (PIIIS2 and PIIIS3 = 10% vol.) were obtained in May/June 04 and February/March 04, respectively. In contrast, at the southeast Harenna sites, soil moisture content increase from spring (13.3% vol.) to winter (16.0% vol.), which is in line with the rainfall patterns between the southwest and southeast of the country (Figure 3.2). In contrast, the values at Harenna were higher in winter than in summer. As a result, significant differences among the forest sites were recorded in autumn (P<0.05) and spring (P<0.001), when Harenna had the lowest soil moisture of 14.7 and 13.3% vol., respectively. However, significantly maximum soil moisture contents were measured at Berhane-Kontir (28.4%) and Bonga (37.4%) soils in autumn and spring, respectively. In winter, soil moisture contents in the four rainforests were not significantly different, with values ranging from 12.8 to 17.1% in Berhane-Kontir and Bonga, respectively (Figure 5.1). From the soil moisture reading and volumetric determination at Harenna, the significantly highest values were obtained in winter, spring/summer and autumn in that order. At Yayu, significantly lowest (13.7% vol.) and highest (36.5% vol.) soil moistures were measured in spring and winter, respectively, with the same patterns at each of the three sub-sites.

Moreover, the results reveal significant differences among sites within each forest site. The lowest values were recorded during the dry season at sub-sites PIS1,

PIIS1, PIIIS2, PIIIS3, PIVS2 and PIVS3. Except PIIIS3, these were those where high plant density was recorded (Table 3.3; Figure 3.4). The low soil moisture status at PIIIS3 could be mainly associated to the reduced plant density, low shade cover, shallow soil depth and loose soil texture. The gradient of the plot was also noticed to slightly influence soil moisture, particularly in the drier Harenna forest. The status of moisture was higher at the bottom of the slope than at the top. This was not the case in the southwest forest sites where moisture was adequate (Figure 5.2). In general, despite the variations in slope ranges, soil moisture gradient was not significant, indicating the contributions of vegetation cover in curtailing run-off and conserving soil moisture.
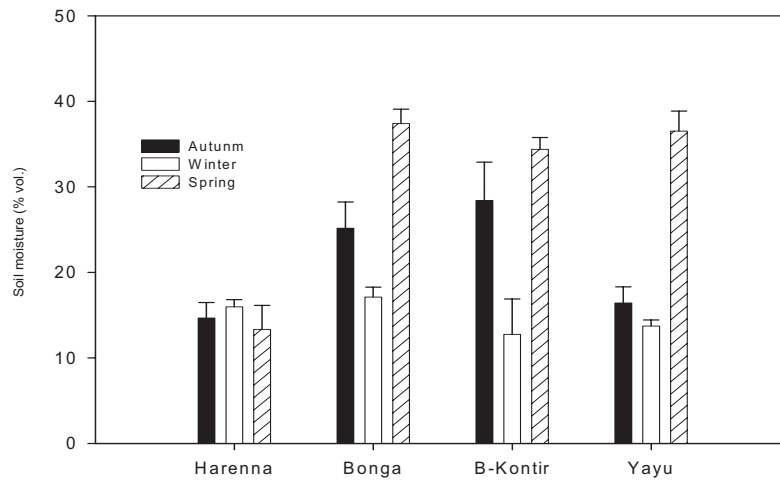

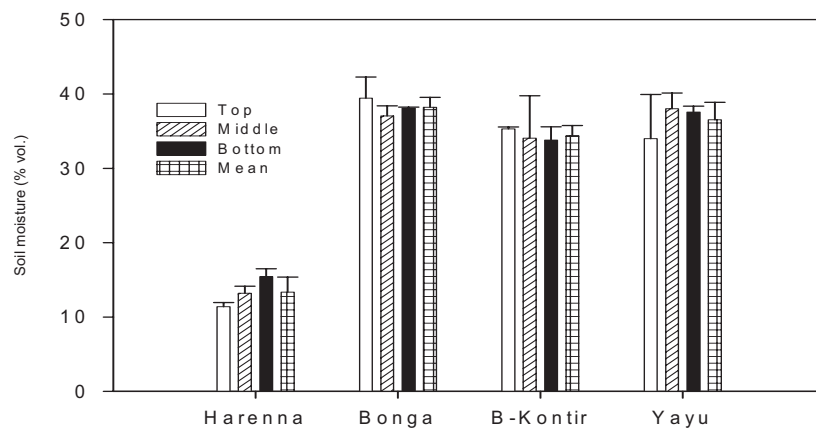Figure 5.1   Seasonal soil moisture dynamics at the four montane rainforests of Ethiopia

Figure 5.2   Soil moisture as influenced by land gradients in the studied montane rainforests of Ethiopia

5.4.2   Leaf water content

The results of midday leaf water potential (LWP) also reveal significant differences due to seasons and sites. At the southwest sites, the diurnal LWP values were much lower in winter than in spring. Thus, the lowest LWP at Bonga and Berhane-Kontir were measured during the dry winter season when the diurnal range was also low (Figure 5.3). Conversely, coffee trees at the Harenna sites had significantly lower LWP values in August (summer), when the diurnal LWP changes were also minimal as compared to the other seasons. Except at Harenna (PIS1) and Berhane-Kontir (PIIIS1), significant predawn LWP variations were detected between the winter and summer seasons. Accordingly, maximum predawn values were measured during the summer season in the southwestern sites as opposed to lower values measured in this season at Harenna.

The diurnal LWP patterns at each site fluctuated over seasons. Hence, the maximum midday LWP results show highly significant seasonal variations at all sites, except at PIS2. At Harenna, the values showed a decreasing trend from autumn to summer. Conversely, there was a highly significant change in midday LWP across seasons at the other sites, where lowest and highest values were measured in winter and summer seasons, respectively (Figure 5.3). This is similar to the status of seasonal soil moisture dynamics (Figure 3.2). However, at Bonga (PIIS1 and PIIS2) the midday LWP showed no significant difference between dry and wet seasons. The range in LWP between autumn and spring was minimum at Harenna as compared to the southwest sites, where high seasonal ranges in the order of Yayu>Berhane-Kontir>Bonga were determined (Figure 5.3). Midday leaf water potential was significantly low at Bonga, Berhane-Kontir, Yayu and Harenna in that sequence. Predawn and midday LWP were significantly ($P<0.001$) lower in the dry winter as compared to wet spring season in the southwest sites. The Harenna coffee trees showed highest predawn LWP and maximum diurnal LWP differences in winter as compared to the southwest sites, particularly the Yayu and Bonga trees. The results of osmotic leaf water content also reveal slight variations between autumn and spring/summer seasons, particularly at Harenna and Yayu (Figure 5.4). Similar to LWP, a higher leaf water content was determined in autumn (December 2003) compared to winter (March 2004) at the three wild coffee populations in the southwest (Figure 5.5). Despite the high soil moisture content, the Bonga coffee trees showed reduced leaf moisture content on dry weight bases. Soil

moisture content was positively and strongly correlated (r = 0.57*) with leaf water contents. Thus, the Harenna and Bonga trees had a low leaf moisture content under limited availability of soil moisture. In contrast, the Yayu trees showed relatively high leaf water content with increased soil moisture (Figure 5.6).
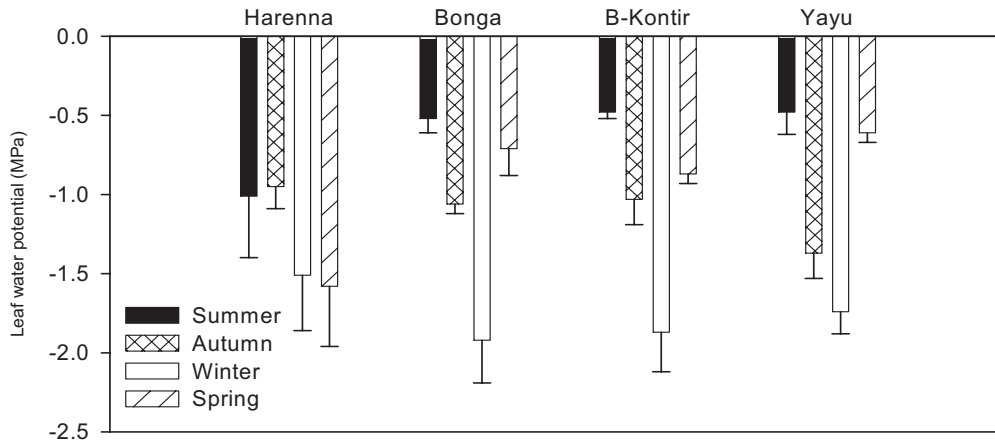

Figure 5.3   Seasonal changes in midday leaf water potential of wild coffee trees at the four montane rainforests of Ethiopia (capacity of the pressure chamber = -2.1 MPa)
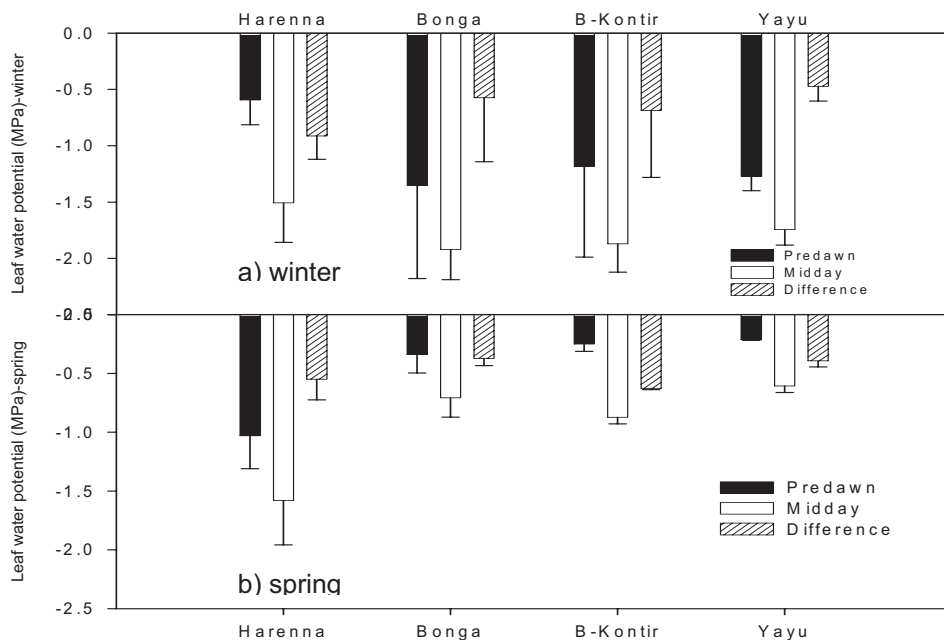

Figure 5.4   Diurnal changes in leaf water potentials of wild coffee trees at the four montane rainforests in a) winter (dry) and b) spring (wet) seasons (capacity of the pressure chamber = -2.1 MPa)

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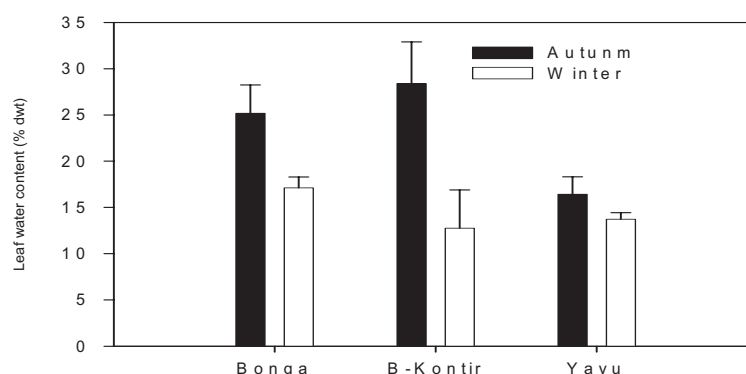
Figure 5.5   Leaf water content determined for autumn (wet) and winter (dry) months at the southwest studied montane rainforests of Ethiopia
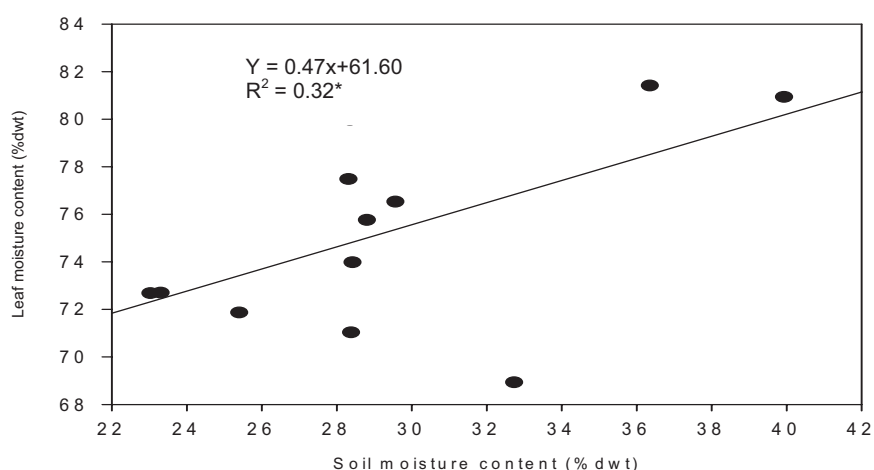
Figure 5.6   Linear regression between soil and leaf moisture contents for the pooled data of the study sites (12 sub-sites) in montane rainforests of Ethiopia

5.4.3   Hydraulic conductance

The coffee trees from the four wild coffee populations did not reveal significant differences in whole-plant, root and shoot hydraulic conductance (Appendix 6). Significant variations (P<0.01) were, however, detected in main stem hydraulic conductance and stem-specific hydraulic conductivity (Table 5.1a). In addition, whole-plant conductance showed significant variations (P<0.05) within the Harenna sites and between coffee trees at Berhane-Kontir and Yayu. At Bonga, this did not change due to sites and coffee trees. Hydraulic conductance in the various parts of coffee plant did not change within sites, except for the significant variations (P<0.05) 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 Berhane-

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Kontir had intermediate stem results (Table 5.1a). 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 Berhane-Kontir (15%) and Yayu (18%). This was positively related to stem size and vegetative growth responses of the coffee trees under the heterogeneous forest environments.

At all study sites, higher conductance was 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 Berhane-Kontir (37%) and Yayu (33%) (Figure 5.7). 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 Berhane-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 Yayu and Berhane-Kontir, respectively (Figure 5.8). The coffee trees from the Berhane-Kontir and Harenna forest stands revealed high hydraulic conductance both in the root and whole-shoot parts as compared to Bonga and Yayu. The overall mean whole-plant hydraulic conductance was significantly ($P<0.05$) higher at Harenna and Berhane-Kontir as opposed to the lowest value for Bonga. The results follow the order of Harenna (2.69×10^{-4} kg s^{-1} m^{-2} MPa^{-1})>Berhane-Kontir (2.30×10^{-4} kg s^{-1} m^{-2} MPa^{-1})>Yayu (1.36×10^{-4} kg s^{-1} m^{-2} MPa^{-1}) >Bonga (1.13×10^{-4} kg s^{-1} m^{-2} MPa^{-1}) (Figure 5.9).

In agreement with the results of the populations, the analysis of variance for hydraulic conductance of root and whole-shoot components revealed insignificant variations within the sites of each population (Table 5.1b). However, relatively high root, whole-shoot and leaf conductance values were measured for the same sites of each population. These included PIS2, PIIS3, PIIIS3 and PIVS2 when compared to the other respective sites. This pattern was found to shift with the removal of fruits and petioles, and maximum conductance was measured at PIS3, PIIS3, PIIIS3 and PIVS2. At Yayu, whole-plant conductance decreased from PIVS1 to PIVS3, which may be related to the

weak growth performances of coffee trees with increased shade cover and plant density (Table 3.3). At Bonga, significant site variations were observed in hydraulic conductance due to removal of all plagiotropic branches and to reduced main stem length. Thus, significantly lower values were measured at PIIS1 as opposed to the value at PIIS3. Unlike the variations among populations, within-site differences in main stem specific hydraulic conductivity were comparable and the results are in consistence with the stem conductance patterns at Harenna and Bonga. Conversely, stem conductivity was reduced at Berhane-Kontir (PIIIS3) and increased at Yayu (PIVS3) due mainly to the more and less favored shoot growths at the two respective sites (Table 5.1b; Figure 5.9). The results of main stem diameter and main stem hydraulic conductance show the same pattern for the wild coffee populations. Consequently, the values were higher for Harenna followed by the Berhane-Kontir coffee trees. These were lowest for Bonga and Yayu (Figure 5.10). Furthermore, the influence of stem size on hydraulic flow was confirmed by the strong positive linear regression (Figure 5.11).

Table 5.1   Variations in hydraulic conductance (means$\pm$SDx10^{-4} kg s^{-1} m^{-2} MPa^{-1}) and stem conductivity (k_hx10^{-4}kg s^{-1}m^{-1} MPa^{-1}) in coffee trees of the four wild populations (a) and sub-sites (b) within each montane rainforest of Ethiopia

a)   Populations

Plant part	Harenna	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	**

b)   Sub-sites

Site	Root	Whole shoot	Leaf	Fruits/petiole	Branch	Stem cut (30 cm)	Stem conductivity
Harenna	NS	Ns	Ns	Ns	Ns	Ns	Ns
PIS1	1.10±0.17	1.02±0.12	1.06±0.05	1.08±0.02	1.30±0.13	4.96±1.39	1.71±0.78
PIS2	2.39±2.53	2.83±2.68	2.47±0.73	1.61±0.02	3.13±1.29	7.26±0.67	1.82±0.18
PIS3	1.80±0.15	2.78±0.75	1.72±0.46	2.10±0.43	3.06±0.23	6.79±0.01	1.65±0.18
Bonga	NS	Ns	Ns	Ns	*	*	Ns
PIIS1	0.64±0.39	0.53±0.11	0.98±0.87	0.52±0.22	0.68±0.31c	1.24±0.57b	0.63±0.10
PIIS2	0.56±0.09	0.86±0.11	0.89±0.09	0.91±0.04	1.26±0.33b	1.86±0.69b	0.83±0.50
PIIS3	0.65±0.04	1.04±0.04	1.07±0.01	1.12±0.01	1.92±0.31a	3.63±0.44a	1.24±0.27
B-Kontir	NS	Ns	Ns	Ns	Ns	Ns	Ns
PIIIS1	1.27±0.11	3.69±0.95	1.22±0.16	1.22±0.04	2.39±0.42	4.41±0.18	1.52±0.08
PIIIS2	1.04±0.16	1.21±0.14	1.00±0.05	0.98±0.03	1.40±0.05	2.43±0.13	0.85±0.07
PIIIS3	2.41±0.01	4.37±2.96	3.82±3.18	2.58±1.61	2.39±0.77	3.66±0.99	1.12±0.33
Yayu	NS	Ns	Ns	Ns	Ns	Ns	Ns
PIVS1	0.74±0.18	1.95±0.45	1.15±0.13	1.07±0.08	1.60±0.27	2.34±0.37	0.71±0.04
PIVS2	1.07±0.37	1.55±0.82	1.26±0.95	1.19±0.08	1.36±0.60	2.05±0.34	0.87±0.33
PIVS3	0.52±0.30	1.30±0.76	0.87±0.38	0.77±0.27	0.93±0.30	2.82±1.02	0.88±0.45

*Ns = not significant; * significant at $P<0.05$ and ** significant at $P<0.01$*
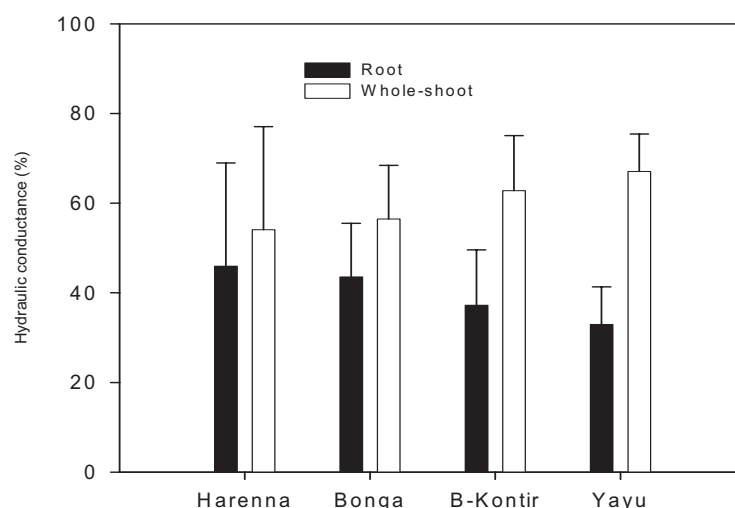
Figure 5.7   Percent whole-plant hydraulic conductance in root and whole shoot of coffee trees of the four montane rainforests of Ethiopia
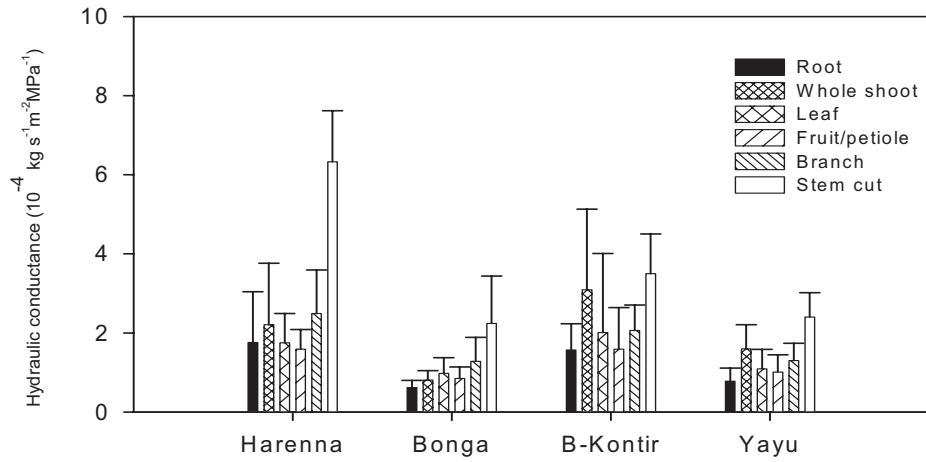
Figure 5.8   Hydraulic conductance in components of the wild coffee trees at the four montane rainforests of Ethiopia
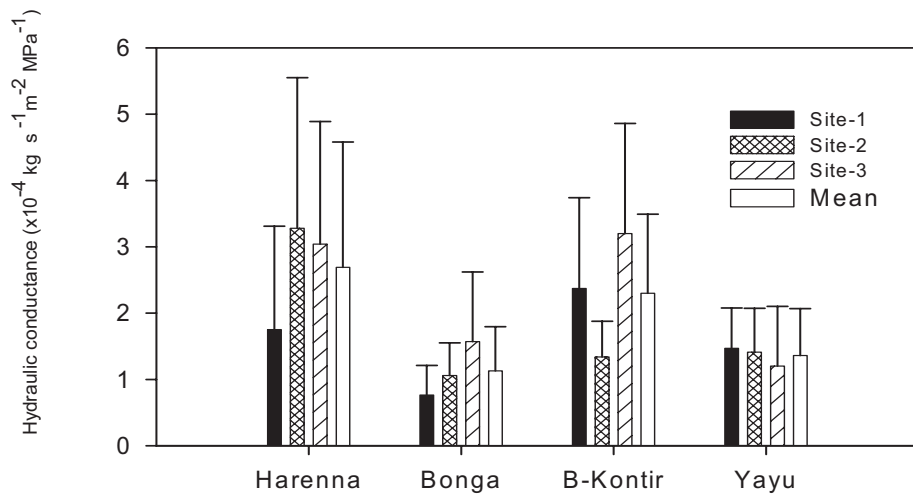
Figure 5.9   Variations in whole-plant hydraulic conductance of coffee trees within sites of each montane rainforest of Ethiopia

Figure 5.10   Diameter of main stem cut and hydraulic conductance of wild coffee trees at the four montane rainforests of Ethiopia
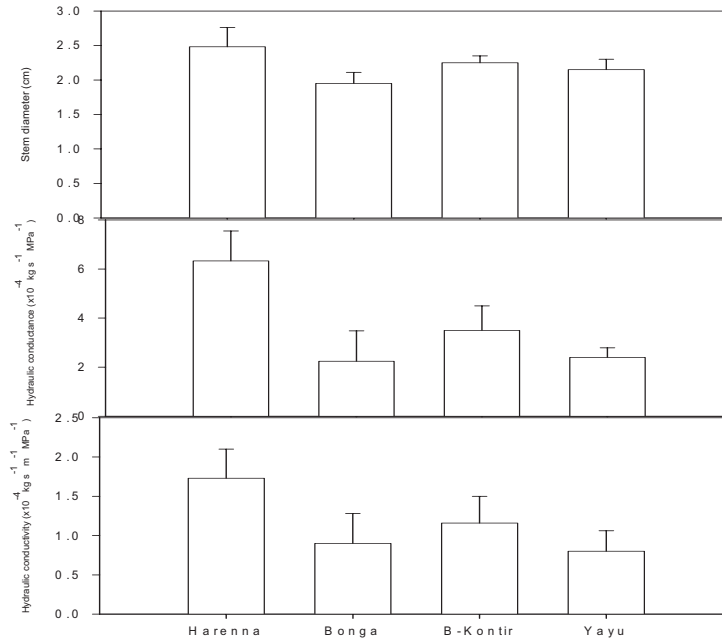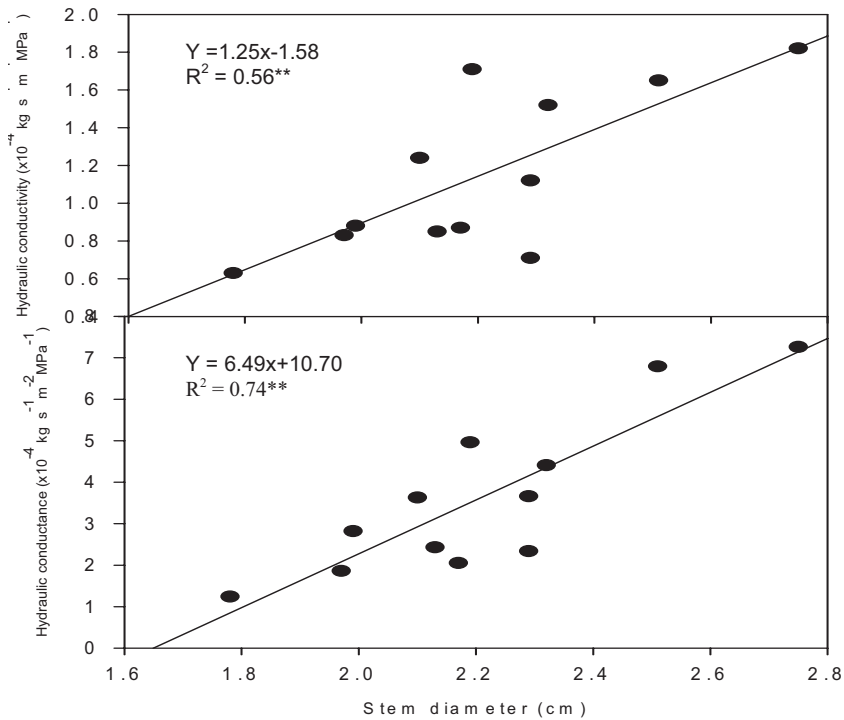

Figure 5.11   Hydraulic conductance and specific hydraulic conductivity of main stem cut (30 cm) plotted against debarked main stem diameter of wild coffee trees using pooled data from the study sites (12 sub-sites)

5.4.4   Relations between growth and hydraulic parameters

Shoot conductance

The correlation results among growth characters and hydraulic conductance measurements for the different coffee populations reveal different patterns and magnitudes for the various plant parts and growth stages. Accordingly, the correlation values were highly significant between stem size and hydraulic conductance due to removal of primary branches ($r = 0.67**$), main stem cut at 30-cm long ($r = 0.56**$) and root conductance ($r = 0.56**$) and with stem hydraulic conductivity ($r = 0.55**$). Similarly, stem size significantly ($P<0.05$) correlated with conductance in the whole shoot and removal of all leaves and lateral branches. The results show that the size of the main stem significantly and positively influenced the water movements in the root and shoot parts of the coffee trees in natural forest ecosystems (Tables 5.2a; 5.2b).

In addition, shoot hydraulic conductances with and without leaves, petioles and branches was negatively correlated with the number of old and young nodes, internodes and lateral branches, while the relationship was insignificant with canopy diameter and crop-bearing growth parameters. The hydraulic conductance due to the removal of branches was significantly associated with main stem size ($r = 0.67**$) and canopy spread ($r = 0.56**$). On the other hand, hydraulic conductance in the absence of leaves showed negative and significant relations with the number of young nodes ($r = -0.44*$) and young stem length ($r = -0.42*$). The conductance in the main stem cut was significantly correlated with most main stem results including cross-sectional area ($r = 0.67**$), moisture content ($r = 0.65**$), fresh ($r = 0.61**$) and dry ($r = 0.52**$) weights and stem volume ($r = 0.59**$). Accordingly, the stiff main stem cuts of the Harenna and Berhane-Kontir trees showed maximum water flow as opposed to the thin and flexible stems of the Bonga and Yayu trees. Similarly, stem hydraulic conductivity was significantly correlated with the height of the coffee tree ($r = 0.50*$), and canopy spread ($r = 0.43*$). The correlation analysis of main stem (30-cm length) diameter and stem hydraulic conductance and hydraulic conductivity revealed positive significant ($P<0.01$) relationships. Average hydraulic conductance values increased with increasing stem size in the wild coffee populations in the ascending order Bonga>Yayu>Berhane-Kontir>Harenna (Figure 5.11).

Main stem conductance

Main stem hydraulic conductance was significantly (r = 0.60**) correlated with most stem attributes such as basal area (stem diameter), stem volume, fresh and dry weight and moisture contents (Table 5.2b). These variables were, however, not significantly correlated with main stem specific hydraulic conductivity, but was rather positively and significantly correlated with plant height, main stem diameter, canopy size and cropping nodes. The hydraulic conductance between shoot and root systems was positive, although insignificant (r = 0.28, P>0.05). However, both root and shoot conductances were significantly (P<0.001) correlated with conductance in the various shoot parts.

Root conductance

Root hydraulic conductance was insignificantly and negatively correlate with the number of large and small lateral roots, which was in contrast to that of medium-sized roots. The total number, diameter and length of lateral roots of varying size (coarse, medium and fine) was positively correlated with hydraulic conductance in root system. In addition, the relationship was significant for lateral root fresh weight (r = 0.50**), dry mass (r = 0.54**) and volume (r = 0.51**). Taproot fresh weight, dry weight and volume were significantly (P<0.0001) correlated with root hydraulic conductance in mature coffee trees. The total number of lateral roots was significantly (P<0.01) correlated with that of the medium and small lateral roots. There was an inverse significant relationship between number and size of large primary roots (r = -0.56**). As a whole, the findings demonstrate that both lateral and taproots significantly influence water flow in the root system and contribute to the exploitation of soil moisture from surface and deeper soil profile.

The correlation between main stem diameter and root (r = 0.56**) and whole-shoot (r = 0.45*) conductance was positive and significant (Table 5.2a). All the other shoot hydraulic conductance components had strong direct relations with stem size, indicating their close relation with growth vigor and productivity of a coffee plant. There was strong and positive correlation value (r = 0.56*) between conductance values measured after the removal of lateral branches. Similar to branch resistances, shoot conductance was negatively correlated with number of nodes and lateral branches, with significant values (P<0.05) obtained for the number of nodes and the young stem length.

In contrast, the increase in these parameters in the crop-bearing surfaces was positively correlated with shoot hydraulic conductance, though insignificantly. This is in contrast to the indirect influence in the old and young growing parts of the coffee plant. This demonstrates the inhibited conductance in old and young growth as compared to medium-aged middle branches (Table 5.2a), which primarly related to functional xylem areas. This could be the possible reason for the significantly reduced hydraulic conductance in the Bonga populations, particularly at PIIS1. In general, the architecture of coffee trees was found to be among the most important aspects for detecting the hydraulic characteristics of wild coffee trees in the montane rainforests of Ethiopia.

Table 5.2   Correlation value (r) between growth parameters and hydraulic conductance in components of the wild coffee trees

a) Extension growth parameters vs. hydraulic conductance components

Parameter	Root	Whole shoot	Leaf	Fruit/petiole	Branch	Stem cut
Height	0.30	-0.07	0.00	0.01	0.31	0.54*
Girth	0.56**	0.45*	0.42*	0.47*	0.67**	0.56**
GBH	0.43*	0.13	0.34	0.27	0.32	0.37
CD	0.43*	0.21	0.36	0.37	0.56**	0.61**
ONN	0.07	-0.28	-0.28	-0.24	-0.05	-0.06
CNN	0.09	0.38	0.29	0.30	0.22	0.39
YNN	-0.34	-0.40	-0.44*	-0.49*	-0.26	-0.26
TNN	0.00	-0.27	-0.32	-0.28	-0.04	0.03
INL	0.24	0.36	0.47*	0.43*	0.30	0.37
OSL	0.41*	-0.19	-0.05	-0.05	0.25	0.26
CSL	-0.01	0.35	0.24	0.27	0.18	0.41*
YSL	-0.36	-0.48*	-0.42*	-0.47*	-0.32	-0.26
TMSL	0.30	-0.09	-0.01	0.00	0.30	0.52*
OBN	0.10	-0.23	-0.11	-0.04	0.15	-0.02
CBN	0.02	0.30	0.24	0.24	0.19	0.39
YBN	-0.18	-0.38	-0.30	-0.35	-0.08	-0.06
TNB	0.01	-0.14	-0.05	-0.02	0.22	0.24

*and ** = significant at P<0.05 and P<0.01 probability levels, respectively (2-tailed). Abbreviations: GBH = girth at breast height, CD = canopy diameter, ONN = old number of nodes, CNN = crop number of nodes, YNN = young number of nodes, TNN = total number of nodes, INL = internode length, OSL = old stem length, CSL = crop stem length, YSL = young tem length, TMSL = total main stem length, OBN = old branch number, CBN = crop branch number, YBN = young branch number, TNB = total number of branches.

b) Main stem parameters vs. conductance components

Parameter	Root	Whole shoot	Leaf	Fruit/petiole	Branch	Stem cut
Girth	0.53*	0.29	0.29	0.39	0.61**	0.65**
Basal area	0.56**	0.27	0.29	0.38	0.63**	0.67**
Length	-0.06	0.14	0.23	0.13	-0.12	-0.13
Volume	0.56**	0.43*	0.38	0.54*	0.63**	0.59**
Fresh mass	0.54*	0.43*	0.37	0.56**	0.69**	0.61**
Dry mass	0.47	0.35	0.33	0.47	0.60	0.52
Moisture content	0.12	0.17	0.05	0.18	0.18	0.16

* and ** = significant at P<0.05 and P<0.01 probability levels, respectively (2-tailed).

5.4.5   Hydraulic resistance

There were no significant differences in branch hydraulic resistances (reciprocal of conductance) among populations, sites and coffee trees. Except at Bonga, remarkable reductions in branch hydraulic resistances were noted with the removal of leaves, fruits and petioles. At Bonga, however, resistances tended to increase with the reduction of lateral branch parts, mostly due to the differences in branch growth characteristics. The average hydraulic conductances increased (Figure 5.8) and the hydraulic resistance in the various branch segments declined in the order of Bonga>Yayu>Berhane-Kontir>Harenna (Figure 5.12). In addition, hydraulic resistance in a 20-cm long branch was found to be highest (6.91×10^5 MPa m^2 s kg^{-1}) and lowest (0.45×10^5 MPa m^2 s kg^{-1}) in the Bonga and Harenna trees, respectively. The same orders were maintained in branch- and leaf- specific resistances. Thus, based on branch resistances, Bonga and Harenna were grouped into the highest and lowest extremes, while Yayu and B-Kontir were intermediate (Figure 5.12).

An independent analysis of varaiance for each population when sites, trees and branches were nested, however, depicted significant (P<0.001) differences in whole-branch hydraulic resistance patterns at the Bonga, Berhane-Kontir and Yayu forests, but not at Harenna (Appendix 5). However, no variations were observed due to the selected coffee trees at all sites. Except at Yayu, reduced whole-branch hydraulic resistances were found from the middle canopy position. The values (Figure 5.13) showed increased resistances with decreased branch age and the uppermost branches exhibited the highest values at Bonga (10.9×10^5 MPa m^2 s kg^{-1}) and Berhane-Kontir (6.52×10^5 MPa m^2 s kg^{-1}). Hence, the reduction in branch hydraulic resistances between bottom (old) and middle (medium age) branches were 8, 25 and 48% at Berhane-Kontir, Bonga and Harenna forests, respectively. At Harenna, 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 Yayu, however, it tended to reduce from middle to top primary branches.

In addition, the reduction of hydraulic resistances in the various component parts of primary branches was only significant at Harenna, 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 was the slight increment for the top juvenile branches in the Bonga forest. The percent hydraulic resistance reductions due to leaf cut were 47, 36 and 33% at Harenna, Yayu and Berhane-Kontir, respectively. There was a direct and significant (r = 0.94***) correlation between the patterns of whole-branch resistances and leaf removal. 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 for the Bonga trees. In addition, decreased resistance was obtained due to subsequent removal of leaf petioles. The resistance contribution of petioles was higher at Harenna (19%) compared to the other populations (Bonga = 3%, Berhane-Kontir and Yayu = 5%).

At Bonga and Berhane-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 1.40×10^5 MPa m^2 s kg^{-1} to 17.5×10^5 MPa m^2 s kg^{-1} (Bonga) and from 0.79×10^5 MPa m^2 s kg^{-1} to 4.40×10^5 MPa m^2 s kg^{-1} (Berhane-Kontir). The hydraulic resistance difference between whole branch and branch cut was higher at Berhane-Kontir (21%) and Harenna (19%) when 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 middle branches at Yayu forest. In general, the mean resistance values followed the descending order of Bonga>Yayu>Berhane-Kontir>Harenna and thus, the reverse holds true for branch hydraulic conductance.

At Bonga, branch- and leaf- specific hydraulic resistances were significantly (P<0.05) high for the upper branches as compared to 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 coffee trees carried fruits. This could also be related to the significantly small branch diameter (P<0.001) recorded for top juvenile branches. Furthermore, the significantly (P<0.01) high total leaf area of the middle branches could lead to enhanced water transport. At the other sites, no significant variations were detected among the selected primary branches. At Harenna and Berhane-Kontir, branch- and leaf-specific hydraulic resistances were negatively correlated along a 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 (3.66×10^2 kg s m^{-2} MPa^{-1}) to top (1.30×10^3 kg s m^{-2} MPa^{-1}) canopy positions (Figure 5.13). This is quite in line with leaf growth characteristics on primary 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 is the position where maximum total leaf areas were estimated, specially for Harenna (45%) and Bonga (47%). This is in contrast to the reduced leaf production in the middle canopy branches at Berhane-Kontir (31%) and Yayu (27%). The results show insignificant differences between the three sub-sites within each wild coffee population. From each population, relatively low values of hydraulic resistances in branch segments and branch-specific hydraulic resistances were measured for PIS3, PIIS3, PIIIS1 and PIVS1. In contrast, coffee trees from site 2 of each montane rainforest were noted to display maximum values for whole-branch hydraulic resistances and branch- and leaf- specific hydraulic resistance patterns, which is in agreement with the reduced branch diameters in the four wild coffee populations (Table 4.7). The highest resistance at Bonga (PIIS2) could be related to young branch age with a significantly maximum branch cross-sectional areas (0.21 cm^2) and leaf surface area (482.24 cm^2). At Harenna, high branch-specific resistance (4.13×10^5 kg s m^{-2} MPa^{-1}) was found at PIS1 where the lowest whole-branch resistance (highest conductance) was also determined and this was related to the increased high leaf area recorded from the same site. Similarly, the correlation between whole-branch hydraulic resistances and leaf number was negatively significant (r = -0.49*). The overall correlation coefficients between branch hydraulic resistance and growth parameters were not significant. Despite this, resistance was directly correlated with branch diameter, number of nodes, branch volume and branch density,

while branch length and total leaf area were negatively correlated. Moreover, the cluster analysis showed the smallest coefficient (0.03) between PIS1 and PIIIS3, and the largest (1.12) between PIS1 and PIIS2 (Figure 5.14). In general, the cluster analysis between growth parameters and hydraulic resistance of primary branches showed close similarity between Bonga and Yayu as well as Harenna and Berhane-Kontir, which is in consistence with the growth parameters of the wild coffee trees.
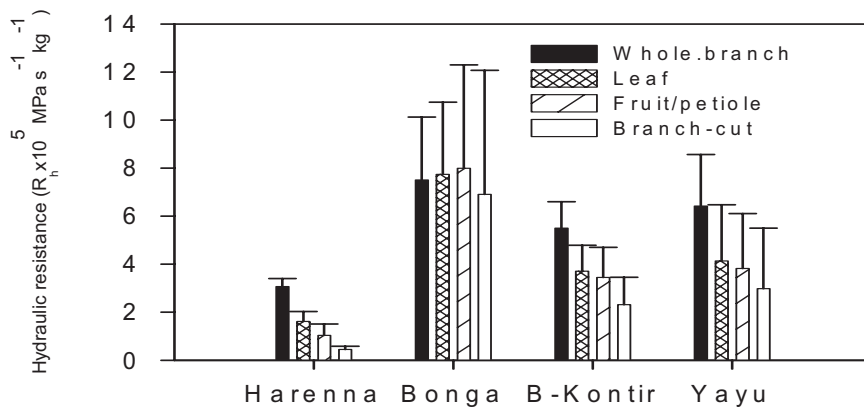

Figure 5.12   Branch hydraulic resistance components in the wild coffee trees at the study montane rainforests of Ethiopia
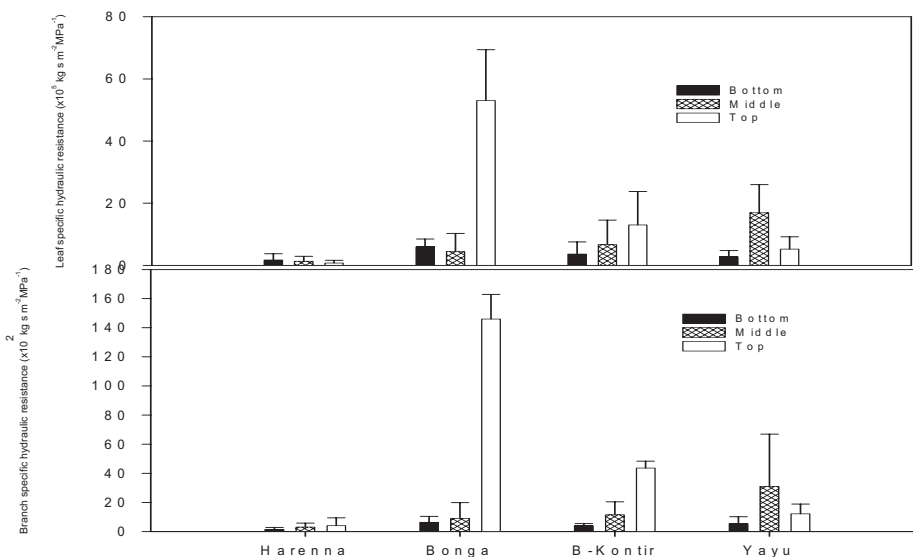

Figure 5.13   Branch- and leaf- specific hydraulic resistance as influenced by branch position in the crown of wild coffee trees at the four montane rainforests of Ethiopia

```
                 Rescaled Distance Cluster Combine
        0         5        10        15        20        25
        +---------+---------+---------+---------+---------+
 PIS1   ─┐
 PIIIS3  ─┤
 PIIS1   ─┤
 PIVS1   ─┤
 PIVS2   ─┤
 PIIIS1  ─┤
 PIS3    ─┘
 PIIS2   ─┐
 PIVS3   ─┤
 PIIS2   ─┤
 PIS2    ─┘
 PIIS2   ─
```
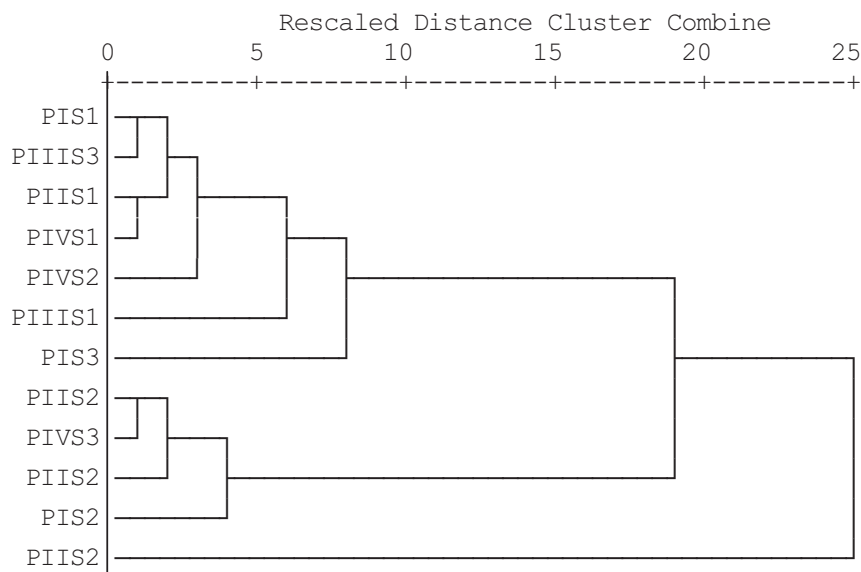
Figure 5.14   Dendrogram using average linkage (between groups) according to growth and branch cut hydraulic resistance of primary branches of the wild coffee trees

5.5   Discussion

Water relations

The results indicate that the soil was driest at Harenna as opposed to the wettest soils in the southwest sites. At Harenna, the high soil moisture contents in spring and autumn may be related to the bimodal rainfall distribution pattern in the area, whereas, though the difference between spring and autumn was high at Yayu, the three forests in southwest showed the same trend, indicating the prevailing similarity in rainfall distribution pattern. These results support the long-term rainfall patterns in the southwestern and southeastern parts of the country (Paulos and Demel, 2000). The significant differences within sites during the dry season could be associated to the variability in shade levels, slope and soil conditions. Taye et al. (2004b) reported on the specific adaptation of coffee landraces along moisture gradients. The results may in part reveal soil moisture competition by the closely spaced coffee trees and associated shade trees, particularly in the drier southeastern sites. The high soil moisture at PIIS2 could be due to the moderate over-shading reducing soil-moisture tensions in the soil-plant-atmosphere continuum. Intermittent drought in most coffee growing regions of Ethiopia at the critical growth stages of the coffee plants considerably affects growth and subsequently yield and quality (Tesfaye, 1995, 2006).

The variability in soil moisture potential indicates the magnitude of soil moisture removed by the roots and lost through transpiration. There were little differences in soil moisture along the land gradients (top, middle and bottom), indicating the contributions of forest canopy cover to control the adverse effects of rainfall on soil conditions. Soil cover especially through broad-leaved weeds and litter fall mainly from the deciduous trees could also help to conserve soil moisture. Nonetheless, there is the possibility of rainwater interception with the upper canopy which is lost by evaporation. Larcher (2003) showed this notion particularly with increasing density of plant cover. The results suggest that stand structures can be used to detect soil moisture dynamics in the natural forests. The results could also reflect the impact of shading to increase air humidity and reduce the vapor pressure gradients between the atmosphere and the leaf, which can ultimately reduce the evaporative soil moisture demands (Wrigley, 1988). Accordingly, at most sites, particularly Bonga, there were little changes in leaf water status between the dry and wet seasons. The physical condition of the soil may also enhance more percolation and maintain residual soil moisture for plant use. The recovery of the leaf water status depends upon the ability of the soil to supply water to the plant in sufficient quantities to recharge the dehydrated plant tissues (Larcher, 2003). No leaf-wilting symptoms were observed on coffee trees during the course of the study at the four rainforest sites.

The diurnal difference in LWP permits rapid characterization of plant species in drought-stress environments. This is because plant water potential indicates the suction force, which a plant actually develops or can develop to extract water from the soil. The LWP fluctuates throughout the day and changes can be considered as the difference between predawn and midday water potential. In this study, the coffee trees showed little diurnal LWP variations during the relatively dry season. At all sites, the minimum change in midday LWP was observed in th dry season, which may reflect the physiological plasticity of coffee trees against fluctuating soil moisture deficits.

The range of diurnal fluctuation in leaf water status is important in plant growth and development. The four wild coffee populations did not differ significantly in terms of the diurnal difference in LWP, indicating the similarity of the forests in maintaining adequate soil moisture but reducing the photosynthetic capacity of coffee trees. This reflects a trade-off between hydraulic capacity and water-use efficiency in

the trees. Nonetheless, the difference between predawn and midday LWP was higher at Harenna and Berhane-Kontir as opposed to Yayu and Bonga in that order. This is in consistence with the shoot (Table 4.1) and root (Table 4.8) growth characteristics of the coffee trees at the respective sites. Such difference in the ability of the trees to recover from maximum drought-stress indicates that wild coffee populations differ in their strategies for coping with low moisture availability. Accordingly, Harenna and Berhane-Kontir populations showed higher leaf water recovery, suggesting their capacity to withstand wider change in water conditions under field conditions, whereas the Yayu and Bonga trees exhibited low diurnal ranges, perhaps indicative of increased xylem resistance and stomatal closure to prevent water loss.

Previous findings in Ethiopia (Taye et al., 2004b; Yacob et al., 1996) show that compact local coffee types flourish ideally on moist flat top and bottom soils, while intermediate and open canopy types adapt and perform well on eroded lands, drier soils and steep slopes besides top and bottomlands. Generally, the normal diurnal range in drought-adapted species is large and the longer the predawn values stay close to the midday values, the smaller the re-saturation opportunity of the plant. According to Whitlow et al. (1992), the failure of the plant to recover to its predawn values has been recognized as evidence of water deficit for that particular species. In those accessions where stomata have the capacity to close rapidly, evaporation is better regulated and, therefore, thus enabling the plant to maintain maximum LWP through which resistance to drought is higher. Therefore, data on the diurnal and seasonal variations in leaf moisture content could provide insight on the behavior of coffee trees under optimum and moderate moisture conditions of the montane rainforests.

Hydraulic conductance

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. The hydraulic conductance corresponded with branch hydraulic resistances as well as with the morphological growth parameters (Table 4.1). The differences in water flow patterns within a relatively saturated main stem suggest the inherent growth variability and impacts of environmental factors, particularly between the geographically distant forests. The enhanced water transport in

the stem segments at the Berhane-Kontir and Harenna sites indicate the high water-use rates, although low leaf conductance can limit water use. The mechanism explaining this follows Ohm's law analogue for water flow in plants (Tyree, 2003; Yang and Tyree, 1992). 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. Stomatal conductance is a function of LWP and often tends to be maximal in high light when LWP is above a threshold value and begins to decline with declining leaf water potential below the threshold value. However, the value of LWP is likely to decrease with decreasing leaf conductance and flow restrictions in the hydraulic system of root and shoot.

At all study sites, particularly at Harenna and Bonga the contribution of root conductance to the whole-tree was 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 was comparable to other reports on other tropical forests (Borchert, 1994; Lawton, 1984; Sobrado, 1993, 2003). 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. In addition, the authors have 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, independent of the differences in wood density.

Hydraulic resistance

The present findings on branch hydraulic resistances clearly demonstrate the influence of branch age and thus, crop to leaf ratio in mature coffee trees. The inherent phenotypic variations between coffee trees, prevailing rainfall patterns and site factors could be among the possible reasons. 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. 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 Berhane-Kontir (PIIIS3) 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, 1984). The greatest resistances with decreased branch age in Bonga and Berhane-Kontir corresponded with the significantly lowest diameters recorded on top branches (Table 5.13). 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. 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. Taken together, the highest and lowest branch specific resistances were from Bonga and Harenna, respectively. Similarly, maximum specific leaf hydraulic resistances were measured for Bonga, Yayu, Berhane-Kontir and Harenna coffee trees in that order. The Harenna trees would thus be more vulnerable to embolism than the other coffee trees. This supports the results from the values of total leaf area, which could be related to the variations in morphological growth (Table 4.7). The results are in consistence with the responses of the seedlings to the imposed drought stress under nursery conditions. Within-tree crown patterns of leaf specific conductivity distribution have been quantified for several angiosperms and conifer tree species (Ewers and Zimmermann, 1984; Tyree et al., 1983; Tyree et al., 1991; Zimmermann, 1978). In most species examined, the values increased with increasing stem diameter and was higher in the main stem than in the branches. Other consistently observed features of tree hydraulic architecture are the increased hydraulic resistance associated with leaf and branch junctions. According to Zimmermann (1983), leaf specific conductivity distribution patterns in tree crowns were evidence of hydraulic segmentation, defined as a structural

feature that confines cavitation events to relatively expendable plant parts in favour of parts more important to plant survival.

Therefore, from the hydraulic resistance characteristics, Bonga (moist) and Harenna (dry) forests were identified to host drought- tolerant and- sensitive coffee populations, respectively. The Yayu and Berhane-Kontir populations had als features less sensitive to drought-stress conditions. Crown structure and consequently hydraulic architecture fundamentally change with increasing age and at later stages of decline (Roloff, 1993, 2001). In pedunculate oak, the active shedding of shoots is the main mechanism for the modification of the crown architecture, while in the nodes of juvenile oaks, the formation of regular xylem disables abscission immediately after flushing, and the frequency of active abscission zones increases with age and declining vigor (Klugmann and Roloff, 1999). In trees, the largest part of the aboveground hydraulic resistance along the soil-root-leaf pathway resides in the smallest shoots of the crown (Yang and Tyree, 1993). The present weak positive correlation between branch hydraulic resistance and number of nodes supports the previous results in that nodes and abscission zones (Rust et al., 2004) further increase hydraulic resistance.

6   GROWTH AND DEVELOPMENT OF COFFEE SEEDLINGS

6.1   Introduction

According to the literature (Hopkins, 1992; Larcher, 2003; Prasad, 1997; Salisbury and Ross, 1992), several external factors affect growth and development of plants in different ways. These include intensity and spectral distribution of radiation, temperature, gravity and the forces imposed by wind, water currents and snow cover as well as wide variety of chemical influences. These include induction, initiating or terminating of developmental processes, thus effecting temporal regulation. Quantitatively, external factors affect the speed and extent of growth, and formatively they influence morphogensis and tropisms. The different modes of action are interwoven with one another and the end result involves the interplay of a large number of processes.

Coffee seeds do not require a period of dormancy and consequently the seeds should be sown as soon as possible after ripening. The seeds are short- lived and, depending on the storage conditions, their viability decreases rapidly after 4 to 6 months when stored at ambient temperature (IAR, 1996; Yacob et al., 1996). Germination is slow taking 30-60 days under the most favourable conditions, which are high rate of ambient humidity, air temperature of 30-35°C and soil temperature of 28-30°C. A drop in temperature slows down germination by up to 90 days (Wintgens, 2004). Despite the maximum pre- and post-sowing care required at the nursery, coffee seedlings in the forest ecosystem, which have established from self-sown seeds have an enormous regeneration capacity. However, there is a lack of information on seed germination and early growth performances of the seedlings in relation to seed and environmental factors. In perennial crops like coffee, basically the ultimate measure of early screening of coffee seedlings is the growth potential that influences the chance of survival of any seedling (Walyaro and Vander Vossen, 1979). Yacob (1993) pointed out the possibility of early screening of Arabica coffee cultivars under specific nursery management inputs. The primary objective of this study was, therefore, to compare the variability in phenological growth in wild Arabica coffee accessions under controlled nursery conditions in southwest Ethiopia. The results will be an input for the understanding of the interaction between coffee seedlings and microenvironmental variables (solar

radiation, soil moisture) in regulating the hydraulic flow in the soil-plant-atmosphere system.

Arabica coffee shows some remarkable features, which distinguish it from the other coffee species. Spontaneous coffee populations and their progenies have distinct genetic variability. The characteristics controlled by major genes from those under polygenic determinations include, among others, branching habit, young leaf color and measured plant morphological parameters. Such response, however, depends upon plant species and cultivar and have been used as criteria to characterize coffee cultivars (Wintgens, 2004). In this study, the orientations of leaves and branches were assessed in seedlings of wild coffee accessions.

It is known that photosynthesis in coffee follows the C_3 or Calvin cycle pathway, as coffee plants placed in darkness after a period of light produce a burst of CO_2 following photorespiration (Hatch and Slack, 1970 as cited by Wrigley, 1988). Work done in Kenya (Cannell, 1971) revealed that about 95% of the photosynthetic products of a plant are derived from the carbohydrates manufactured in the green parts by the process of photosynthesis and the remaining 5% come from mineral elements absorbed by the roots. Large regular yields of coffee can be obtained only when both the carbohydrates and mineral element supplies within the tree are adequate to meet the needs both of the developing fruits and the shoots and roots which will support the following year's crop. The capacity of the plant to produce carbohydrate depends mainly on the total green (mainly leaf) area engaged in photosynthesis and the net photosynthetic rate per unit green surface area (Cannell, 1971). The same author showed that dry matter production in any crop depends upon leaf area index, structure of the canopy, photosynthetic rate per unit of leaf area and strength of the metabolic sinks in attracting assimilates.

The need to know how the coffee plant accumulates and partitions dry matter to the various plant organs under a given management cannot be overemphasized. Moreover, this information is necessary as a selection criterion for coffee cultivars as well as for determining optimum management inputs. This aspect, however, has not yet deserved focused attention in the evaluation of different coffee cultivars under the diverse agro-ecology of Ethiopia. The principal interest of this study was, therefore, to determine the impacts of different shade and irrigation levels on qualitative as well as

morphological and physiological growth parameters of coffee seedlings of the four wild coffee populations in the montane rainforests of Ethiopia.

As a shade-tolerant species, coffee can be constrained by an inherently low photosynthetic capacity and may suffer from photo inhibition (Wrigley, 1984). According to Carr (2001), commercial cultivars have retained many of the characteristics adapted to the shady environment of the forests in the Ethiopian highlands in which *Coffea arabica* is believed to have originated. These include partial closure of the stomata when evaporation rates are high as a result of large leaf-to-air saturation deficits (>1.6 kPa), even if the soil is at field capacity. However, the cultivation of coffee under full sunlight conditions is not uncommon in many countries. This has been successful due to the high adaptability of coffee plants to different irradiance levels (Fahl et al., 1994). Light provides the energy needed for photosynthesis, and canopy shading from trees may influence plant productivity and seedling survival. Irradiance (quantum flux density) is a key factor in the field, and varies seasonally, diurnally and spatially (Salisbury and Ross, 1992). The net energy capture hypothesis of adaptation to sun and shade (Givnish, 1988) proposes that the consequences of natural selection in shaded habitats should parallel the phenotypic responses shown by seedlings in acclimation to low light. The variability in leaf parameters is of broad scientific interest. From an ecophysiological perspective, it may provide clues as to how plants acclimate to their environment, and plastic plant structural characteristics. It has been proposed, for example, that variability in leaf mass area within the crowns of individual plants optimizes the allocation of leaf carbon with respect to photosynthetic carbon assimilation (Gutschick and Weigel, 1988), although it is currently not known whether the variation in leaf-specific area within canopies is adaptive or simply a passive response to an environmental gradient such as light.

Shade plants essentially follow strategies of optimum use and conservation of available energy. The physiological mechanisms involved in the adaptation of the juvenile trees to light have remained less investigated in the diverse coffee production systems of Ethiopia. Knowledge of physiological adaptation strategies and growth requirements is important for the successful cultivation and sustained utilization of the wild coffee gene pool in its natural habitat and hence, be amongst the priority research areas. Moreover, there is little information on the phenotypic plasticity and biomass

partitioning of coffee trees under varying light gradients in heterogeneous field and experimental conditions. Therefore, knowledge of the effects of irradiance levels on growth and physiology of coffee plant is important to examine the mechanism involved in the shade-adapted Arabica coffees. Therefore, an *ex-situ* study was conducted at the Jimma Research Center, southwestern Ethiopia to describe growth, biomass allocation, and morphology and architecture of seedlings of the wild coffee accessions in full sunlight and moderate shade conditions. The findings will provide an insight to better understand and predict the variability in ecophysiological growth responses of various coffee accessions under contrasting light and drought stress conditions.

6.2   Material and methods

6.2.1   Microclimatic measurements

The rate of transpiration can be naturally 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. Hence, microclimatic variables (air temperature, soil temperature and relative humidity) were monitored in potted coffee seedlings in the sun and moderate shade 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 microclimatic data were recorded from the seedlings arranged in sun and shade plots. The seedlings received all the conventional nursery practices (IAR, 1996).

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 and labelled. The data was 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) from the same leaf spot. This was accomplished in the relatively hot month (May 2005) and cloudless hours of the day. In addition, ResiWin 0.12 (Gademann Instruments GmbH, Schweinfurt, Germany) was used to measure leaf microclimate and conductivity in shade and sun conditions. Maximum care was taken to ensure that leaves were not shaded by side seedlings. Moisture drops and dust particles were cleaned from the sample leaves before recording leaf temperature.

6.2.2   Phenological parameters

Starting from the appearance of the seedlings above the soil surface, the number of emerged seedlings and subsequent growth stages (butterfly, soldier and first true leaf pairs) were counted at a 7-day intervals between May 24, 2004 and July 12, 2004 (55-112 days after sowing; DAS). From this, germination percent, germination rate and mean days to each stage were calculated following the procedures outlined by Steiner (1990). After most seedlings produced the first true leaf pairs, thinning to one seedling per pot was conducted on July 12, 2004. The uprooted seedlings were pricked-off to empty pots of the same accession. Subsequently, five uniform seedlings were selected and arranged in the central row of each plot and morphological growth parameters were recorded on a monthly basis between 10 and 13 November 2004 (224-227 DAS). Parameters included seedling height, diameter at base, number of main stem nodes, main stem internode length, leaf number, maximum leaf length and width. Intact leaf area was estimated using leaf dimensions (maximum length and width) and a constant (K = 0.66) developed by Yacob et al. (1993) for Arabica coffee seedlings. Further, seedling vigor indices (SVI) were determined for two growth stages (55 and 112 DAS) using the measurements of percent germination, girth and height of coffee seedlings as described by Steiner (1990).

6.2.3   Leaf and branch orientations

Leaf and branch angles were examined on one-year-old seedlings of the coffee accessions in the moderate shade condition. Five seedlings per accession and two primary branches per seedling were sampled for measurement. The angle between the main trunk and lateral branch as well as leaf angle at the base of the petiole (bottom and upper nodes) were measured using a protractor compass (0-180°). In addition, visual scores on the frequency of young leaf color (deep bronze, light bronze, deep green and light green) were recorded for the same seedlings. A plot consisted of 25 seedlings per accession. The well-watered seedlings were placed in the light and moderate shade conditions using an elephant grass and the bamboo slants, respectively.

6.2.4   Leaf chlorophyll contents

Leaf chlorophyll was determined for the sun and shade coffee seedlings. In the laboratory, leaf chlorophyll concentration was determined from 1 ml of the chlorophyll extract diluted with 5 ml 80% acetone (V/V). The concentration of chlorophyll a and chlorophyll b was obtained at the respective optical densities of 645 and 663 nm against 80% acetone as a blank. The absorbance of the extract was measured using a spectrophotometer. The equations used to estimate chlorophyll a, b and total chlorophyll were as follows (Barnes et al., 1992; Hopkins, 1995):

Total chlorophyll (μ g/ml) = $20.2xA_{645}+8.02xA_{663}$ (chlorophyll a + chloprophyll b)

Chlorophyll a (μg/ml) = $12.7xA_{663}-2.69xA_{645}$

Chlorophyll b (μg/ml) = $22.9xA_{645}-4.68xA_{663}$, where A_{645} and A_{663} were the optical densities at wavelengths of 645 and 663 nm, respectively.

In addition to the laboratory method, the amount of chlorophyll present in the intact coffee leaf was measured using a SPAD-502 chlorophyll meter (Minolta Co., Ltd, Tokyo). The values are calculated based on the amount of light transmitted by the leaf in two wavelength regions (red and infrared) in which the absorbance is different. For this, well-developed and healthy leaves were sampled from five central coffee seedlings. The seedlings were well watered in the two light regimes (sun and shade). The leaves were located on the second to third nodes of the lateral branches and an average of 20 readings was taken on each seedling. This was done on four consecutive days (between May 30 and June 02, 2005) three times a day (morning, midday and afternoon).

6.2.5   Shoot and root morphology

The coffee seedlings of the wild coffee accessions were grown under optimal nursery environments. Five central seedlings per plot were used to record intact and destructive morphological growth parameters. The non-destructive vegetative data were recorded at monthly intervals starting from 7 to 12 months after sowing. Intact leaf area, crown area and leaf area index were derived from the collected primary data on the coffee seedlings. The shade treatment was applied between March and May 2005. One-year-old seedlings were used to record dry weight of leaves, main stem, primary branches and root growth. The roots were immersed and washed in water to remove adhering

soil. Measurements on root parameters (lateral root number, lateral root length, taproot length, root volume) were made for each treatment. Subsequently, each plant part was oven-dried at 105°C for 24 h and weighed using a sensitive balance. Total dry matter production and allocation patterns were determined for the variables studied. In addition, the growth rate of the accessions was calculated for both light treatments using the difference between final and the first data divided by the time of the study period (one month).

6.2.6   Response to light regimes

The experiment was conducted in a split-split plot design with three replications of shade, irrigation and coffee accessions. Twenty-five seedlings per plot were arranged on a nursery bed at a distance of 50 cm spacing. Subsequently, measurements were taken with the aim to examine the growth responses and characterize accessions of different wild coffee populations. The coffee seedlings that were used for transient hydraulic measurements were compared for their early growth and morphological responses to contrasting levels of shade and irrigation. In this case, two shade levels (full sun and moderate shade), two irrigation treatments (with and without) and 12 accessions were arranged as main, sub-plot and sub-sub-plot treatments, respectively. The sun and shade plots were designed to mimic deforested and forest-covered lands, respectively.

The seedlings were arranged in full sun on May 28 and hydraulic and destructive data measurements were started on June 02 2005. The shade treatments lasted for only a short time as the drought-stressed seedlings in the sun showed rapid dehydration during the 16-day drying period. After all intact growth parameters have been recorded, the seedlings were brought to laboratory for destructive measurements on root and aboveground parts. Intact leaf area was measured by multiplying average of maximum leaf dimensions (length and width) by a constant (K = 0.66) developed by Yacob et al. (1993, 1998) for Arabica coffee seedlings. During each harvesting, the seedlings were separated into roots, leaves, stems and branches and placed in individual bags. The root parts were carefully washed to remove adhering soil. The different seedling component parts were separately oven dried at 105°C for 24 h and immediately weighed.

Subsequently, derivative variables were computed according to Poorter (1999) and Christopher (2002): Leaf mass ratio (LMR; leaf mass over total plant mass, g g^{-1}), root mass ratio (RMR; root mass over total plant mass, g g^{-1}), stem mass ratio (SMR; stem + petiole mass/total plant mass, g g^{-1}), specific leaf area (SLA; leaf area/leaf mass, cm^2 g^{-1}), leaf area ratio (LAR; leaf area/total plant mass, cm^2 g^{-1}), leaf area root mass ratio (LARMR; total leaf area/root mass, cm^{2}g^{-1}), mean leaf size (MLS; total leaf area/total leaf number, cm^2), specific stem length (SSL; stem length/(stem + petiole dry mass), cm g^{-1}) and crown area (CA; πx0.25x average crown width^2, cm^2) and leaf area index (LAI; total leaf area/crown area, cm^2 cm^{-2}). According to Poorter (1999), these variables refer, respectively, to biomass allocation (RMR, SMR, LMR), leaf display (SLA, LAR), the balance between investment in light intercepting organs against water and nutrient uptaking organs (LARMR), the efficiency of biomass investment for height gain (SSL) and crown architecture (CA, LAI). Besides physiological parameters, the frequency and incidence of coffee leaf rust were recorded during the dry month (March 2006) on wild coffee accessions maintained in sun and shade plots with the view to correlated with leaf moisture contents.

6.3   Statistical analysis

Analysis of variance (ANOVA) was carried out using SAS system for Windows version 8.1 (SAS Institute Inc., Cary, NC). Owing to inter-monthly differences in climatic variables, shoot morphological characters and seedling growth rates were evaluated in a two-way ANOVA for shade levels, months and accessions as independent variables. In case of growth rate analysis, all variables were transformed to natural logarithms with the assumption of the additive effects of the independent variables and avoid to interaction effects. This also stabilizes variances (Poorter and Garnier, 1996).

The Pearson correlation matrix was run between the most relevant dependent variables studied. Moreover, principal component analysis and cluster analysis of the growth parameters were computed to describe the extent of variability among the accessions. Moreover, Canonical Correspondence Analysis ordination technique was carried out using CANOCO for Windows version 4.52 (ter Braak and Smilauer, 2003). This was undertaken to determine the relationships between different coffee accessions and physiological growth variables. In ordination, the angle of the lines with a particular

axis is a measure of the degree of correlation (shallow angle means higher correlation). The length of the lines illustrates the significance of the axis in explaining seedling growth variables.

6.4   Results

6.4.1   Characteristics of potting medium

The results of soil physical and chemical analyses are presented in Appendix 4. Hence, the potting soil medium was clay loam in texture with ideal physico-chemical conditions for growth and development of coffee seedlings. This was confirmed from the absence of nutrient deficiency symptoms and thus no mineral fertilizer was applied throughout the study period. The use of decomposed coffee composts improved physico-chemical conditions of the medium through better moisture retention capacity. The physical conditions were ideal, which might be due to the high organic matter content (9.2%). According to the general guidelines on soil rating, the potting medium had high total nitrogen, high organic carbon and high available potassium. However, available magnesium was medium and calcium was low. This supports the previous report on the use of coffee composts as principal media ingredients for production of high quality coffee seedlings (Taye et al., 2002b).

6.4.2   Microclimatic variables

The results of microclimatic monitoring indicate 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 (Table 6.1). However, the difference between day and night soil temperatures was not significant, though it was higher during the day (23.83°C). The optimum temperature for the germination of coffee seeds is about 30 to 32°C, the most favourable being between 28°C and 30°C (Coste, 1992). The influence of shade level either singly or in combination with times of the day on the microclimatic elements considered was not statistically significant. 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 the sun-exposed than in the shaded pots. This means that artificial shading was seen to create more favourable microclimates by

decreasing air temperature by up to 0.47°C (2.5%) and soil temperature by 5.13°C (21.4%) compared to the sun-exposed plots. With reference to shade by time interactions, coffee seedlings in the sun showed higher soil temperature both during the day and at night (Figure 6.1).

The influence of shade regime on daily leaf temperature was significant ($P<0.001$) in midday and afternoon, but not in the morning. In the morning, leaf temperature was slightly higher to the shaded seedlings than for those in the sun plots, and the increment was about 2%. However, during the later hours of the day, leaf temperature was significantly higher in sun than in shaded leaves (Figure 6.2). The reductions in leaf temperature under moderate shade were 16 and 14% in midday and afternoon, respectively. This might be due to the effects of low humidity and high irradiances under the sun-exposed conditions. There were slight differences in diurnal change in average leaf temperature among coffee accessions. The difference between predawn and midday leaf temperature was low in the Berhane-Kontir and high in Harenna seedlings, reflecting the variability in leaf characteristics (size, shape, texture, roughness and orientation).

Table 6.1   Microclimate variables in sun and moderate shade plots under 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
Irradiance	Ns	Ns	Ns
Sun	73.42±8.57	18.75±3.17	24.03±5.95
Shade	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.*
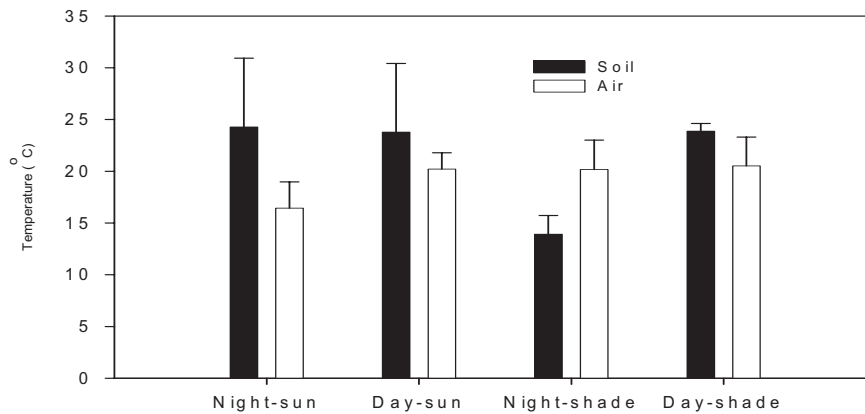
Figure 6.1   Daily variations in average air and soil temperatures in sun and moderate shade plots under nursery conditions
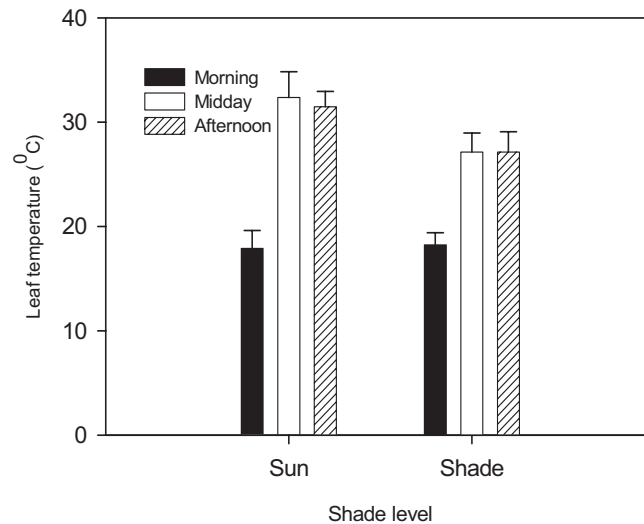
Figure 6.2   Diurnal average leaf temperature recorded for coffee seedlings in sun moderate shade conditions

6.4.3   Seedling emergence and early growth

Coffee seeds started to emerge above the potting soil 55 DAS, though this varied among coffee accessions. This was longer than the normal nursery calendars, due primarily to the reduced temperatures and hard seed cover. Accordingly, the results of the analysis of variance depict highly significant variations among the coffee accessions between 55 and 97 DAS. Furthermore, the growth response of coffee seedlings on 55 and 112 DAS indicated highly significant differences in the rates of emergence, germination, growth stages and vigor index. Although there were no significant variations during the initial stage (55 DAS), the seedlings exhibited highly significant differences in the rapidity of

growth stages. There were remarkable differences within accessions of each forest coffee population, particularly between Bonga and Yayu (Table 6.3a). Accessions from Berhane-Kontir, II-2 and IV-3 had significantly low mean percent emergence values. This corresponds with early harvesting and prolonged storage time, indicating in part the decline in seed viability with increased time of storage; which depends on the moisture content of seeds (Wondifraw, 1994) and storage conditions (Yacob et al., 1996). In addition, the reduced germination percent for the Berhane-Kontir and Yayu accessions could be attributed to seed damage by the Antestia bug (*Antestiopsis intricatata*). Consequently, the overall percent emergence values ranged between 48.3 and 83.5% for III-2 and I-3, respectively. However, the slightly lower mean emergence for 97 than for 90 DAS shows that the seedlings attained the subsequent growth stage. As a result, except Berhane-Kontir accessions, the seedlings produced the first true leaf pair on 112 DAS (Table 6.3b). Above all, the significantly prolonged mean days to the germination and subsequent early growth of the Berhane-Kontir accessions indicate their specific microclimatic requirements (e.g., soil and air temperatures) similar to the area of origin, i.e., a hot humid agroecological zone.

During the initial stage, the lowest and highest values of emergence, germination rates, soldier stage and seedling vigor were obtained from accessions III-3 and IV-2. The same growth responses were observed with time and on 112 DAS the Yayu accessions had significantly the highest first true leaf stage, followed by the Harenna and Bonga populations. During this time, significantly highest germination rates (0.79) and seedling vigor (487.62) were calculated for the Harenna accessions, followed by Yayu. In contrast, most Berhane-Kontir accessions were at a soldier stage, and the appearance of a true leaf was accordingly inhibited as compared to the others. As a result, the most inferior seedling vigor was determined for the Berhane-Kontir accessions (Tables 6.3a and 6.3b).

Most accessions attained peak emergence on 62 DAS and sharply declined thereafter (Figure 6.3) with the highest and lowest values obtained for accessions IV-1 and III-3, respectively. Accordingly, coffee accessions from Yayu were fast to reach the soldier stage, followed by Harenna, the lowest being Berhane-Kontir accessions. Most seedlings attained a butterfly growth stage on 69-DAS (Figure 6.3) and the results increased with increased DAS. Thus, significantly highest mean percent butterfly stage

was obtained for the accessions IV-1 and IV-2, but the coffee seeds from accession IV-3 were significantly slow to reach this stage. This was the slowest for the Berhane-Kontir accessions (Figure 6.4). The findings correspond to the characteristics of the seeds, especially seed density (Table 4.4). The final data recorded on October 20, 2004 (204 DAS, 7 months old) also reveal that most coffee seedlings produced three to four pairs of true leaves, whereas accessions from Berhane-Kontir had only two to three pairs of true leaves. This might also reflect the imprints of the mother coffee trees and adaptation to specific ecological factors, which calls for further research.

Table 6.3   Growth stages (means±SD) of coffee seedlings on: (a) 55 and (b) 112 days after sowing (DAS)

a) 55 DAS

Accession	ER	SR	GR	MDE	MDS	SVI
Pr>F	***	**	***	Ns	*	***
I-1	0.07±0.08abc	0.15±0.20ab	0.22±0.24abc	16.00±12.15	39.00±12.15	70.96±85.88ab
I-2	0.09±0.04abc	0.07±0.07b	0.15±0.10bc	35.14±12.67	19.86±12.67	42.13±30.07b
I-3	0.13±0.06a	0.16±0.11ab	0.29±0.13ab	27.92±11.61	27.08±11.61	72.18±41.83ab
II-1	0.05±0.03bc	0.19±0.18ab	0.24±0.20abc	15.29±13.84	39.71±13.84	66.18±64.60ab
II-2	0.03±0.03bc	0.04±0.03b	0.07±0.06bc	25.48±18.08	20.35±16.45	15.99±14.14b
II-3	0.09±0.07abc	0.12±0.11ab	0.21±0.17abc	24.14±9.79	30.87±9.79	49.86±43.10b
III-1	0.04±0.03bc	0.06±0.04b	0.09±0.06bc	19.72±14.22	26.12±16.51	19.29±14.26b
III-2	0.04±0.03bc	0.04±0.04b	0.07±0.07bc	25.72±19.29	20.12±17.62	15.28±16.21b
III-3	0.01±0.02c	0.02±0.04b	0.03±0.06c	12.22±22.20	15.28±24.37	6.06±11.30b
IV-1	0.09±0.04ab	0.19±0.08ab	0.28±0.08abc	19.42±6.77	35.58±6.77	77.87±29.16ab
IV-2	0.13±0.03a	0.29±0.25a	0.42±0.28a	20.55±9.13	34.45±9.13	126.08±77.82a
IV-3	0.06±0.04abc	0.08±0.04ab	0.14±0.07bc	19.43±12.04	35.57±12.04	30.81±19.98b
Mean	0.07	0.12	0.18	21.75	28.66	49.39
CV (%)	57.85	95.93	69.50	66.40	49.50	76.42

Growth and development of coffee seedlings

b) 112 DAS

Accession	SR	BR	FTLR	GR	MDS	MDB	MDFTL	SVI
Pr>F	***	***	***	***	***	***	***	***
I-1	0.12±0.06bc	0.60±0.02ab	0.07±0.07bc	0.78±0.04a	16.23±8.76cd	85.75±3.80ab	10.02±9.98bc	487.62±88.47a
I-2	0.09±0.03bcd	0.66±0.04a	0.04±0.05bc	0.79±0.02a	12.88±4.66cde	92.95±5.30a	6.17±7.36bc	420.60±81.43ab
I-3	0.10±0.07bc	0.65±0.08a	0.04±0.05bc	0.79±0.04a	14.30±9.60cd	91.69±7.25ab	6.02±6.78bc	378.22±80.89bc
II-1	0.11±0.03bc	0.51±0.03bcd	0.07±0.07bc	0.69±0.03b	17.13±5.35cd	83.68±6.36ab	11.19±10.41bc	360.20±66.73bc
II-2	0.07±0.03cde	0.45±0.05c-f	0.03±0.03bc	0.54±0.05cde	13.52±6.37cd	92.51±7.11a	5.97±6.73bc	232.54±51.87d
II-3	0.05±0.02cde	0.58±0.08ab	0.04±0.06bc	0.67±0.03b	9.42±2.18def	96.40±10.18a	6.18±10.30bc	316.55±56.29c
III-1	0.11±0.04bc	0.44±0.04c-f	0.01±0.01c	0.55±0.02cd	22.33±7.40bc	87.28±5.27ab	2.39±3.31c	223.78±45.00d
III-2	0.14±0.03ab	0.37±0.07f	0.00±0.00c	0.50±0.05de	30.91±8.78ab	81.10±8.78ab	0.00±0.00c	196.99±63.05d
III-3	0.19±0.07a	0.38±0.08ef	0.00±0.01c	0.58±0.04c	37.08±13.19a	74.35±13.05b	0.57±0.88c	220.03±62.58d
IV-1	0.02±0.02e	0.55±0.07abc	0.11±0.09ab	0.68±0.02b	2.76±3.21ef	90.81±12.97ab	18.43±14.66ab	378.74±62.21bc
IV-2	0.01±0.01e	0.51±0.09b-e	0.17±0.10a	0.68±0.03b	1.70±1.42f	82.52±15.93ab	27.79±16.63a	432.28±90.44ab
IV-3	0.04±0.02de	0.42±0.03def	0.02±0.02c	0.48±0.02e	8.43±4.40def	98.79±4.59a	4.78±4.18c	202.87±46.56d
Mean	0.09	0.51	0.05	0.64	15.56	88.15	8.29	320.87
CV (%)	37.23	12.33	81.90	5.30	34.90	10.45	80.44	13.25

*Ns = Not significant, ** and *** = significant at P≤0.01 and P≤0.001 significance levels, respectively. Means with the same letter within each column are not significantly different. Abbreviations: ER = emergence rate, SR = soldier rate, GR = germination rate, MDE = mean days of emergence, MDS = mean days of soldier, BR = butterfly rate, MDB = mean days of butterfly, FTLR = first true leaf rate, MDFTL = mean days of first true leaf and SVI = seedling vigor index.*
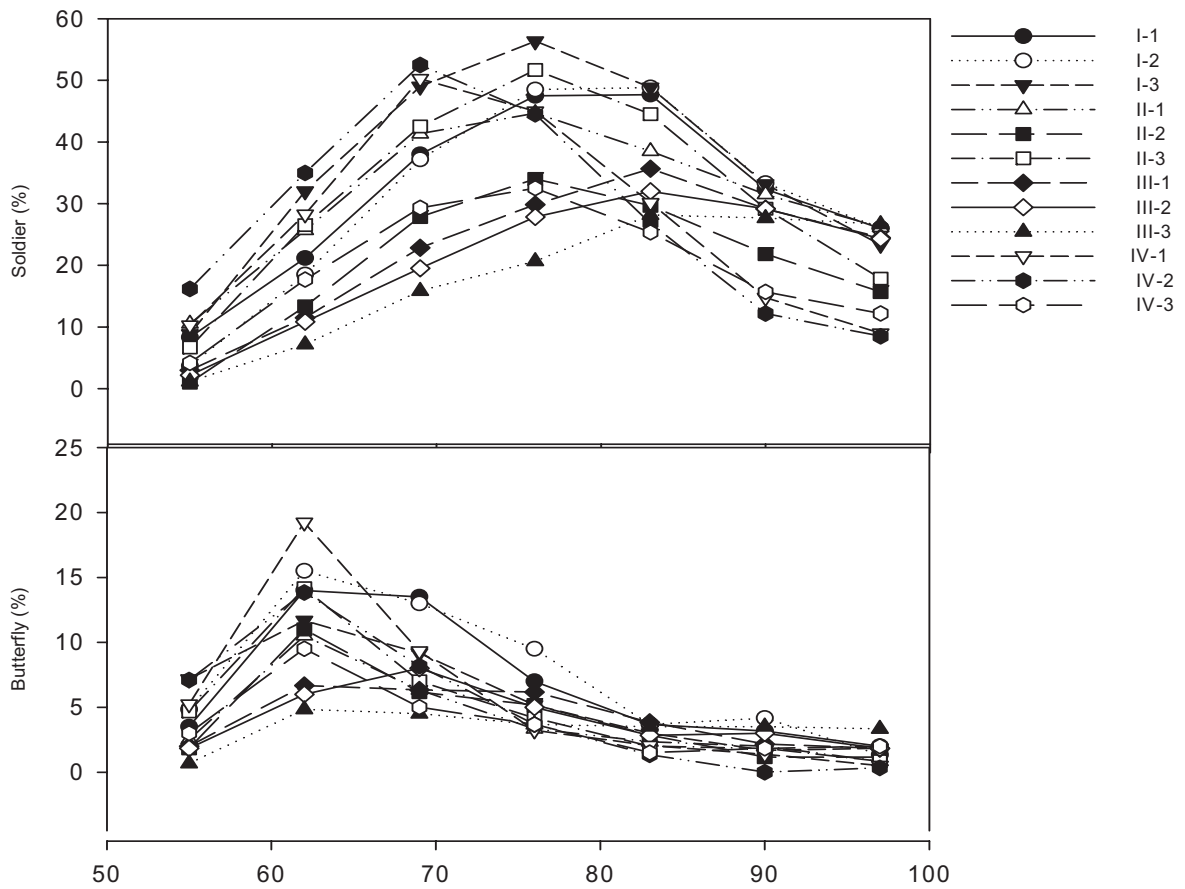
127

Figure 6.3   Mean percent of soldier and butterfly growth stages in seedlings of wild coffee accessions for different days after sowing (55-97 DAS)

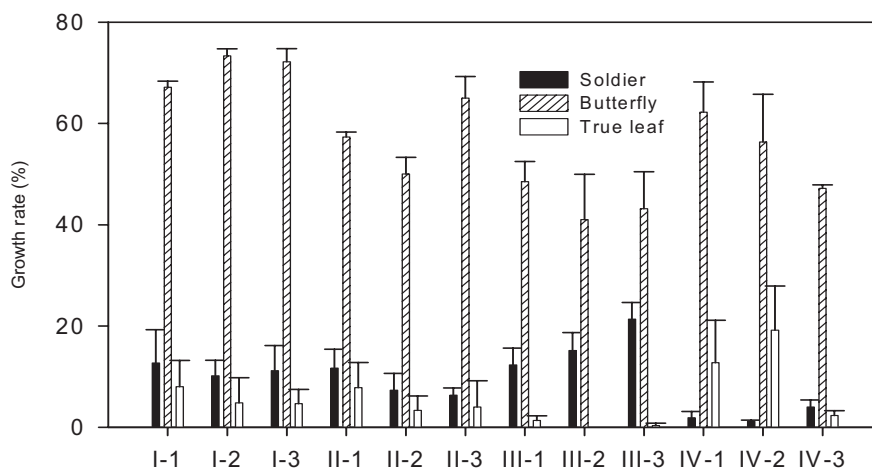Figure 6.4   Mean proportion of soldier and butterfly stage and true leaf pairs in seedlings of 12 coffee accessions (112 DAS)

6.4.4   Growth characteristics of coffee seedlings

Branch and leaf orientation

One-way ANOVA depicted that coffee seedlings of the 12 accessions uniformly managed under partial shading differed significantly (P<0.001) in the orientation (angle) of the primary branch measured at the junction to the main stem axis. Consequently, the accessions from Harenna (I-1 = 48.83° and I-2 = 46.67°) and Yayu (IV-1 = 45.50° and IV-2 = 43.50°) exhibited maximum horizontal branch angles as opposed to the Berhane-Kontir progenies with reduced acute branch angles, ranging from 40 to 42° (Figure 6.5). On the other hand, coffee seedlings did not show significant variations in leaf angle measured at the base of the petiole. The results show that the acute leaf angle was greater than that of the primary branch. In the Harenna and Yayu accessions, leaf orientation was close to a right angle, i.e., almost double that of the branch angle. The most horizontal and vertical leaf angles were measured on the Yayu (IV-2 = 75°) and Berhane-Kontir (III-2 = 66°) accessions (Figure 6.5), respectively. In general, the degree of branch orientation followed the descending order: Yayu>Harenna>Bonga>Berhane-Kontir, most likely reflecting the differences among the wild coffee populations in the growth stage of coffee seedlings. The Bonga accessions were intermediate in leaf and branching habits. Nevertheless, the pattern is similar to that of the branching habit and this was confirmed by the positive and significant correlation value (r = 0.27*) between branch and leaf angles. Hence, based on leaf and branch orientation, the Harenna and Yayu seedlings had semi-horizontal, while those in Bonga and Berhane-Kontir showed semi-erect growth. This supports the crown habits of the respective mother trees in field conditions at the four rainforests.
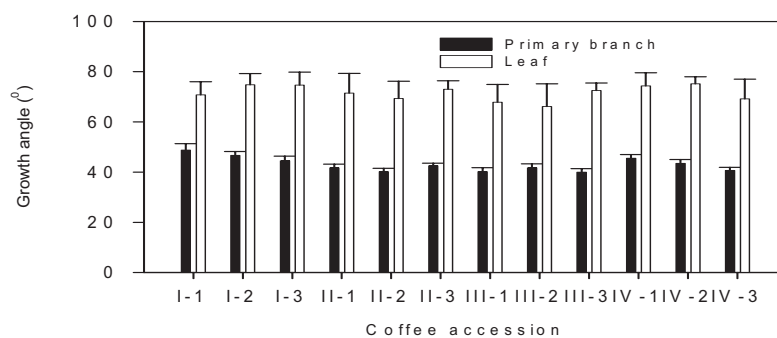

Figure 6.5   Primary branch and leaf orientation in seedlings of coffee accessions in modrate shade environments

Leaf color

The results indicate that the coffee seedlings exhibited distinct young leaf colors due to shade, coffee accession and their interaction effects. The accessions of the coffee populations were characterized by three major young leaf colors: deep bronze (12.8%), light bronze (24.6%) and light green (62.6%) with the variability coefficients of 7.0, 18.3 and 19.8%, respectively. Consequently, the accessions from the Harenna forest sites had exclusively deep and light bronze-tipped seedlings, whereas light green was the feature of those from southwest populations. The most reddish brawn and bronze types were recorded from Harenna population, though there were still significant variations among the progenies of the three sites (Table 6.4). Consequently, the highest mean results of bronze for accessions from I-1 (66.5%) and I-2 (47%) and light green-tipped were recorded from I-3 (46.7%), reflecting the occurrence of intra-variability within the same population. Similarly, the light green-tipped leaves were observed in the accessions of Bonga (II-1 = 82.7%) and Yayu (IV-2 = 91.3% and IV-3 = 90%).

The two-way ANOVA also depicted that the interaction between coffee accession and shade regime was significant in the frequency of accessions with deep bronze ($P<0.001$) and light green ($P<0.05$) leaf tip colors. In contrast, the light bronze leaves did not change significantly and their proportion was high with reduced shading. Beside genetic factors, this may be related to reduce the concentration of leaf chloroplast. Deep bronze-tipped leaves even under light shade dominantly characterized coffee seedlings from the Harenna forest. Light green-colored leaves also highly prevailed in most coffee seedlings of the southwest accessions. Accordingly, light bronze was much more frequent in moderate shade, and deep bronze and light green leaves in light shade environments (Figure 6.6).

Table 6.4   Percent of young leaf tip colors (means±SD) in seedlings of coffee accessions

Accession	Deep bronze	Light bronze	Light green
I-1	74.13±9.37 a	21.22±5.82 bc	4.65±4.47 g
I-2	57.89±12.65b	16.81±6.22 bcd	25.31±7.08 f
I-3	29.78±4.98 c	20.11±13.13 bc	50.11±9.39 e
II-1	0.00±0.00 d	13.89±12.20 cde	86.11±12.20ab
II-2	0.00±0.00 d	19.11±19.03 bc	80.89±19.03 bc
II-3	1.33±2.42 d	24.89±11.68 b	73.78±12.01 cd
III-1	0.00±0.00 d	35.78±22.46 a	64.22±22.46 d
III-2	2.33±5.72 d	18.78±11.40 bc	78.89±12.58 bc
III-3	1.67±4.08 d	27.33±13.95 ab	71.00±16.43cd
IV-1	1.33±3.27 d	18.78±15.73 bc	79.89±18.05 bc
IV-2	0.00±0.00 d	5.00±7.13 e	95.00±7.13 a
IV-3	0.00±0.00 d	6.11±6.20 de	93.89±6.20 a
Mean	14.04	18.98	66.98
CV (%)	22.96	48.84	14.56
Shade	**	***	***
Accession	***	***	***
Shade*acc	***	NS	*

Within a column, means followed by the same letters are not significantly different according to Tukey test at P = 0.05.
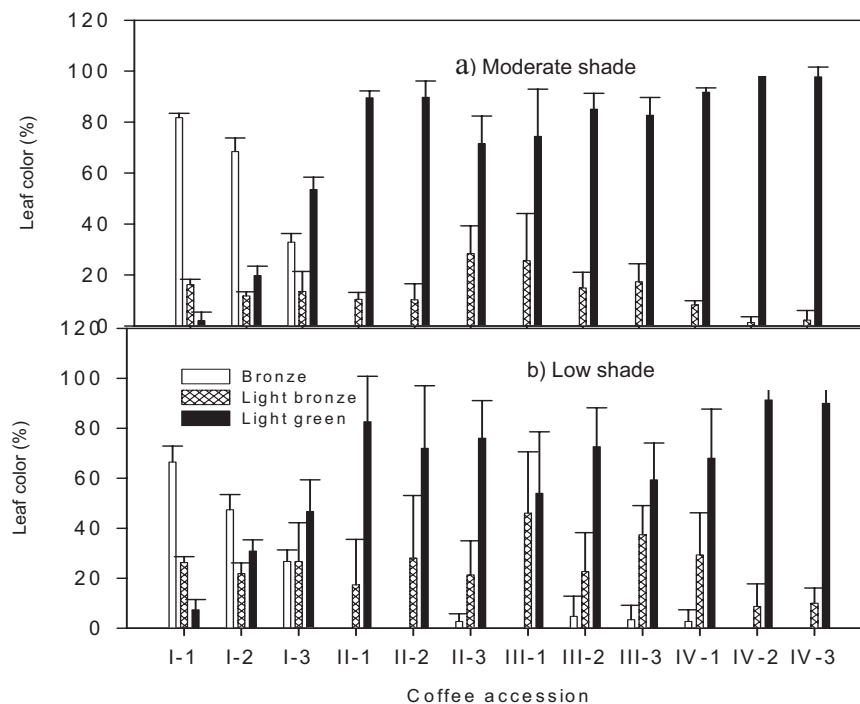

Figure 6.6   Proportion of coffee seedlings with bronze, light bronze and light green young leaf colors in (a) moderate and (b) low shade environments

Leaf chlorophyll

Diurnal change in the amount of leaf chlorophyll was neither significant nor consistent for the different data recording days. The influence of shade was, however, significant ($P<0.001$) and the readings were consistently higher in sun than in shade plots. As a result, the average values of 53.53±4.09 and 45.93±5.45 (with a difference of 15%) were determined from sun and shade seedlings, respectively. Although not significant, sun leaves also had higher concentrations of leaf chlorophyll (Table 6.5). Statistically significant ($P<0.001$) variation was displayed among coffee accessions in the amount of chlorophyll, but not in chlorophyll concentration. The highest average amount of foliar chlorophyll was recorded for Harenna (I-1 = 55.10±2.36) and the lowest in the Bonga accession (II-1 = 43.98±7.50). The concentrations of leaf chlorophyll (chl a, chl b and total chlorophyll) were not different among coffee accessions and their interaction with shade regimes. These were determined to be highest and lowest for the Yayu (IV-2) and Berhane-Kontir (III-1) accessions, respectively. Despite the absence of significant interactions with shade treatment, all accessions had higher values in the sun than in the shade (Figure 6.7; Figure 6.8). This indicates that foliar chlorophyll in coffee seems to be more controlled by innate plant characteristics. However, the influence of other plant and environmental factors, e.g., mineral fertilization is a question for further research. The results reveal that coffee accessions from the same area of collection or wild coffee population were different in leaf chlorophyll contents. This was particularly noticed for the Harenna (I-3) and Yayu (IV-2) accessions. However, the Harenna and Berhane-Kontir seedlings had maximum readings as compared to the Bonga and Yayu accessions (Table 6.5; Figures 6.7, 6.8).

Table 6.5   Amount (SPAD-502) and concentrations (µg ml^{-1}) of chlorophyll in leaves of coffee seedlings managed in contrasting shade regimes

Treatment	SPAD-reading	Chl-a	Chl-b	Total chl.
Shading	***	Ns	Ns	Ns
Sun	53.53±4-09a	4.21±2.56	2.50±1.15	6.71±3.59
Shade	45.93±5-45b	3.73±3.78	2.47±2.07	6.20±5.72
Accession	***	Ns	Ns	Ns
I-1	55.10±2.36a	5.05±2.95	2.76±1.00	7.80±3.94
I-2	53.05±8.08abc	4.82±2.56	3.09±1.69	7.91±3.35
I-3	45.08±4.31cd	2.12±1.47	1.61±0.53	3.73±1.97
II-1	43.98±7.50d	4.53±3.10	2.94±1.89	7.47±4.75
II-2	52.80±4.81abc	4.33±2.27	3.25±1.44	7.58±3.26
II-3	45.08±3.18cd	1.94±1.39	1.50±0.46	3.43±1.74
III-1	50.48±2.54a-d	1.63±0.26	1.23±0.38	2.85±0.53
III-2	49.60±8.58a-d	5.86±3.06	3.13±1.66	8.99±4.67
III-3	52.40±5.71abc	2.55±1.63	1.88±0.74	4.43±2.32
IV-1	49.78±5.50a-d	2.75±2.71	1.78±0.84	4.53±3.54
IV-2	53.25±5.04ab	7.39±5.91	4.10±3.54	11.50±9.43
IV-3	46.20±5.34bcd	4.66±5.09	2.59±2.24	7.26±7.31
Mean	49.73	3.97	2.49	6.45
CV (%)	6.38	71.23	64.08	65.74
ShadexAcc	Ns	Ns	Ns	Ns

*Ns = Not significant; *P<0.05; ***P<0.001 significance level. Means with the same letters within a column are not significantly different from each other at P = 0.05 (Tukey test).*
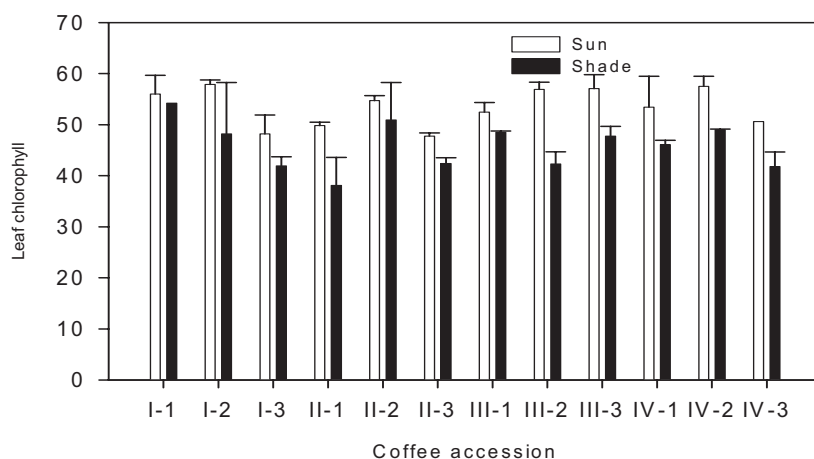

Figure 6.7   Chlorophyll meter (SPAD-502) reading on the amount of chlorophyll present in sun and shade leaves of coffee accessions
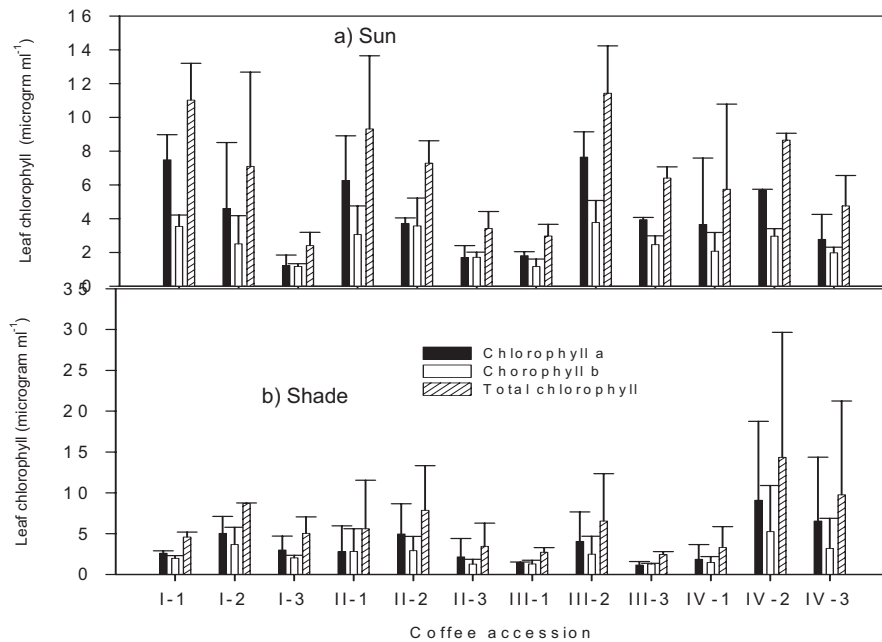
Figure 6.8　　Variability in concentration of leaf chlorophyll (μg/ml) in seedlings of coffee accessions in (a) full sun and (b) moderate shade environments

The relationship between leaf chlorophyll and leaf composition is indicated in Table 6.6. Intact chlorophyll reading with SPAD-502 had a weak positive correlation with leaf dry matter in both sun (r = 0.43) and shade (r = 0.51) plots, but its indicative ability was better in shade environments. This correlation was, however, stronger than the correlation values obtained between leaf dry matter and concentrations of chlorophyll types determined in the laboratory. Although insignificant, leaf organic carbon showed direct and indirect associations with the concentrations of leaf chlorophyll in sun and shade environments, respectively. In full sunlit, foliar chlorophyll contents (amount and concentration) were negatively associated with the concentration of inorganic ions such as K, Ca, Mg and N. Leaf TN was indirectly and significantly correlated with chlorophyll a (r = -0.62*) and total chlorophyll (r = -0.61*). This was different under shade conditions where SPAD-502 had a weak positive correlation with leaf K and N contents, while the correlation with leaf Mg content was negative. Here, chlorophyll concentrations were indirectly related to leaf K, but directly with leaf N content. The regression coefficients of the SPAD-502 reading with chlorophyll a, b and total chlorophyll depicted significant relations in full sun and partial shadow environments. The relationships were stronger in shade than in open sun

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(Figure 6.9); indicating that the chlorophyll meter (SPAD-502) may be suitable for predicting the greenness and hence nitrogen requirement of a coffee plant under specific environmental conditions.

Table 6.6　　Pearson correlation coefficients between leaf chlorophyll (SPAD-502 and laboratory analysis), leaf nitrogen (LN) and leaf organic carbon (LOC) in well-irrigated coffee seedlings in sun and moderate shade plots

Light regime	Variable	SPAD-502	Chl-a	Chl-b	Total-chl	LN
Sun	Chl-a	0.62*				
	Chl-b	0.61*	0.88***			
	Total chl	0.63*	0.99***	0.94***		
	LN	-0.24	-0.62*	-0.54	-0.61*	
	LOC	0.05	0.17	0.26	0.20	0.01
Shade	Chl-a	0.07				
	Chl-b	0.07	0.95***			
	Total chl	0.07	0.99***	0.98***		
	LN	0.13	0.10	0.07	0.09	
	LOC	0.42	-0.26	-0.09	-0.20	0.43

*$P<0.05$; **$P<0.001$ significance levels (2- tailed).*
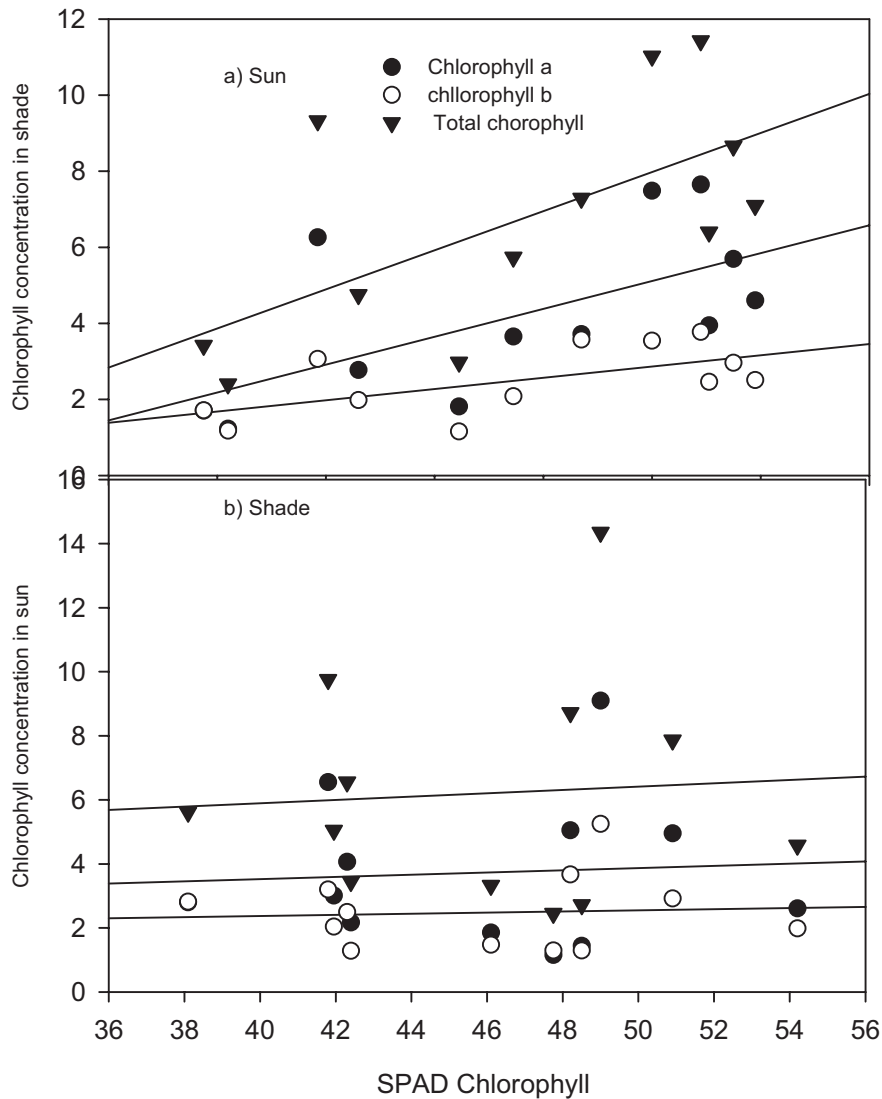
Figure 6.9   Regression between SPAD-502 and laboratory analyzed concentrations of chlorophyll in (a) full sun and (b) shaded leaves of coffee seedlings

Based on the concentration of leaf chlorophyll, the accessions were broadly clustered into 4 groups using the rescaled cluster distances between 5 and 10. Group 1 consisted of the accessions III-1, III-3, IV-1; group 2 of I-1, I-2, II-2; group 3 of I-3, II-1, II-2, III-2, IV-3; and group 4 consisted of the Yayu accession (IV-2), which was exceptional in terms of its chlorophyll a and total chlorophyll concentrations (Figure 6.10). The high total chlorophyll content in the leaves of III-2 and IV-3 seedlings could be due to the high chlorophyll concentrations observed at both wavelengths. The results, in general, do not follow consistent pattern for accessions of the same wild coffee

population, indicating intra-population variations in leaf chlorophyll contents under similar micro-environmental situations.

```
                Rescaled Distance Cluster Combine
      0         5         10        15        20        25
      +---------+---------+---------+---------+---------+
III-1 
III-3 
 IV-1 
  I-2 
 II-2 
  I-1 
  I-3 
III-2 
 II-3 
 II-1 
 IV-3 
 IV-2 
```
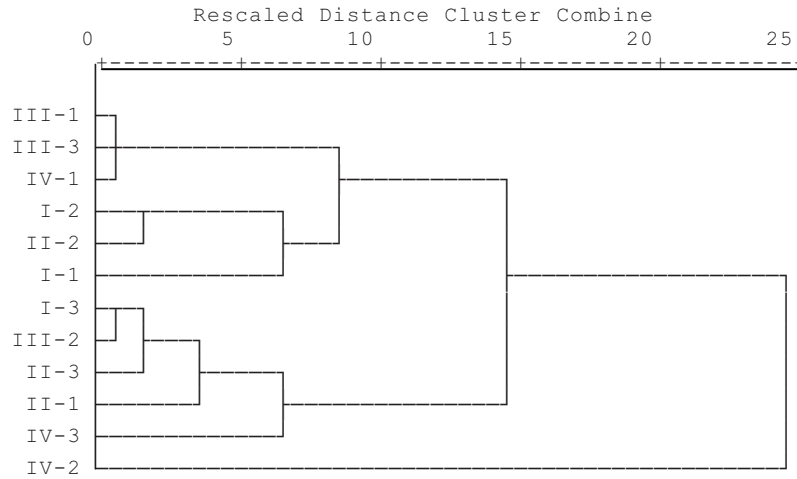
Figure 6.10   Dendrogram of the cluster analysis of leaf chlorophyll contents in seedlings of wild coffee accessions

Shoot morphology

The extent of morphological variability among coffee seedlings was different during the different growth stages. The accessions showed significant differences in the early growth performance, but this disappeared with increased seedling age. The results of the extension growth parameters recorded in 7- and 12-month-old seedlings are presented in Tables 6.7a and 6.7b, respectively. Accordingly, the early stage results show that seedlings of wild Arabica coffee accessions were highly significant in all parameters considered. Accordingly, most of the accessions collected from the Harenna and Yayu forests had maximum values as opposed to the lowest values obtained from the Berhane-Kontir population. The tallest seedlings with the highest leaf dimensions were found in the IV-2 accessions, followed by seedlings from I-1 with significantly higher numbers of leaves and nodes. Moreover, significant variations in growth parameters were observed among seedlings raised from coffee seeds collected from the three sites within each forest coffee unit. This is more prominent for the lowest seedling height and length of main stem internode length for accessions I-3, III-3 and IV-3. Similarly, leaf number and leaf dimensions were lowest for the II-2 and IV-3 (Table 6.7a).

Shade treatments were applied in the later stage of the seedlings and lasted only for a 2-month period (between June and July 2005). As a result, no significant differences were observed for most extension and destructive parameters. However, slightly higher values of main stem diameter, number of lateral branches and number of nodes on main stem were recorded for sun-exposed seedlings than for those in shade plots. The influence of shade treatment was more noticeable on leaf growth as compared to stem and root parameters. Consequently, the seedlings produced a significantly ($P<0.001$) higher leaf number in full sun than in shade environments (Figure 6.11). However, there were significant ($P<0.05$) reductions in leaf dimensions (length and width) and thus average leaf area in unshaded plot, although higher total leaf surface area and leaf area index were obtained in partial shadow conditions.

However, with increasing age of the seedlings (Table 6.7b), the results depict no significant growth response among accessions in all the morphological parameters considered. There was even a change in the order of ranking among the accessions, like for example in height elongation pattern, between Yayu and Harenna seedlings. At this stage, the Harenna seedlings exhibited the greatest average values for most variables such as seedling height (75.23 cm), main stem diameter (1.33 cm) and length of internode on primary branch (5.89 cm). The overall average seedling height was about 65 cm, while the undebarked main stem diameter was about 1.2 cm. Similarly, the Berhane-Kontir seedlings had reduced main stem nodes and long internodes on the primary branch, whereas the shortest seedlings with thin main stem diameter and short internodes on lateral branches were found in the Bonga coffee accession (II-1). This was followed by Yayu seedlings with higher values of leaf growths. These are some of the features of compact coffee types. In a similar fashion, the average leaf areas of the seedlings were different among accessions, and maximum values were determined for Harenna (I-3 = 31.71 cm^2) and Berane-Kontir (III-2 = 33.29 cm^2) seedlings. This was in contrast to the reduced average leaf size in Bonga (II-3 0 25.50 cm^2) and Yayu (IV-2 = 25.90 cm^2). Accordingly, the total leaf area ranged from 1162.75 cm^2 to 1787.26 cm^2 for Berhane-Kontir (III-1) and Harenna (I-3) accessions, respectively. Despite the narrow and small leaf size, unlike Bonga coffees, Yayu accessions had maximum total leaf surface area and leaf area index (Table 6.7b), indicating the indirect association between leaf number and leaf size. Hence, the leaf area index ranged from 3.36 to 5.10

for the same accessions, indicating the direct strong link between total leaf surface area and leaf area index. Unlike the Bonga accessions, the higher leaf production in the Yayu accessions contributed to the increased leaf area index. Leaf length ranged from 9.82 to 10.68 cm for the corresponding accessions from the Harenna and Berhane-Kontir seedlings. However, the maximum leaf width (I-3 = 4.73 cm) was recorded in Harenna and the narrowest leaves in Bonga (II-3 = 3.81 cm). The magnitude of variation was minimal for leaf dimensions (length and width), and mean leaf area was more dependent on leaf width. This resulted in the overall average results of 10.19 and 4.25 cm for leaf length and width, respectively. The accessions also showed maximum variations in the growth of primary branches, which was highest for Harenna (I-3 = 10.50) as opposed to the lowest growth for Yayu (IV-1 = 7.00). Further evaluation should, therefore, confirm whether or not such growth response remain at the later stages in field conditions.

Growth and development of coffee seedlings

Table 6.7a   Morphological characteristics of 7-month-old seedlings of coffee accessions under nursery conditions

Accession	Height (cm)	Girth (cm)	Leaf growth						Node number	Internode length (cm)
			Number	Length (cm)	Width (cm)	Total area (cm²)	Mean area (cm²)	LAI		
I-1	16.39a	0.33a	8.52a	7.09abc	3.05a	122.47ab	14.35ab	0.35ab	4.33a	3.77ab
I-2	15.05bc	0.30ab	8.50ab	6.97bcd	3.07a	121.09ab	14.18ab	0.35ab	4.23ab	3.55bc
I-3	13.23de	0.31ab	8.37abc	6.53def	2.90abc	106.81a-d	12.67bcd	0.31a-d	4.20ab	3.14d
II-1	14.17dc	0.31ab	8.02dc	6.79cde	2.85abc	103.73a-d	12.88bc	0.30bcd	4.02bcd	3.52bc
II-2	13.42de	0.29bcd	7.62e	6.33def	2.72cd	87.62de	11.48cd	0.25de	3.82d	3.52bc
II-3	13.89dc	0.29bc	8.10bcd	6.75cdef	2.79bcd	101.64b-e	12.50cd	0.29b-e	4.03bcd	3.45c
III-1	13.19e	0.27cd	7.08f	6.30f	2.63d	78.07e	10.97d	0.23e	3.47e	3.81a
III-2	12.37e	0.27cd	7.07f	6.80cde	2.71cd	87.09de	12.25cd	0.25de	3.52e	3.52bc
III-3	12.18e	0.26d	6.85f	6.53def	2.81bcd	84.57de	12.22cd	0.25de	3.51e	3.48c
IV-1	15.71ab	0.30ab	8.07dc	7.32ab	2.94ab	115.49abc	14.29ab	0.34abc	4.05bc	3.87a
IV-2	16.78a	0.33a	8.37abc	7.53a	3.06a	128.16a	15.30a	0.37a	4.18ab	4.01a
IV-3	13.46de	0.29bcd	7.73de	6.59def	2.74bcd	93.42cde	12.01cd	0.27cde	3.95cd	3.41c
Pr>F	**	**	**	**	**	***	**	***	**	**
Mean	14.15	0.30	7.86	6.79	2.86	102.51	12.93	0.30	3.94	3.59
CV (%)	10.24	10.47	5.78	7.69	8.36	12.23	14.75	12.15	6.33	8.16

, * = significant at P≤0.01 and P≤0.001 levels, respectively. Subscripts with the same letter(s) within a column are not significantly different at P=0.05 significance level according to Tukey test at P = 0.05.

Growth and development of coffee seedlings

Table 6.7b   Morphological growth of 12-month old seedlings of wild coffee accessions under nursery conditions

Accession	Height	Girth	NMSN	NPrBr	NBrN	BrIL	MSIL	LN	LL	LB	MLA	TLA	LAI
I-1	75.23	1.33	13.50	8.25	24.75	5.89	5.90	48.00	9.97	4.53	29.99	1385.27	4.00
I-2	74.45	1.27	12.75	7.50	21.00	5.54	7.28	47.00	9.82	4.36	28.46	1326.26	3.83
I-3	68.23	1.23	10.25	10.50	27.50	5.59	6.22	58.00	10.10	4.73	31.71	1787.26	5.17
II-1	58.38	1.18	12.50	8.75	28.50	4.82	6.27	58.00	10.29	4.32	29.57	1635.60	4.72
II-2	61.38	1.10	13.25	8.50	25.25	4.51	5.98	47.75	9.90	4.11	27.01	1269.05	3.67
II-3	60.75	1.09	12.25	7.50	23.25	4.90	6.39	49.50	10.21	3.81	25.50	1275.13	3.69
III-1	60.88	1.18	12.25	7.00	21.50	5.09	5.98	45.25	9.79	4.02	26.09	1162.75	3.36
III-2	61.55	1.13	12.00	8.50	21.25	5.44	6.91	48.50	10.97	4.59	33.29	1591.02	4.60
III-3	64.43	1.17	12.25	8.00	23.25	5.19	7.24	55.25	10.68	4.15	29.32	1575.88	4.56
IV-1	62.90	1.26	11.25	7.00	25.00	5.53	6.84	58.50	10.35	4.16	28.39	1657.16	4.79
IV-2	65.13	1.18	13.00	8.50	31.25	5.22	6.19	58.75	9.90	3.96	25.90	1506.59	4.36
IV-3	62.65	1.24	12.25	7.75	27.25	5.05	6.09	61.00	10.33	4.26	29.32	1664.95	4.81
Pr>F	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns
Mean	64.66	1.19	12.29	8.15	24.98	5.23	6.44	52.96	10.19	4.25	28.71	1486.41	4.29
CV (%)	7.85	7.04	9.00	17.41	21.89	7.21	10.09	14.64	4.11	6.54	10.09	11.97	11.99

*Ns = Not significant; * = P<0.05; ** = P<0.01. Within a column, figures followed by different letters are significantly different at P = 0.05 (Tukey test). Abbreviations: NMSN = Number of main stem node, NPrBr = number of primary branch, NBrN = number of branch nodes, BrIL = branch internode length, MSIL = main stem internode length, LN = leaf number, LL = leaf length, LB = leaf breadth, MLA = mean leaf area, TLA = total leaf area and LAI = leaf area index.*

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There were no significant interactions between shade and coffee accessions for most of the morphological growth parameters studied. However, most accessions exposed to direct sunlight had higher results for leaf variables, except average leaf area. However, few accessions, particularly from Berhane-Kontir, had higher leaf growth in shade comparted to sun conditions (Figure 6.11). In other words, the variations were very pronounced between the Harenna and Berhane-Kontir seedlings, which is in line with the results of seed germination and early stage growth performance of the seedlings as discussed above. In essence, although intra-population variations in morphological responses were evident, the wild coffee accessions were identified to have varying growth habits: open type (Harenna and Berhane-Kontir) and compact (Bonga and Yayu) canopy natures and hence, their hydraulic properties could differ accordingly.
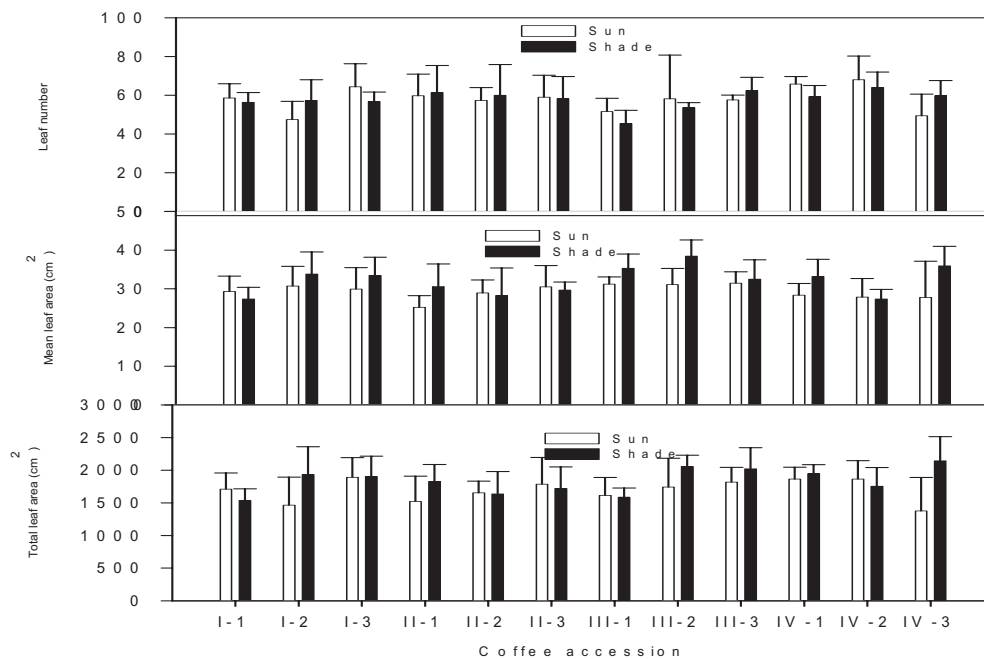

Figure 6.11   Leaf growth parameters of coffee seedlings as influenced by contrasting shade regimes

The results of the Pearson correlation matrix among the morphological parameters of coffee seedlings under optimal environments showed significant positive relations between seedling height and stem size (r = 0.74**). The internode length on the primary branch was strongly related to seedling height and stem diameter. Leaf area index was directly and significantly (r = 0.83**) influenced by the number of leaves.

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Similarly, average leaf area was strongly dependent on leaf dimensions and the correlation was higher due to leaf width (Table 6.8).

Table 6.8   Pearson correlation values among non-destructive morphological parameters of coffee seedlings under optimal environment (shaded and irrigated plot)

Parameter	Height	Girth	NMSN	NPRBr	NBrN	PrBrIL	MSIL	LN	LL	LB	MLA	LAI
Height	1.00	0.74	0.17	0.12	-0.13	0.75	0.15	-0.22	-0.36	0.46	0.20	-0.06
Girth	0.74**	1.00	-0.03	-0.04	0.08	0.77	0.01	0.18	-0.26	0.49	0.28	0.25
NMSN	0.17	-0.03	1.00	-0.33	-0.02	-0.25	-0.21	-0.42	-0.32	-0.34	-0.39	-0.62
NPRBr	0.12	-0.04	-0.33	1.00	0.48	0.10	-0.23	0.30	0.07	0.62	0.53	0.53
NBrN	-0.13	0.08	-0.02	0.48	1.00	-0.17	-0.48	0.77	-0.18	-0.04	-0.11	0.49
PrBrIL	0.75**	0.77**	-0.25	0.10	-0.17	1.00	0.26	-0.01	0.06	0.60	0.49	0.29
MSIL	0.15	0.01	-0.2	-0.23	-0.48	0.26	1.00	-0.02	0.50	0.09	0.27	0.20
LN	-0.22	0.18	-0.42	0.30	0.77**	-0.01	-0.02	1.00	0.26	0.05	0.15	0.83
LL	-0.36	-0.26	-0.32	0.07	-0.18	0.06	0.50	0.26	1.00	0.25	0.62	0.55
LB	0.46	0.49	-0.34	0.62*	-0.04	0.60*	0.09	0.05	0.25	1.00	0.91	0.53
MLA	0.20	0.28	-0.39	0.53	-0.11	0.49	0.27	0.15	0.62*	0.91**	1.00	0.66
LAI	0.06	0.25	-0.62*	0.53	0.49	0.29	0.20	0.83**	0.55	0.53	0.66*	1.00

*, ** = Correlation is significant at the 0.05 land 0.01 level (2-tailed), respectively. Abbreviations: see Table 6.7b.

With regard to the coordination and classification of the accessions, the results of the principal component analysis for the extension data reveal that in principal axis-1 leaf growth parameters (total leaf area, average leaf size, leaf width, leaf number and leaf length) were the major variables for the variances among accessions. In principal axis-2, seedling height (50%), stem size (38%) and internode length of primary branch (44%) were responsible for the variability among accessions. Accordingly, coffee accessions were located along the axis on the basis of their geographical closeness, particularly between the southeast and southwest populations (Figure 6.12). Such differentiation was observed for the Bonga and Harenna accessions, which were located at a far distance. About 50% of the accessions, however, did not reveal this pattern. Likewise, the result of the cluster analysis for shoot morphological parameters also depicts the same patterns of grouping the coffee accessions. Consequently, at a rescaled distance between 10 and 15, the accessions were clustered into 5 classes: group 1 consisted of Yayu and Berhane-Kontir, group 2 of an accession from Berhane-Kontir, III-2, group 3 of a Harenna accession alone-I-3, group 4 of Bonga accessions, and group 5 of Harenna accessions (Figure 6.13).
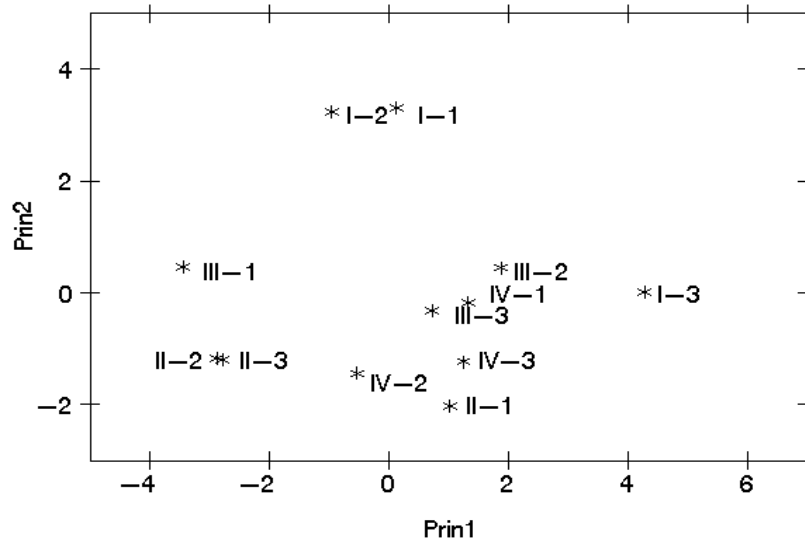
Figure 6.12   Principal component analysis for extension growth parameters of coffee seedlings under optimal shade and irrigation condition
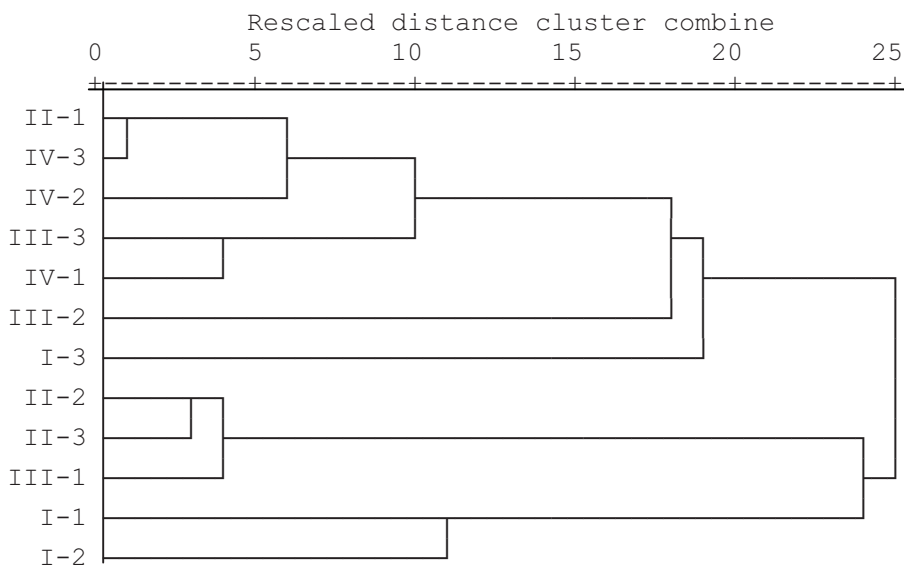

Figure 6.13   Dendrogram for clustering of wild coffee accessions according to results of extension growth parameters

Root morphology

Although insignificant, the number and volume of lateral roots was higher for unshaded seedlings. Taproot and lateral roots were slightly longer in the shade, though not significantly different to those of unshaded seedlings. On the other hand, coffee

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accessions significantly differed in total root volume (P<0.001), taproot length (P<0.05) and length of lateral roots (P<0.01). The accessions, however, did not differ in the number of lateral roots, though the respective maximum and minimum counts were obtained from the Harenna and Berhane-Kontir accessions. The longest (19.19±0.45 cm) and shortest (17.03±0.99 cm) lateral roots were obtained from Yayu (IV-1) and Harenna (I-3) seedlings, respectively. This reflects that coffee saplings can adapt to drought situations by extending the root system into deeper soil layers. Berhane-Kontir accessions had the significantly lowest root volume (28.80±4.67 cm^{-3}) as opposed to the highest value (48.50±2.78 cm^{-3}) for the Harenna seedlings (Table 6.9).

6.4.5   Biomass production and partitioning

Biomass production

Shoot biomass

Significantly (P<0.001) higher stem (main stem and branch) dry mass (17.48±2.49 g) was obtained from unshaded plots than from those in partial shade. In addition, insignificantly higher leaf dry weight (13.58 g) was found for sun-exposed seedlings (Table 6.9). Similarly, most shoot growth parameters were higher for drought-subjected seedlings. Hence, significantly (P<0.05) higher leaf dry mass and main stem plus branch (P<0.05) values were obtained for non-irrigated than for well-watered seedlings. With regard to shade or irrigation, stem biomass was higher (17.48 g) in the sun than the shade (15.60 g) with about 11% difference. Coffee accessions significantly (P<0.05) differed in stem dry weight, with average results ranging from 14.36±1.85 to 19.08±2.01g for Berhane-Kontir (III-2) and Harenna (I-1) seedlings, respectively (Table 6.9). Most accessions had relatively lower growth responses in shade conditions as compared to the sun plots. As a result, higher dry mass of leaf, root and total dry matter were recorded for seedlings exposed to direct sunlight (Figure 6.14). There was a considerable difference among accessions in root dry mass and root to shoot ratio; the values followed the order of Harenna>Yayu>Bonga>Berhane-Kontir accessions. This reflects the variations in growth rate and productivity among the accessions, which in turn can be associated with the stem natures (stiff or flexible, stem density) and attributes of the water-conducting xylem tissue. The result shows that stem growth is

one of the strongest parameters affecting water flow in coffee trees and hence can be used as a selection criteria in the breeding program

Root biomass

A significantly (P<0.01) higher root dry weight (8.93 g) was obtained from unshaded than from partially shaded seedlings (7.89 g), where a reduction of about 12% was noted. The difference between watering regimes was also significant (P<0.01) for root dry mass and was higher for drought-stressed (8.90 g) than for well-irrigated (7.92 g) seedlings. In the same manner, coffee accessions significantly differed (P<0.01) in root dry mass and consequently, the lowest (III-1 = 6.48 g) and highest (I-2 = 10.43 g) average values were obtained from Berhane-Kontir and Harenna seedlings, respectively (Table 6.9). In general, the Harenna seedlings had a higher root mass than the others, particularly the Berhane-Kontir accessions, which had a low root biomass ranging between 6.48 and 7.22 g. This was less than the overall average root dry weight of 8.41 g. The ratios of root to shoot dry mass of the seedlings also significantly differed among the accessions, but not between shade and irrigation levels. The absence of significant differences due to shade and irrigation suggests that the duration of the treatments was too short to considerably change root biomass accumulation. However, root to shoot ratio of some seedlings surpassed those in shadow conditions. The significantly lowest (III-3 = 0.23) and highest (I-2 = 0.33) root to shoot values were determined for the Berhane-Kontir and Harenna accessions, respectively (Figure 6.15). As a whole, root to shoot ratio was higher for the other accessions from Harenna than those from Berhane-Kontir.

Total biomass

The analysis of variance comparing the total dry matter production of coffee seedlings depicts significant (P<0.01) differences between the two shade and irrigation treatments as well as due to accessions (P<0.05). Significantly (P<0.001) higher total dry matter yields (39.99±5.31 g) were obtained from the sun than from the shaded plots. There was about 9 % reduction in total dry matter production of seedlings in moderate shade as compared to those in full sunlight. Similarly, significantly (P<0.01) higher total dry matter was obtained from drought-stressed than well-watered seedlings. The results also

reveal significantly lowest (III-1 = 33.23 g) and highest (I-1= 42.34 g) total biomass from the Berhane-Kontir and Harenna coffee accessions, respectively (Table 6.9; Figure 6.15). Accessions from Harenna (I-2 = 41.95 g) and Berhane-Kontir (III-2 = 34.54 g) had the next maximum and low average values, respectively, though no significance was detected among the other accessions.

Growth and development of coffee seedlings

Table 6.9   Shoot and root growth parameters (means±SD) in coffee seedlings according to shade, irrigation and accession treatments

Treatment	LDW (g)	SDW (g)	RDW (g)	RV (cm⁻³)	TRL (cm)	LRN	LRL (cm)	R:S	TDM (g)
Shading	Ns	**	**	*	*	Ns	Ns	Ns	**
Sun	13.58±1.59	17.48±2.49	8.93±1.64	38.52±7.32	29.57±5.91	38.73±4.17	17.97±1.05	0.29±0.03	39.99±5.31
Shade	13.06±0.91	15.60±1.55	7.89±1.52	36.03±7.09	32.03±4.20	37.84±4.64	18.42±1.46	0.28±0.04	36.54±3.13
Irrigation	*	*	**	Ns	***	*	Ns	Ns	**
Stressed	13.68±1.40	17.14±2.53	8.90±1.52	36.36±6.03	33.68±4.90	39.52±4.00	18.42±1.19	0.29±0.03	39.72±4.95
Watered	12.95±1.12	15.94±1.81	7.92±1.66	38.18±8.31	27.91±3.80	37.05±4.48	17.98±1.35	0.27±0.04	36.81±3.92
Accession	Ns	*	**	***	*	Ns	*	**	*
I-1	13.25±0.80	19.08±2.01a	10.02±1.11a	46.25±9.19ab	34.45±5.00	41.10±2.68	19.62±1.35	0.31±0.04ab	42.34±3.43a
I-2	13.06±0.89	18.47±2.09ab	10.43±1.23a	48.50±2.78a	35.42±6.13	43.20±5.60	19.45±0.63	0.33±0.01a	41.95±4.03ab
I-3	13.73±1.85	16.63±1.78ab	9.22±0.95ab	42.70±2.55abc	34.06±6.35	38.43±0.97	19.19±0.45	0.31±0.02ab	39.57±4.52ab
II-1	13.63±1.78	16.65±2.47ab	8.30±1.44abc	34.95±4.99cd	28.78±3.76	39.25±7.93	17.07±0.97	0.28±0.02abc	38.58±5.57ab
II-2	12.34±0.66	15.52±1.33ab	7.97±1.11abc	35.25±5.54bcd	31.74±5.06	39.70±3.50	17.77±0.77	0.28±0.03abc	35.82±2.90ab
II-3	12.81±0.68	15.29±1.66ab	8.15±1.34abc	37.55±4.35a-d	30.71±6.20	36.58±1.83	19.16±0.61	0.29±0.04abc	36.24±2.84ab
III-1	11.91±0.51	14.84±1.45ab	6.48±1.09c	32.70±5.13cd	27.38±4.15	33.08±3.74	17.99±1.18	0.25±0.04 bc	33.23±1.93b
III-2	12.97±1.29	14.36±1.85b	7.22±1.66bc	31.20±4.98d	28.73±4.53	36.50±4.89	18.11±1.41	0.27±0.04abc	34.54±4.21ab
III-3	14.37±1.45	16.11±2.41ab	6.86±1.20bc	28.80±4.67d	27.39±6.56	36.60±2.15	17.31±0.91	0.23±0.03c	37.33±4.65ab
IV-1	13.87±0.76	17.16±1.50ab	8.67±0.30abc	37.25±4.33a-d	27.14±2.74	38.15±4.83	17.03±0.99	0.28±0.02abc	39.69±2.09ab
IV-2	14.41±0.67	18.06±1.24ab	9.39±1.00ab	38.65±3.22a-d	30.58±1.25	39.75±2.71	18.38±1.34	0.29±0.01abc	41.87±2.81ab
IV-3	13.52±2.12	16.29±3.37ab	8.23±2.43abc	33.45±4.89cd	33.21±5.18	37.10±3.19	17.32±1.03	0.27±0.05abc	38.03±7.63ab
Mean	13.32	16.54	8.41	37.27	30.80	38.29	18.20	0.28	38.26
CV (%)	7.95	9.35	10.72	10.61	10.38	9.77	5.05	9.31	8.20

Ns = Not significant; *, ** and *** = significant at P<0.05, P<0.01 and P<0.001, respectively. Means followed by same letter with in a column are not different from each other (Tukey test at P = 0.05). Abbreviations: LDW = leaf dry weight, SDW = stem dry weight, RDW= root dry weight, RV = root volume, TRL = taproot length, LRL = lateral root length, R:S = root to shoot ratio, TDM = total dry matter.
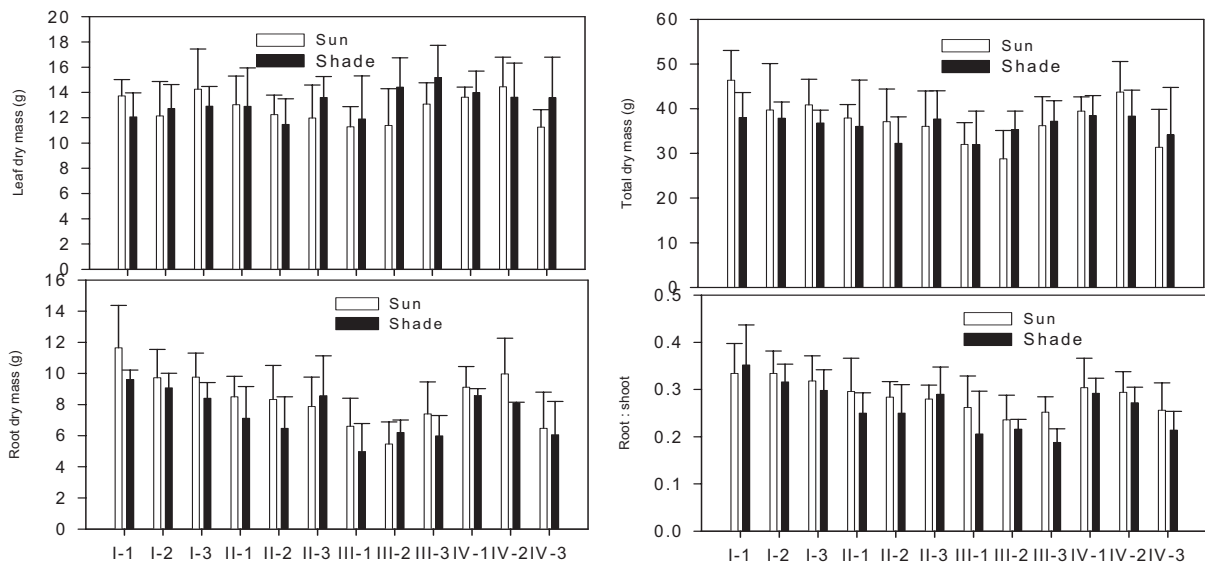
Figure 6.14   Biomass yield and root to shoot ratio of wild coffee accessions under sun and shaded conditions
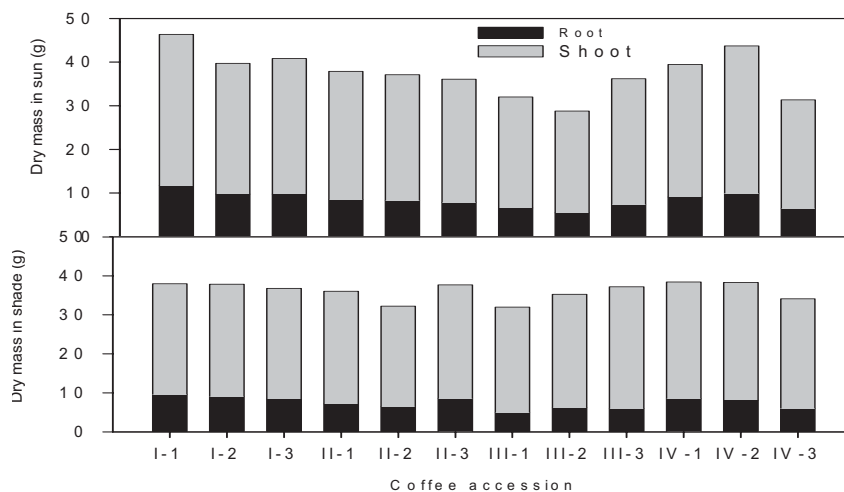

Figure 6.15   Root and shoot dry mass for seedlings of wild coffee accessions under (a) sun and (b) shade conditions

There were positive and significant associations between most root and shoot growth characteristics of coffee seedlings (Table 6.10), and stem and root dry weights were equally and significantly ($r = 0.96^{**}$) correlated to total biomass yield. Moreover, leaf dry matter was significantly associated with root biomass ($r = 0.71^{**}$) and total dry matter ($r = 0.85^{**}$), indicating the role of leaves in carbon assimilation and distribution to different plant parts. Moreover, the principal component analysis demonstrated that all destructive parameters were increased in axis 1. In axis 2, root parameters showed

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decreased values while shoots were positive. The proportion of leaf dry weight in the correlation matrix was about 71% and the cumulative value increased thereafter (Figure 6.16). According to the hierarchical cluster analysis, coffee accessions were grouped into 3 broad classes at about 10 cluster distance dissimilarity. The groups consisted of 5, 5 and 2 accessions, respectively (Figure 6.17). The first group consisted of a mixture of accessions from Yayu (IV-1 and IV-2), Bonga (II-1), Berhane-Kontir (III-3) and Harenna (I-3). Bonga and Harenna accessions were classified into the second and the third cluster, reflecting the close similarity between the two forest units. The results of the destructive parameters show that seedlings of different wild coffee accessions did not show great variations and thus grouped into few clusters, Harenna seedlings being the most dissimilar accessions from the southwest materials.

Table 6.10   Pearson correlation values between shoot and root destructive parameters

Parameter	LDW	SFW	SDW	RFW	RDW	RV	TRL	LRN	LRL	TDM
SFW	0.49									
SDW	0.46	0.93**								
RFW	0.20	0.91**	0.88**							
RDW	0.44	0.94**	0.96**	0.94**						
RV	0.13	0.89**	0.86**	0.99**	0.92*					
TRL	0.05	0.31	0.48	0.51	0.53	0.51				
LRN	0.18	0.59*	0.65*	0.74**	0.79**	0.73**	0.73**			
LRL	0.10	0.76**	0.66*	0.81**	0.73**	0.81**	0.32	0.51		
TSDW	0.75**	0.89**	0.93**	0.73*	0.89**	0.69*	0.37	0.56	0.53	
TPDM	0.68*	0.93**	0.96**	0.81**	0.94**	0.77**	0.43	0.64*	0.60*	
R:S	-0.26	0.63*	0.65*	0.82**	0.73**	0.84**	0.46	0.75**	0.70*	0.49

*, ** = Correlations are significant at 0.05 and 0.01 levels, respectively (2-tailed). For abbreviation see Table 6.9.
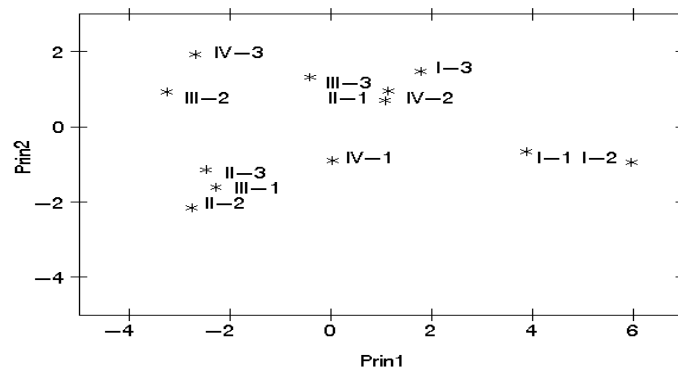

Figure 6.16   Principal component analysis for destructive growth parameters of coffee seedlings maintained under optimal environmental conditions
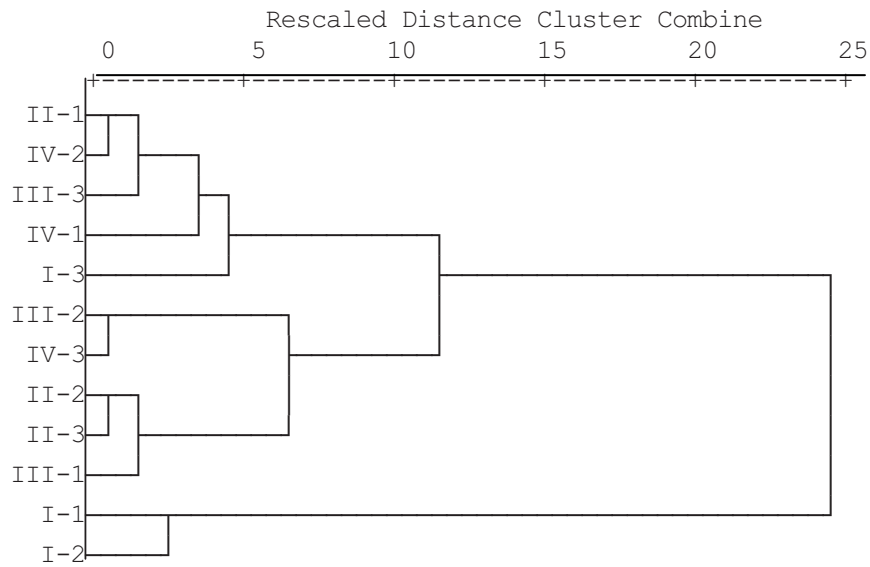
150

```
              Rescaled Distance Cluster Combine
        0         5        10        15        20        25
        +---------+---------+---------+---------+---------+
  II-1  ─┐
  IV-2  ─┤
 III-3  ─┴─┐
  IV-1  ───┴─────┐
   I-3  ─────────┴─────────┐
 III-2  ─┐                 │
  IV-3  ─┴───────┐         │
  II-2  ─┐       │         │
  II-3  ─┤       │         │
 III-1  ─┴───────┴─────────┤
   I-1  ─┐                 │
   I-2  ─┴─────────────────┘
```

Figure 6.17   Dendrogram of cluster analysis of coffee accessions based on root and
                shoot destructive growth parameters

Total biomass partitioning

Though insignificant, the amount of total dry mass partitioned to the root part was
higher in sun (22.22±1.89%) and drought stressed (22.35±2.02%) seedlings as
compared to the lower shares in partial shading (21.45±2.81%) and well-watered
(21.33±2.68%) seedlings. In contrast, leaf partitioning was significantly different
according to the level of shade (P<0.001) and irrigation (P<0.05). As a result, the mean
values ranged from 34.11±2.19 to 35.89±2.92% and 34.63±2.50 to 35.37±2.90%
between full sun and shade and drought-stressed and irrigated seedlings, respectively.
Furthermore, in full sunlight, the stem plus branch part shared significantly (P<0.05)
more of the total assimilates (43.67±1.55%) as opposed to seedlings arranged in partial
shade conditions.

The total dry matter yield distributed to leaf and total shoot part was, however,
not altered due to irrigation treatment. Hence, the average leaf and shoot shares ranged
between 43.03±1.75 and 43.30±1.53% and 77.66±2.02 and 78.67±2.68%, respectively.
This was similar to the slightly higher assimilate amounts (78.55±2.81%) stored in the
shoot part of shaded seedlings, though the allocation to the root part was low (Table
6.11). This corresponds with the more luxurious shoot growth of coffee seedlings at
resource rich environments as opposed to deep root systems in drought-stressed

situations. The coffee accessions from Berhane-Kontir had significantly (P<0.01) the lowest (18.3%) root partitioning as compared to the Harenna seedlings, which had the highest (38.6%) root share. The results indicate significant differences among accessions in the patterns of total biomass partitioned in leaf (P<0.001) and shoot (P<0.01) parts. Consequently, the values ranged between 31.2 and 38.6% for leaves and between 75.2 and 81.7% for the shoot. Under ideal shade and irrigation regimes, differences among accessions in the allocation of total biomass were not significant. However, low leaf partitioning was observed in the Harenna accessions as compared to those from the Bonga and Berhane-Kontir forests. Maximum leaf partitioning was also observed in one of the accessions from the Yayu populations (IV-3 = 35.8%). On the other hand, stem plus branch partitioning did not vary among accessions, with the values ranging between 41.5 and 44.6% for III-2 and III-3 of the Berhane-Kontir accessions, respectively (Table 6.11; Figure 6.18).

Table 6.11   Total dry matter partitioning (%, means±SD) in coffee seedlings according to shade, irrigation and accessions

Treatment	Root	Leaf	Stem	Whole shoot
Shading	Ns	***	*	Ns
Sun	22.22±1.89	34.11±2.19b	43.67±1.55a	77.78±1.90
Shade	21.45±2.81	35.89±2.92a	42.66±1.58b	78.55±2.81
Irrigation	Ns	*	Ns	Ns
Stressed	22.35±2.02	34.63±2.50b	43.03±1.75b	77.66±2.02
Watered	21.33±2.68	35.37±2.90a	43.30±1.53a	78.67±2.68
Accession	**	***	Ns	**
I-1	23.68±1.89ab	31.33±1.14de	45.00±1.55	76.33±1.89bc
I-2	24.82±0.87a	31.21±1.61e	43.98±1.19	75.18±0.87c
I-3	23.33±0.66ab	34.62±0.99bc	42.05±0.73	76.67±0.66bc
II-1	21.48±1.19abc	35.38±0.92bc	43.15±1.05	78.53±1.19abc
II-2	22.16±1.45abc	34.52±1.50c	43.32±1.48	77.84±1.44abc
II-3	22.37±2.04abc	35.51±3.48abc	42.13±2.20	77.64±2.04abc
III-1	19.50±3.15bc	35.87±1.09abc	44.64±2.90	80.50±3.15ab
III-2	20.75±2.89abc	37.71±3.00ab	41.54±0.57	79.25±2.89abc
III-3	18.34±1.86c	38.62±2.52a	43.05±1.16	81.66±1.85a
IV-1	21.88±1.32abc	34.94±1.00bc	43.18±1.73	78.13±1.33abc
IV-2	22.39±0.92abc	34.47±1.07cd	43.15±0.76	77.62±0.93abc
IV-3	21.38±2.81abc	35.81±2.85abc	42.82±0.74	78.62±2.81abc
Mean	21.84	35.00	43.17	78.16
CV (%)	7.67	3.18	3.30	2.14

*Ns = Not significant; *, ** and *** = significant at P<0.05, P<0.01 and P<0.001, respectively. Means followed by same letter with in a column are not different from each other (Tukey test at P = 0.05).*
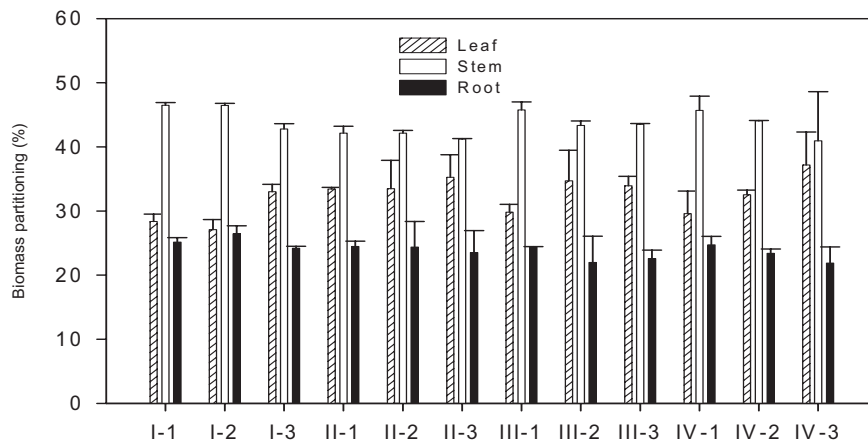
Figure 6.18   Total dry matter partitioning in seedlings of wild coffee accessions

6.4.6   Growth rate of coffee seedlings

Most morphological parameters of the coffee seedlings were significantly increased with seedling age between March and April, most likely reflecting the increased vegetative growth rate due to the prevailing climatic variables during the study period. The length of internodes on the orthotropic branch, leaf dimensions and thus, average leaf size, however, did not reveal significant changes, most likely due to the short duration of the shade treatment. All parameters showed a similar increasing trend from March to April, with varying magnitudes. Consequently, the least (2.5%) and greatest (25.6%) change in growth was determined for leaf width and total leaf area. The maximum total leaf turnover (19.4%) may be contributed to the greatest percent growth in total leaf surface and hence, leaf area index. Seedling variables, which were highly significantly different between the months, showed varying rates of growth over the study period. These included seedling height (10.5%), stem diameter (18.2%) and production of nodes (7.6%), suggesting variations in dry mass allocation and seedling vigor. Although node growth increased over the months, values were negative when sun seedlings were compared to shade seedlings. Percent growth change between March and May also revealed highly significant changes during the study period (110 days). In addition, the two-way analysis of variance for growth rates of seedlings was significantly ($P<0.01$) higher in April than in May owing to inter-monthly differences in radiation and related climatic variables, particularly air temperature (Figure 6.1).

With regard to seedling response to light regimes, except for the seedling height, number of primary branches and total leaf area, all the other parameters revealed significant differences between the two shade treatments. Shade treatments significantly influenced growth rates of stem diameter (P<0.01), number of nodes (P<0.05), number of primary branches (P<0.01), leaf numbers (P<0.001) and mean leaf area (P<0.05). Accordingly, except for number of main stem nodes and leaf number, the values were higher under sun than in shade. Leaf growth showed an increment of 12.5% under sun as compared to moderate shading. This resulted in an increment of 3.9% in total leaf area compared to shade leaves.

In contrast, relative growth patterns for average leaf size revealed negative values based on shade and accessions, reflecting the reduced leaf sizes with increased seedling age. This was particularly the case for seedlings with increased light intensity, where a reduction of 65.2% in average leaf size was determined as compared to shade environments. This could be due to the reduced leaf dimensions in full sun environments. Similarly, production of lateral branches was significantly higher (5.7%) with increased light intensity. However, the length of the main stem internode was inhibited and the reduction was 33.9% in the open sun plots compared to the shade plots. In general, most variables showed increased growth rate according to light levels and months, high influence noted for the shade treatment. In contrast, higher growth changes in such parameters as stem size, number of nodes and lateral branches, and total leaf area were obsereved with ageing.

Coffee accessions displayed significant variations in seedling height (P<0.001), number of nodes (P<0.01) on the main stem. The Harenna and Berhane-Kontir accessions had the highest and lowest average values for these growth parameters, respectively (Table 6.12). Though the statistical analysis did not detect significant differences for the other traits, maximum average values were determined for the Harenna and Yayu seedlings. This is in line with the seed germination and early stage growth performance of the accessions. Moreover, accessions of the same forest population were different in morphological growth habits in a controlled nursery environment, indicating inter- and intra-regional variability among the wild coffee populations. In general, based on the growth of internode length and leaf characteristics, the Harenna and Berhane-Kontir coffee accessions can be groups as open crown, while

the Yayu and Bonga accessions were dominated by compact to intermediate canopy natures. Similar to the shoot and root growth responses elaborated earlier, natural resource-use efficiency of the seedlings could also vary accordingly. Hence, an attempt was made to assess the hydraulic conditions of the different accessions (chapter 7).

In addition, there were significant accession differences in growth rate (log transformed) of seedling height ($P<0.001$), number of nodes ($P<0.01$), number of main stem nodes ($P<0.01$), number of primary branches ($P<0.05$), leaf number ($P<0.001$) and total leaf are and leaf area index ($P<0.01$). The lowest and highest growth rates in stem elongation were found in Harenna (I-1 = 0.04 ± 0.02 cm cm^{-1}month^{-1}) and Berhane Kontir (III-1= 0.09 ± 0.03 cm cm^{-1}month^{-1}). The growth rate of number of nodes ranged from 0.04 ± 0.01 to 0.07 ± 0.01 for the Yayu (IV-1) and Berhane-Kontir (III-1) accessions, respectively. In addition, the accessions from Harenna (I-1) and Berhane-Kontir (III-1) displayed significantly the lowest and highest respective growth rates in total leaf surface area and leaf area index ($P<0.05$), compared to the other coffee seedlings (Table 6.12). As a result, the accessions from Harenna showed the lowest change in total leaf area (I-1 = 0.06 ± 0.07 cm cm^{-2} month^{-1}) as opposed to the highest value (III-1 = 0.21 ± 0.10 cm cm^{-2} month^{-1}) observed from the Berhane-Kontir accessions in the youngest seedlings. The remaining parameters also showed similar patterns among accessions, though not significantly different within the short experimental period. There was a consistent ranking among coffee accessions; seedlings that were fast growing in a low-light environment were fast growing in a high-light environment. Hence, the ranking of growth parameters could be attributed to the age variations among the wild coffee accessions and thus show their potentials to grow and invest carbon under specific environmental conditions.

Although not statistically significant, about 50% of the accessions maintained higher growth in height under reduced light regimes. Accordingly, the values of most of the accessions from Bonga and Berhane-Kontir were higher in sun and shade, respectively. In contrast, the Harenna and Yayu accessions showed reduced growth rate. The average growth rate in average leaf area and in total leaf area showed inverse relationships, and the results were inconsistent between the shade plots and coffee accessions. However, the results follow similar patterns to those of stem elongation.

This is in line with seed germination rate and early stage growth performance of the accessions as discussed in section 6.4 (Table 6.3; Figure 6.3).

According to the ANOVA for month, shade and accession there were significant interactions between shade and accession in the number of leaves ($P<0.05$) and average leaf size ($P<0.05$). Similarly, the interaction between month and shade treatment had a significant influence on stem length ($P<0.001$), stem diameter ($P<0.05$) and total leaf area ($P<0.001$). In addition, intenode length on the main stem was significantly ($P<0.01$) changed based on the combined effects of month and accession. However, the other interactions did not depict statistically significant variations of seedling growth response (Table 6.12). In full sunlight, seedlings revealed little change in height growth rate as opposed to a 54.4% increment for the shade plots between March and May. In May, seedlings in partial shade showed a 28.4% height increase over sun-exposed seedlings. On the other hand, there was an increment in stem size between March and May that were 53.5% and 30.9% for open sun and shaded seedlings, respectively. The difference between shade treatments varied with increasing age and hence, shaded seedlings exhibited increasing (25.6%) and decreasing (10.7%) growth rate of main stem size in March and May, respectively. On the other hand, partially shaded seedlings revealed an increase in total leaf surface areas by 9.3%, when compared to those in open sun. In contrast, full sunlight was found to significantly decrease total leaf area between the two months. This could be associated with the contribution of shade in extending the lifespan of the coffee leaves. This means that leaves in the sun require relatively maximum photosynthetic active radiation and low biomass partitioning patterns. These can result in the reduced leaf retention capacity of the seedlings, particularly in open sun conditions and in the drier month of May. This was evident from the differences between shade levels, where shaded plots were noted to have reduced and increased values of growth rate of total leaf area and leaf area index in the two experimental periods, respectively.

The morphological growth parameters of coffee seedlings were not significantly influenced by treatment interactions (Table 6.12). This could be explained in terms of the slow growth rate of the perennial coffee plant and the short experimental period. Thus, it is imperative to repeat the investigations over seasons and locations with the purpose to determine the relative rankings of the morphological and

physiological traits of Arabica coffee types in relation to climatic gradients. In contrast, the relative growth rates of stem diameter (RGR_D) and of leaf number (RGR_{LN}) were significantly influenced by the interaction between shade and accessions (Table 6.12). Consequently, 75% of the accessions had higher growth values for these parameters in full sunlight than in partial shade. Only 25% of the accessions, i.e., seedlings from Harenna (I-3), Berhane-Kontir (III-3) and Yayu (IV-1), showed greater RGR_D in moderate shade (Figure 6.19). In terms of RLG_{LN}, the accessions showed inconsistent responses to shading and the lowest and highest values were determined for the shaded seedlings in the Bonga (II-1) and Berhane-Kontir (III-1) accessions. Moreover, seedlings from Bonga forest had a higher RGR_{LN} in the open sun plots as opposed to accessions from Berhane-Kontir. This could be attributed to variations in seedling age, and the physiological activity of the leaves could also vary accordingly.

Growth and development of coffee seedlings

Table 6.12 Relative growth rate (means±SD) in shoot parameters for seedlings of coffee accessions in sun and shade environments (log transformed data)

Variable	Height	Stem size	NN	NMSN	NPB	LN	MLS	TLA
			Light regime					
Sun	0.07±0.03	0.18±0.04a	0.05±0.02a	0.04±0.04b	0.24±0.08	0.20±0.07a	-0.11±0.07b	0.15±0.07
Shade	0.07±0.03	0.16±0.03b	0.05±0.01b	0.07±0.04a	0.23±0.07	0.16±0.07b	-0.07±0.08a	0.15±0.08
			Accession					
I-1	0.04±0.02c	0.17±0.04	0.05±0.01ab	0.00±0.03b	0.19±0.07ab	0.14±0.06b	-0.15±0.06	0.06±0.07b
I-2	0.07±0.03abc	0.15±0.03	0.05±0.02ab	0.05±0.05ab	0.27±0.06ab	0.19±0.06ab	-0.15±0.08	0.15±0.10ab
I-3	0.05±0.01bc	0.17±0.02	0.04±0.01b	0.04±0.03ab	0.24±0.07ab	0.19±0.05ab	-0.15±0.05	0.13±0.03ab
II-1	0.06±0.02abc	0.17±0.06	0.05±0.02ab	0.07±0.03a	0.23±0.06ab	0.15±0.10b	-0.11±0.09	0.10±0.04ab
II-2	0.08±0.03ab	0.15±0.03	0.05±0.02ab	0.08±0.03a	0.23±0.08ab	0.19±0.11ab	-0.11±0.08	0.19±0.08a
II-3	0.08±0.02ab	0.18±0.03	0.06±0.01a	0.07±0.04a	0.21±0.11ab	0.18±0.06ab	-0.04±0.04	0.17±0.07ab
III-1	0.09±0.03a	0.17±0.03	0.07±0.01a	0.07±0.04a	0.31±0.05a	0.23±0.07a	-0.03±0.15	0.21±0.10a
III-2	0.08±0.03ab	0.18±0.06	0.06±0.02a	0.08±0.03a	0.29±0.04ab	0.23±0.08a	-0.08±0.06	0.17±0.08ab
III-3	0.08±0.02ab	0.17±0.03	0.06±0.02ab	0.07±0.05a	0.26±0.02ab	0.20±0.07ab	-0.08±0.04	0.19±0.06a
IV-1	0.06±0.02abc	0.15±0.04	0.04±0.01ab	0.05±0.04ab	0.21±0.05ab	0.19±0.06ab	-0.06±0.02	0.15±0.05ab
IV-2	0.05±0.02abc	0.17±0.02	0.05±0.02ab	0.02±0.04ab	0.17±0.04b	0.15±0.04b	-0.06±0.05	0.12±0.03ab
IV-3	0.08±0.02ab	0.16±0.02	0.05±0.01ab	0.07±0.02a	0.23±0.07ab	0.17±0.05ab	-0.05±0.03	0.16±0.05ab
			ANOVA (Pr>F)					
Shade	Ns	**	*	**	Ns	***	*	Ns
Accession	***	Ns	**	***	*	***	Ns	**
Shade*acc	Ns	*	Ns	Ns	Ns	**	Ns	Ns

Ns = Not significant $P>0.05$; *$P<0.05$, **$P<0.01$, ***$P<0.001$. Means with different letters within a column are significantly different at the 5% level of probability (Tukey). Abbreviations: NN = No of nodes, NMSN = No of main stem nodes, NPB = No of primary branch, LN =No of leaves, MLA = mean leaf area, TLA = total leaf area.
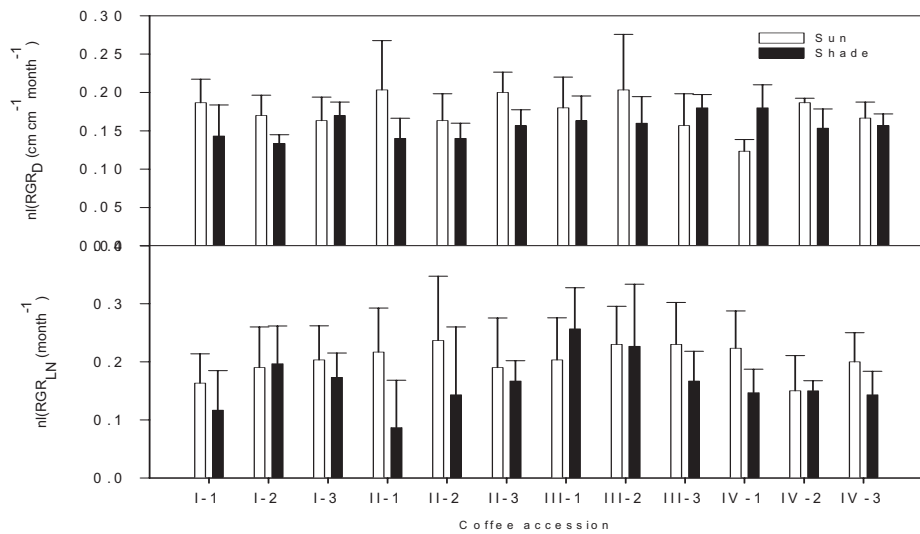
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Figure 6.19 Natural logarithm of relative growth rate in stem diameter (nl (RGR$_D$)) and leaf production (nl(RGR$_{LN}$)) of coffee seedlings of wild accessions under sun and shade conditions

6.4.7   Growth response to light regimes

Shade had a significant (P<0.01) effect on leaf mass ratio (LMR) with the higher value (0.36±0.03 g g^{-1}) recorded in reduced light conditions. In contrast, seedlings in full sun produced significantly (P<0.05) higher shoot mass ratio (SMR = 0.44±0.02 g g^{-1}) than those in the shade (0.43±0.02 g g^{-1}), indicating the plasticity in dry mass allocation to the main stem parts. On the other hand, LMR was significantly affected by shade (P<0.001), irrigation (P<0.05) and accession (P<0.001) as well as by two-way interaction effects (P<0.05) (Table 6.13). Hence, moderately shaded and irrigated seedlings had a higher LMR, which indicates the increased biomass allocation to leaves than to the other parts. This was as opposed to most other variables, which showed no significant variations, neither due to single nor to interaction effects. However, seedlings exposed to direct sunlight had relatively higher root mass ratio (RMR), SMR, canopy area (CA) and leaf area index (LAI).

Well-irrigated seedlings in full sunlight showed considerable reductions in growth, especially in LMR, compared to shaded seedlings. The correlation results (Table 6.14a, 6.14b) also show that RMR was negatively (P<0.0001) associated with LMW and LARMR in both open sun and shade conditions. Its association with SMR, SLA, LAR and SSL was also indirect, but not significant. In the open sun, RMR was positively related with the other variables, but only significant with TDM (P<0.05) and

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RDW (P<0.0001). In the sun and shade, the relationship between RMR and SLA was indirect and direct, respectively. In contrast to shaded seedlings, RMR was negatively related to the SDW, CA and LAI of the sun plots. However, the correlations were weak. The results may indicate that plant responses to light are governed by different resource constraints at each end of the light gradient. In low light, plants enhance light interception by means of a high biomass allocation to leaves and the formation of thin leaves with a high SLA, leading to a high LAR. This was evident from the positive and significant correlations (r = 0.92-0.93, P<0.001) between SLA and LAR under both light conditions (Tables 6.14a, 6.14b).

The results depict significant accession differences in RMR (P<0.05) and LMR (P<0.001), but not for all the other variables compared. Accordingly, the accession from Harenna showed the highest RMR (I-2 = 0.25±0.01 g^1 g^{-1}), but the lowest LMR (0.31±02 g^1 g^{-1}). However, the reverse was true for the seedlings of the Berhane-Kontir accessions (Figure 6.20). These traits were strongly negatively correlated (Table 6.14) in open sun (r = -0.70***) and shade plots (r = -0.85***). The accession from Bonga (II-1) had the highest specific leaf area (SLA) (155.50±27.75 cm^2 g^{-1}) and leaf area ratio (LAR) (53.83±11.23 cm^2 g^{-1}) as opposed to the lowest SLA (IV-3 = 116.98±39.67 cm^2 g^{-1}) and LAR (I-2 = 37.35±8.83 cm^2 g^{-1}) in the Yayu and Harenna accessions, respectively. This demonstrates the increased leaf thickness of these accessions as compared to the others and may be related to relative growth and net assimilation rates in coffee seedlings as found in other tropical tree species (Poorter, 1999). This underscores the importance of SLA in explaining differences in accession performances in contrasting light environments.

Unlike RMR, LARMR was linked to LMR and was low for Harenna (I-2 = 151.52±40.41 cm^2 g^{-1}) and high for Berhane-Kontir (III-3 = 261.71±26.54 cm^2 g^{-1}). The results also show reduced specific stem lengths for Harenna and Yayu, indicating their superior shoot growth and maximum biomass allocation in stems and petioles. On the other hand, the smallest and largest crown areas were calculated for Bonga (II-3 = 146.86±42.33 cm^2) and Yayu (IV-2= 313.62±38.27 cm^2) seedlings, respectively. As a result, a high coefficient of variations (36.8%) was obtained for the crown area as compared to all other variables. However, the Yayu (IV-3 = 4.45±1.06) and Harenna (I-3 = 5.56±0.64) accessions had the lowest and highest LAI, respectively (Table 6.13).

This may reflect the variability in seedling size, i.e., growth habits of the seedlings. The plasticity in average leaf size and crown size could also affect the leaf area index and thus photosynthetic capacity and partitioning patterns.

With regard to interactions, LMR was more sensitive to compare coffee accessions along varying natural resource gradients. In full sunlit, LMR was reduced for both drought-stressed and irrigated seedlings. Except for three (I-3, III-2 and IV-1), the other accessions (75%) showed higher LMR in the shade than in open sun (Figure 6.21). This was particularly observeved with the Bonga and Berhane-Kontir accessions, indicating accession by environment interactions. However, two accessions (17%) had almost equal LMR values under low and high light conditions, which indicates their broader tolerance to different light regimes with regard to this trait. Moreover, a few accessions (33%) revealed higher LMR in drought-stressed plots. This was especially noted for Bonga (II-3 = 0.37 g g^{-1}). But, the other accessions particularly those from Berhane-Kontir (III-2 = 0.41 g g^{-1}) and Yayu (IV-3 = 0.38 g g^{-1}) had increased LMR with increased soil moisture status in shade conditions (Figure 6.21). Though no significant interactions were detected, increased RMR and SMR were recorded for drought-stressed seedlings in shade and open sun plots, respectively. In the shade, however, well-irrigated and drought-stressed seedlings showed reduced RMR, owing to the higher partitioning of assimilates to the leaves than to the root and stem parts. As a whole, with increased sunlight LMR, SLA, LAR, LARMR, mean leaf size and SSL decreased, whereas leaf thickness and RMR increased. In this case, water uptake by the plant can be higher due to the increased biomass investment in the roots, resulting in a high RMR and a better balance between transpiring leaf surface and root biomass. This has been reported by Poorter (1999), who has shown that light is the most important determinant of variation in leaf (LMR, SLA, LAR) and water (RMR and LARMR) related growth characteristics of the plant. In contrast, SMR, SLM and LAI seem to be more accession specific.

Growth efficiency of the seedlings did not differ between shade levels, though it decreased with reduced light intensity, averaging 0.010±0.002 g cm^{-2} and 0.009±0.002 g cm^{-2} for sun and moderate shade, respectively. Average growth efficiency values were slightly higher for the Harenna and Yayu accessions as opposed to Bonga and Berhane-Kontir (Table 6.13). Consequently, the lowest and highest

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average results were determined for the Bonga (II-2= 0.008 ± 0.002 g cm^{-2}) and Harenna (I-2 = 0.012 ± 0.003 g cm^{-2}) accessions, respectively. This is consistence with SMR, but reciprocal to LMR (Table 6.13).

The formation of a wide crown can diminish self-shading, but cannot lead to a lower LAI. In direct sunlight, canopy area (CA) was indirectly influenced by all aboveground growth variables, but with significant links between SLA, LAR, LARMR (P<0.05) and SSL (P<0.01). In contrast, its relation with LMR was positive and significant (r = 0.41*). On the other hand, SLA, LAR and LARMR were significantly correlated with LAI in both shade treatments. In full sun, root and shoot biomass showed consistent patterns and were significantly and indirectly related to LAR, LARMR and SSL. In sun seedlings, SDW, RDW and TDW showed consistent and significant correlations with morphological and architecture variables. In the shade plots, however, TDM was significantly correlated with LMR (r = -0.64**), LARMR (r = -0.58**) and SSL (r = -0.47*), but directly and significantly related to leaf (P<0.05) and stem (P<0.001) dry matter accumulations (Tables 6.14a, 6.14b).

The results also show that the incidence of leaf rust was significantly (P<0.01) higher in the shade than in the open sun, though the frequency was not different due to shade regime and accessions. Nevertheless, the average frequency was higher in shade (83.1%) than in sun plots (80.6%). The coffee populations did not differ in leaf rust infestation, though the Bonga and Harenna accessions had the lowest and highest incidences, respectively. In terms of leaf rust incidence, the populations followed the order Yayu>Harenna>Berhane-Kontir>Bonga. Similarily, the frequency values ranged from 57.9 to 93.8% for the Bonga and Berhane-Kontir populations, respectively, with the order Berhane-Kontir>Harenna>Yayu >Bonga. The results support the occurance of leaf rust at field levels in the four wild coffee areas following the altitudinal and related climatic gradients. The correlations between leaf moisture contents and stomatal density were not significant. Nonetheless, frequency of leaf rust was indirectly correlated with leaf moisture contents both in sun and shade plots, whereas, leaf moisture content and stomatal density were negatively related to incidence of leaf rust in full sunlight, but the association was positive in more humid shade conditions. The results thus demonstrate the influence of plot-specific microclimatic situations on the infestation of coffee leaf rust at a nursery site. Further research is, however, necessary.

Growth and development of coffee seedlings

Table 6.13 Architectural characteristics (means±SD) of wild coffee seedlings based on shade and coffee accessions

Treatment	RMR	LMR	SMR	SLA	LAR	LARMR	SSL	CA	LAI	GE
Shade level										
Sun	0.22±0.02	0.34±0.02b	0.44±0.02a	128.80±18.77	43.89±6.74	199.88±40.66	3.80±0.54	233.06±80.18	5.01±0.64	0.010±0.002
Shade	0.21±0.03	0.36±0.03a	0.43±0.02b	131.38±25.95	47.18±9.85	225.45±58.97	4.17±0.47	208.87±73.34	4.95±1.00	0.009±0.002
Accession (Acc)										
I-1	0.24±0.02ab	0.32±0.01d	0.45±0.02	133.82±12.47	41.95±4.47	179.04±33.64	3.83±0.68	259.65±53.07	5.13±0.67	0.011±0.001
I-2	0.25±0.01a	0.31±0.02d	0.44±0.01	119.10±23.89	37.35±8.83	151.52±40.41	3.77±0.58	185.48±67.34	4.48±0.85	0.012±0.003
I-3	0.24±0.01ab	0.35±0.01c	0.42±0.01	141.60±20.21	49.02±7.21	210.42±33.31	3.99±0.25	213.69±107.86	5.56±0.64	0.009±0.001
II-1	0.22±0.01abc	0.35±0.01bc	0.43±0.01	129.73±26.37	46.04±10.17	216.65±59.25	4.02±0.68	222.87±70.61	5.09±1.13	0.010±0.002
II-2	0.22±0.01abc	0.35±0.02c	0.43±0.02	155.50±27.75	53.83±11.23	243.08±47.91	4.24±0.30	201.78±74.86	5.55±1.12	0.008±0.002
II-3	0.23±0.02abc	0.36±0.03bc	0.42±0.02	125.63±21.30	44.32±6.23	200.53±41.40	3.99±0.59	146.86±42.33	4.62±0.53	0.010±0.002
III-1	0.20±0.03bc	0.36±0.01bc	0.45±0.03	137.27±14.43	49.19±4.72	255.08±28.30	4.01±0.53	217.22±61.23	4.71±0.38	0.009±0.001
III-2	0.21±0.03abc	0.38±0.03ab	0.42±0.01	120.48±10.95	45.38±4.96	223.35±50.90	4.48±0.30	165.65±101.85	4.54±0.79	0.009±0.001
III-3	0.18±0.02 c	0.39±0.03a	0.43±0.01	123.98±12.27	47.73±3.58	261.71±26.54	3.86±0.79	229.94±40.13	5.12±0.37	0.009±0.001
IV-1	0.22±0.01abc	0.35±0.01c	0.43±0.02	128.17±13.47	44.86±5.86	205.50±27.50	3.82±0.23	263.96±76.63	5.13±0.59	0.010±0.001
IV-2	0.22±0.01abc	0.35±0.01c	0.43±0.01	128.82±29.66	44.43±10.63	198.70±47.99	3.50±0.28	313.62±38.27	5.36±1.24	0.010±0.002
IV-3	0.22±0.03abc	0.36±0.03abc	0.43±0.01	116.98±39.67	42.32±15.91	206.45±96.48	4.31±0.79	230.85±92.82	4.45±1.06	0.011±0.004
Mean	0.22	0.35	0.43	130.09	45.53	212.67	3.98	220.96	4.98	0.010
CV (%)	7.63	2.81	3.14	17.15	18.50	19.82	12.81	36.83	19.72	18.52
ANOVA (Pr>F)										
Shading	Ns	***	*	Ns	Ns	Ns	Ns	Ns	Ns	Ns
Accession	*	***	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns
Shade*Acc	Ns	*	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns

Ns = Not significant P>0.05; * P<0.05; ** P<0.01; ***P<0.001. Means with the same letter in a column are not significantly different from each other at P<0.05 (Tukey test). Abbreviations: RMR = root mass ratio, LMR = leaf mass ratio, SMR = stem mass ratio, SLA = specific leaf area, LAR = leaf area ratio, LARMR = leaf area root mass ratio, SSL = specific stem length, CA = canopy area, LAI = leaf area index; GE= growth efficiency.
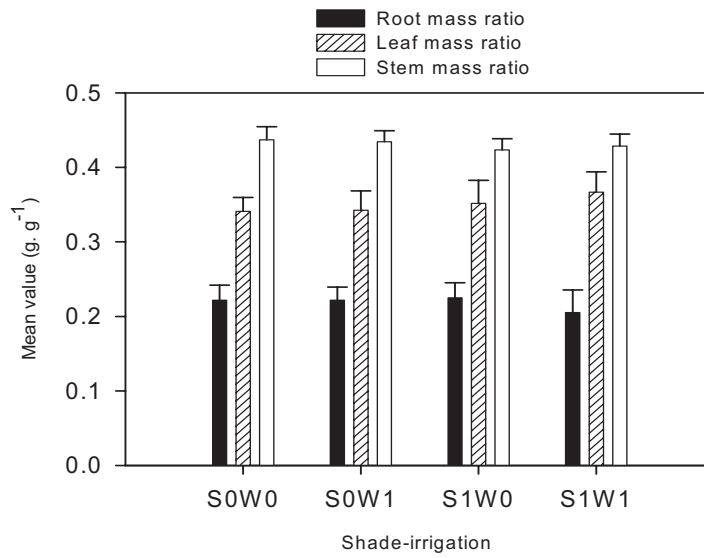
Figure 6.20   Root, leaf and stem mass ratio of coffee seedlings as influenced by the interaction of shade and irrigation levels
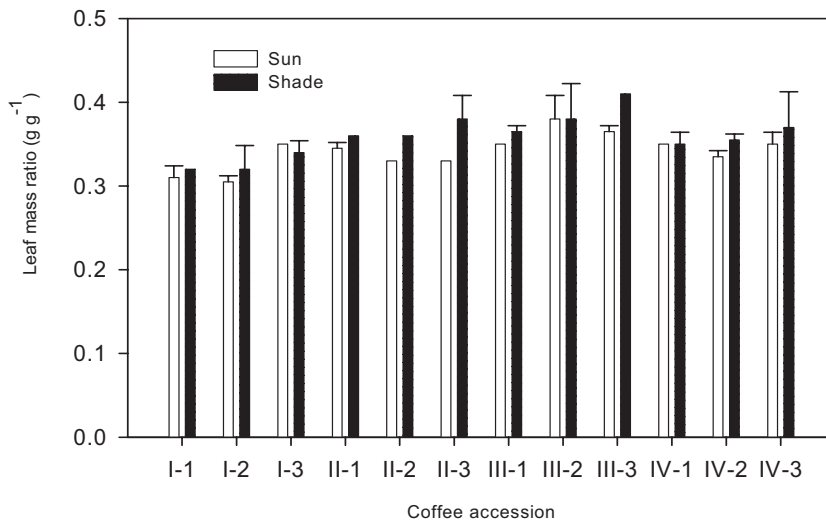

Figure 6.21   Influence of two shade levels on leaf mass ratio of the seedlings of coffee accessions

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Table 6.14   Correlation values between growth variables of coffee seedlings under sun and (a) and shade (b) conditions

a)   Full sunlight

Variable	RMR	LMR	SMR	SLA	LAR	LARMR	SSL	CA	LAI	LDW	SDW	STW	TDM
LMR	-0.70**												
SMR	-0.13	-0.58**											
SLA	-0.11	-0.15	0.35										
LAR	-0.38	0.26	0.09	0.92**									
LARMR	-0.70**	0.49*	0.14	0.74**	0.92**								
SSL	-0.29	0.49*	-0.34	0.37	0.56*	0.54*							
CA	0.13	-0.04	-0.11	-0.51*	-0.49*	-0.43*	-0.59**						
LAI	0.01	-0.22	0.30	0.64**	0.55*	0.40*	-0.17	0.32					
LDW	0.15	-0.07	-0.10	-0.51*	-0.51*	-0.45*	-0.61**	1.00**	0.33				
SDW	0.38	-0.61**	0.42*	-0.30	-0.54*	-0.56**	-0.78**	0.78**	0.37	0.79**			
STW	0.30	-0.42*	0.23	-0.40*	-0.55*	-0.55**	-0.76**	0.91**	0.37	0.92**	0.97**		
TDM	0.46*	-0.52**	0.19	-0.40	-0.59**	-0.64**	-0.76**	0.87**	0.34	0.88**	0.97**	0.99**	
RDW	0.78**	-0.69**	0.08	-0.35	-0.61**	-0.79**	-0.67**	0.66**	0.21	0.67**	0.85**	0.83**	0.91**

b)   Shade plot

Variable	RMR	LMR	SMR	SLA	LAR	LARMR	SSL	CA	LAI	LDW	SDW	STW	TDM
LMR	-0.85**												
SMR	-0.17	-0.36											
SLA	0.02	0.04	-0.14										
LAR	-0.27	0.39	-0.26	0.94**									
LARMR	-0.74**	0.73**	-0.06	0.64**	0.84**								
SSL	-0.10	0.39	-0.51*	0.41*	0.51*	0.44*							
CA	-0.33	0.41*	-0.18	-0.14	0.01	0.18	-0.17						
LAI	-0.08	0.17	-0.19	0.94**	0.92**	0.68**	0.34	0.21					
LDW	-0.32	0.40	-0.19	-0.14	0.01	0.17	-0.16	1.00**	0.21				
SDW	0.42*	-0.67**	0.53**	-0.21	-0.43*	-0.52*	-0.57**	0.31	-0.08	0.32			
STW	0.18	-0.34	0.32	-0.22	-0.32	-0.32	-0.51*	0.69**	0.03	0.69**	0.91**		
TDM	0.56**	-0.64**	0.21	-0.19	-0.40	-0.58**	-0.47*	0.44*	-0.02	0.45*	0.94**	0.92**	
RDW	0.92***	-0.87**	0.00	-0.10	-0.39	-0.77**	-0.30	-0.02	-0.09	-0.001	0.72**	0.55*	0.84**

*, ** = *Correlations are significant at <0.05 and <0.01 levels, respectively (2- tailed).*

In addition, at a 15 rescaled cluster distance (85% similarity), the accessions were grouped into four broad classes with a different number of accessions (Figure 6.22). Group 1: I-1, I-3, II-1, II-2, IV-1, IV-2; group 2: III-1, III-2; group 3: II-3, III-2, IV-3 and group 4: I-2. Consequently, half of the accessions were classified in the same category (group 1), while the extremely distant group had only one accession. Accessions from Bonga, Yayu and Harenna were included in the largest groups. Most accessions (17%) were in a separate class, while the most distant accession was from Harenna (I-2). According to the principal component analysis (Figure 6.23), the variables that contributed most to the dissimilarity among the seedlings include LAR, LARMR, LMR, LAI, SLA and RMR. The accessions were comparable in SMR.


```
                 Rescaled Distance Cluster Combine
        0         5        10        15        20        25
        +---------+---------+---------+---------+---------+
  II-1─┐
  IV-1─┤
  IV-2─┤
   I-1─┤
   I-3─┤
  II-2─┤
 III-1─┤
 III-3─┤
 III-2─┤
  IV-3─┤
  II-3─┤
   I-2─┘
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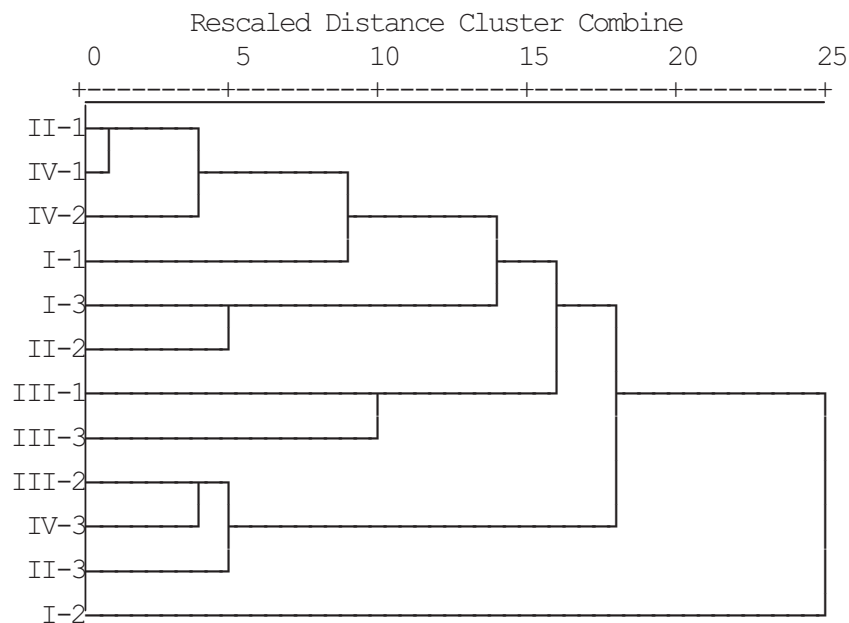
Figure 6.22.   Dendrogram using average linkage (between groups) for cluster analysis of coffee accessions based on morphological and physiological traits. The groups were identified according to dissimilarity measures.
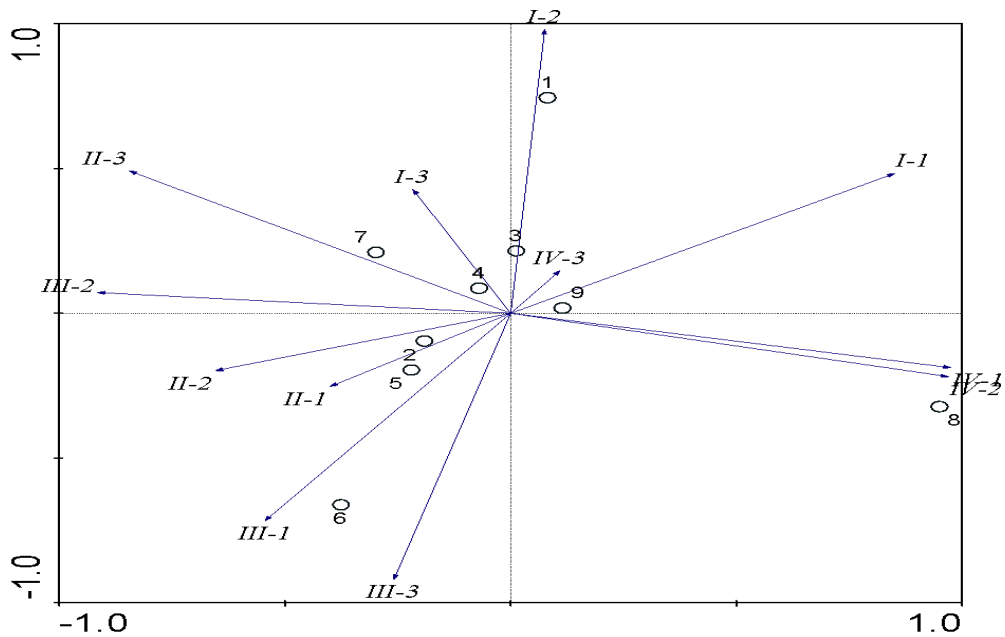
Figure 6.23   Principal component analysis biplot of coffee accessions and physiological growth parameters in coffee seedlings (accessions = I-1 to IV-3; parameters 1 = RMR, 2 = LMR, 3 = SMR, 4 = SLA, 5 = LAR, 6 = LARMR, 7 = SSL, 8 = CA, 9 = LAI)

6.5   Discussion

6.5.1   Microclimate

Shaded pots showed a drop in soil temperature as compared to the other interaction effects, indicating the role of shading to conserve and minimize diurnal variations in soil temperature for ideal root growth. This supports previous reports (Coste, 1992; Wrigley, 1988) that show the role of shade in creating a more favourable microclimate for coffee cultivation. The reductions in leaf temperature in moderate shade varied for the midday and afternoon. This might be due to the effect of low humidity and high solar radiation in exposed conditions. There were slight differences in diurnal change in average leaf temperature among the coffee accessions. The difference between predawn and midday leaf temperature was low in the Berhane-Kontir and high in the Harenna seedlings. This could be the reason for increased water transport and high productivity of the latter accessions, though they showed the highest water losses. This could reflect the intensity of the coupling of seedling canopy to the atmosphere, primarily due to variations in phenology and leaf growth parameters in the different coffee accessions. This corroborates with the findings of Goldberg et al. (1984), who reported a negative

correlation between leaf temperature and stomatal conductance in pot experiments. Other authors (Barros et al., 1997; Sila et al., 2004) also reported declined vegetative growth rate in coffee with lowering seasonal temperatures and reduced stomatal conductance, with major growth occurring during the warm rainy seasons. Leaf wetness and the angle of the incoming solar radiation could also be amongst the possible reasons for the difference in leaf temperature and thus evapotranspiration water losses. Further investigation is required to examine the interaction between seedling water flux and environmental variables. This would help to determine optimum irrigation requirements for production of high quality and reliable coffee seedlings.

6.5.2   Growth characteristics of coffee seedlings

The results of the early growth response of the accessions are in agreement with the speed of seed germination, due largely to differences in seed attributes (size, stored reserves). The tallest and shortest seedlings were from the Harenna and Bonga accessions, respectively. The other parameters also showed accession-specific growth performances. Accordingly, the results of seedling branching habit and leaf tip colors corroborates with the findings on the morphological variability of the same coffee accessions in field conditions. Montagnon and Bouharmont (1996) reported similar more erect branching habits and narrower leaves in sub-spontaneous genotypes from the west of the Great Rift Valley as compared to those accessions collected from east Ethiopia. Most morphological growth parameters at the early and later growth stages were high for the Harenna accessions than for the others, probably indicating their increased vigor and later reproductive performance. The Harenna and Berhane-Kontir accessions have broader leaves than the two other populations, suggesting wide-open and compact-narrow growth habits, respectively. The light response of these accessions to incoming light and transpiration can also vary accordingly. Hence, it is advisable to consider such growth variations in relation to the external factors (moisture, light, plant nutrients). Vegetative parameters (earlier and current season node number) were indirect indicatives of optimum coffee productivity, especially in coffee of homogenous genetic character (TewodeBerhane, 1986). The finding also supports the studies by Walyaro and Vander Vossen (1979) and Yacob (1993), who showed the possibility to screen and predict later performance of coffee cultivars using early growth responses.

Based on different morphological and agronomic traits, Montagnon and Bouharmont (1996) also identified two main groups of coffee accessions from the west and east of the Great Rift Valley. Seedlings of coffee accessions of the four wild coffee populations were field transplanted at Jimma Research Center field gene bank. Further characterization and improvement works are required to identify and conserve the promising coffee accessions as a complementary and back up to the *in-situ* conservation of the respective forests.

There is no standardized growth stage for the evaluation of coffee seedlings for specific traits including drought tolerance. The phenology of the coffee plant can, however, influence resource-use efficiency and thus capacity to withstand physical or biological stresses. In this regard, the available information is limited to the stage of the seedling for field transplanting (IAR, 1996). The results of morphological parameters recorded at early and later growth stages can signify the need to consider a series of phenological performances to evaluate coffee materials for specific traits. This would minimize the risks of discarding potential coffee types. This is in consistence with the growth variations obtained in the forest ecosystem and with the previous reports on improved Arabica coffee cultivars (IAR, 1996; Yacob et al., 1996) and coffee landraces (Taye and Alemseged, 2004) in Ethiopia. The later stage growth was changed in comparison to the initial morphological variables, and their resource-use efficiency could also vary accordingly. Most shoot and root characteristics were significantly related to root to shoot ratio, which suggests the strong ties and inherent interdependency between below- and above-ground growth responces of coffee plants.

Photosynthetic rates depend on the total leaf area, the architecture of the canopy and the amount of light intercepted by leaves in addition to other environmental factors. Canopies with more vertically inclined leaves have a high photosynthetic rate with maximum leaf area, since they are more efficient in the interception of light (Larcher, 2003). The degree of leaf and branch orientation was different among accessions and followed the order of Yayu>Harenna>Bonga>Berhane-Kontir, most likely reflecting the difference in the growth stage of the seedlings. The Bonga accessions were intermediate in leaf and branching habits. Leaf and branch orientations followed similar pattern and this was confirmed by positive and significant correlations. Therefore, the Harenna and Yayu seedlings showed semi-horizontal, while Bonga and

Berhane-Kontir showed semi-erect growth habits. This supports the findings on the phenotypic diversity between accessions of *Coffea arabica* collected from southwest and east of the Great Rift Valley in Ethiopia (Montagnon and Bouharmont, 1996). Erect (erectophile) leaves have a higher optimum leaf area index (LAI) than those with horizontal (planophile) leaves. Because of their orientation to the sun, erect leaves intercept less photosynthetically active radiation (PAR) than the horizontal leaves. Hence, a lower leaf area on a plant with erectophile leaves receives adequate PAR for net positive photosynthesis and such a crop can effectively function with a higher LAI. The optimum LAI of tree crops is usually between 6 and 10 depending on the type of leaf and the height of the tree (Larcher, 2003; Prasad, 1997).

The analysis of variance depicted significant interaction between coffee accession and shade regimes through the frequency of deep bronze and light green leaf tip colors. In contrast, light bronze leaves did not change significantly and the proportion was high with reduced shading. Beside genetic factors, this may be related to the reduction in the concentration of leaf chloroplast. This may reflect the occurrence of phenotypic and genetic variability within the population, supporting the work of Meyer et al. (1968), who reported the variability in young leaf colors among Ethiopian coffee populations. For this, the presence of two alleles has been described for the color of the growing leaf tip. These are Br (bronze) and br (green), which are characteristics of the Typica and Bourbon varieties, respectively, in accordance with the former phenotypic description of *C. arabica* by Montagnon and Bouharmont (1996).

Coffee leaves are extremely variable according to the season and the growing conditions and thus, the value is relative in any comparison involving plants growing under different light intensities. There is a correlation between water availability and leaf size, and the largest leaves are found in tropical rainforest and small leaves in dry or cold environments. The longevity of the leaves also differs markedly both between species within a habitat and between environments of different kinds. Venkataramanan (1988) observed that the chlorophyll content in coffee increased with leaf expansion up to the fourth pair of leaves but subsequently decreased during later stages of leaf growth (fifth and sixth pairs of leaves). In the present study, in all the xamined coffee accessions, the content of chl-a was found to be higher than that of chl-b, as in many crops. Furthermore, a higher chl-a ratio was observed in low temperature regimes.

There was a considerable variations both in incidence and frequency of coffee leaf rust (*Hemileia vastatrix*) in the seedlings in sun and shade environments, demonstrating variations in leaf wetness due to accession and shade regime. This also suggests the existence of immense ecophysiological diversity in the natural coffee populations. Kassahun (2006) also found genetic variability among the same wild coffee populations, though the closeness of the wild populations differ from the results of the phenotypic diversity. Hence, detailed research is required to assess the importance of plant-environment interactions and biochemical analysis on the underlying changes in leaf color. The association between morphological and genetic traits is of great importance for a more comprehensive breading system in wild coffee populations of distant geographic origin. This would help to associate this phenotypic attribute with the other desirable traits like disease tolerance and quality attributes in coffee plants.

The influence of shade was not significant on root growth characteristics, indicating the limited time for the shade treatment to cause differences. Nevertheless, full sun-exposed seedlings had a slightly higher number and volume of lateral roots. In contrast, a longer taproot and lateral roots were observed for shaded seedlings than unshaded ones. This indicates the influence of short-term drought stress in affecting root growth. On the other hand, there were significant differences among the coffee accessions in total root volume, taproot length and length of lateral roots. Root morphological parameters were significantly highest for Harenna opposed to the lowest values obtained from the Berhane-Kontir accessions. Similar to shoot, the Yayu and Bonga accessions were intermediate in root characteristics. The higher lateral root count and volume in full sun seedlings were in line with the root dry weight and root to shoot ratio recorded on the same coffee seedlings. This could be an indicative of high root access to maximize soil water uptake in limited soil-water conditions. Hence, the significantly better root growth in the Harenna accessions could be related to their drought-stress avoidance mechanism as compared to the southwest coffee accessions. The variation in seed germination, early growth and restricted root growth in the plastic pots might also be among the possible reasons for the response of the seedlings to soil moisture deficits. Further evaluation of the accessions using large containers or under field conditions is crucial to generate information on the genetic variability of the accessions to drought stress situations.

Root characteristics are considered to play an important role with regard to survival and better performance of perennial crops like coffee. Therefore, identification of efficient accessions with respect to ideal root traits is essential. Drought-adapted plants are often characterized by deep and vigorous root systems. In this regard, Daniel et al. (2004) found that total transpiration was high in coffee genotypes with relatively high root biomass. They reported positive relationships between water-use efficiency, total dry matter production and photosynthesis in robusta coffee. The correlations between root growth parameters and root hydraulic resistance were strong and indirect in well-irrigated coffee seedlings, i.e., seedlings with better root systems showed significantly higher root hydraulic conductances and were more productive in terms of biomass production. This was observed in the sun-exposed seedlings and Harenna accessions. Thus, the results obtained provide information on the closeness of shoot and root physiological events under drought-stress environments, which ultimately lead to the control of transpirational water loss and total dry matter distribution patterns. Several studies (TewoldeBerhan, 1986; Pinheiro et al., 2005; Yacob et al., 1996) show correlations between morphological and yield components. The knowledge of the correlation is invaluable to the breeder in selecting desirable morphological traits. In this study simple correlation was computed between morphological parameters, which show a different magnitude of relationships. The interplay between root and shoot system depends on environmental and plant factors, and the physiological root to shoot behaviors vis-à-vis plant age and environmental influences remains to be investigated. The present findings reveal the existence of inter-and intra-regional morphologically variability among wild Arabica coffee with regard to seed germination and seedling growth architecture in controlled nursery environments. This supports the work by Kassahun (2006) on the genetic diversity of the same wild coffee populations. Hence, evaluation of coffee cultivars for specific traits, e.g., drought tolerance, needs to consider both below- and above-ground growth attributes. To this end, further investigations are necessary to assess the underlying mechanisms and identify drought-tolerant accessions along varying amplitudes of environmental stresses.

6.5.3   Biomass assimilation and distribution

The results show significantly higher shoot dry mass production in sun and progressively drought-stressed seedlings. This could be related to reduced stomatal conductance and concomitantly lower rate of net carbon assimilation in shade and irrigated plants compared to short-term drought-stressed seedlings. Moreover, a reduced leaf number was noted in shade compared to sun plots, and such smaller leaf area may alter assimilate partitioning among the tree organs and decrease shoot dry matter yield. This pattern suggests that a major mode of adjustment to reduced soil water demand by the coffee seedlings, at least in the early stages of soil water shortage, could consist of the maintenance of nearly constant assimilation on an area basis through a reduction in the rate of increase in average leaf size. The positive correlation between leaf area and leaf dry weight indicates that leaf expansion can be accompanied by growth and development as well as accumulation and synthesis of the leaf cell components. Similar results were also reported for field-grown robusta coffee (DaMatta, 2004b). On the other hand, coffee accessions significantly differed in stem dry weight with the lowest and highest average results obtained from the Berhane-Kontir and Harenna seedlings, respectively. This could reflect the variations in growth rate and productivity among the accessions, which in turn depend upon stem nature (stiff or flexible) and size of the water conducting tissue. Though insignificant, the amount of total dry mass partitioned to the root part was higher in sun-and drought-stressed seedlings as compared to partial shading and well-irrigated seedlings. The results of dry matter production and partitioning are in line with the maximum hydraulic conductance measured in full sun and irrigated seedlings, indicating the more enhanced water use of the coffee seedlings during the short (2 week) period of drought-stress. This could be associated, among others, with the specific growth responses shown by the increased number of lateral roots, higher root to shoot ratio as well as decreased leaf-specific area determined from drought-stressed seedlings.

The relationships between growth parameters and hydraulic resistance indicate similar patterns, largely demonstrating the differences in root and shoot growth habits of coffee seedlings. The response of the coffee seedlings could also suggest a drought-stress resistance strategy investing more of the daily biomass production in the root system while penalizing the shoot system. In Ethiopia, Tesfaye (1995) reported ideal

growth of coffee seedlings under limited irrigation, and their capacity to establish in more stressful field conditions could vary accordingly. The results show no treatment interactions on root and shoot growths of the coffee accessions. Taye et al. (2004a) reported similar patterns of total dry matter production and allocation in Arabica coffee seedlings grown in various potting media. According to literature (Hale and Orcutt, 1987; Larcher, 2003; Salisbury and Ross, 1992; Prasad, 1997), plants withstand drought stress by drought tolerance (higher biomass allocation to vegetative organs and root to shoot ratio), whereas drought escape strategies involve early flower set and leaf senescence. According to DaMatta et al. (2002), water deficit led to marked decreases in net carbon assimilation rate and to a lesser extent in stomatal conductance, regardless of the low and high nitrogen levels.

For maximum rate of production of dry matter within the plant as a whole it is important that a high proportion of assimilates as possible should be returned to the leaf tissue, which will further increase the productive capacity of the plant, and that expenditure of dry matter on the rest of the plant (stems, petioles and roots) should be no more than is required to efficiently support the leaves and supply sufficient mineral nutrients and water. The overall rate of utilization of assimilates in leaf production will depend upon the rate of new leaf initiation, the rate of growth and final leaf size and the branching habit. Under field conditions, assimilate utilization may be limited by various external factors including temperature, and the supply of water and mineral elements. However, there is evidently some homeostatic mechanism maintaining a given root-shoot balance under any given set of conditions, and this in turn implies an interplay between growth in root and shoot (Wareing, 1970). Russell (1977) reported that changes in the partitioning of dry matter between roots and shoots brought about by environmental factors suggest that when the size of the source is reduced, the growth of organs most remote from it is often particularly affected. Hence, the manner in which dry matter is partitioned between the different parts of the plant is clearly of great importance both in natural vegetation and in crop plants.

In essence, the growth and seed production of a plant is a result of the integrated processes of photosynthetic carbon dioxide assimilation and subsequent partitioning and utilization of the assimilated carbon. This requires efficient translocation of photo-assimilates to the developing plant parts (Devlin and Witham,

1983; Hale and Orcutt, 1987). Gathaara et al. (1997) cited Harper and Ogden (1970), who described a method of studying energy allocation in plants that requires separating individual plants into component tissues according to their function, and expressing energy allocation as a proportion of total biomass stored in each tissue type. There are several reasons why weight is used to measure biomass allocation patterns. Energy content and dry weight equally reflect energy allocation pattern and dry weight is reported to reflect the integration of all physiological processes throughout the growing season. In addition, dry weight reflects the functional aspects of all assimilation (Devlin and Witham, 1983; Pandey and Sinha, 1996). In many crop species, increased yields of improved cultivars have been related to changes in partitioning as opposed to increase in total biomass (Egli, 1988). In the tall, mature field-grown Arabica coffee trees in Kenya, shoot growth is reported to be associated with seasonal changes in dry matter distribution within the tree (Cannell, 1971). Gathaara et al. (1997) quoted the work of Gathaara (1990), who reported that work in greenhouse-grown Arabica coffee cultivar-Ruiru 11 showed that dry matter partitioning to above- and below-ground parts varied with accessions.

6.5.4   Growth rate of coffee seedlings

Growth rates of seedlings were highly significantly higher in April than May, which is in line with the increased amount of rainfall and decrease in maximum air temperature (Figure 3.3). This indicates the effect of monthly differences in radiation and related climatic variables particularly air temperature and availability of soil moisture. It may also be due to a combination of plant and environmental factors such as seedling age, mutual shading particularly in the shade, and inhibited growth in the sun plots. The monthly growth rate could be linked to changes in light intensity and soil temperature, especially under conditions of limited water availability. The results suggest that soil temperature must explicitly be taken into account as a driving variable when relating the growth of young coffee plants to photosynthetic radiation. This is in agreement with many authors (Coste, 1992; Wrigley, 1988), who reported on the influence of high light intensity in enhancing the growth of more nodes with short internodes. This is in agreement with Poorter (1999, 2001), who found reduced relative growth rates (RGR) in stressed plants. According to Poorter and Remkes (1990), larger plants have lower

RGRs because of increased self-shading and high investment in supporting plant fractions. The findings could also demonstrate the influence of monthly climatic conditions on the growth of coffee seedlings under more controlled nursery environments. Except for basal diameter, significant positive relationships between RGRH and other parameters were determined for each shade level. The magnitudes of the associations were, however, stronger in open sun, which could indicate that the increase in other parameters might explain the interdependence among growth attributes and sapling height in differing wild coffee accessions. The growth response of the seedlings to contrasting light regimes was in consistence with other studies (Poorter, 1999; Sack and Grubb, 2001; Shipley, 2000; Walters et al., 1993b). The difference in the growth rate between the months was in line with that of Barros et al. (1997) and Silva et al. (2004), who reported increased vegetative growth in coffee with increased daily and seasonal air temperatures. Of the total growth over the 12-month study period, 78% occurred in the warm, rainy season and 22% during the cool dry season. In contrast to the period of reduced growth, during the active period, growth was strongly negatively correlated with air temperature.

The Berhane-Kontir seedlings showed slow growth rates compared to the other populations, particularly Harenna and Yayu. This is reflected in the other parameters (relative growth rate, morphological and physiological response) and hydraulic conditions. Cornelissen et al. (1996) reported on the positive link between RGR and xylem size as a result of a close relationship between RGR and leaf area ratio (LAR). The work of Castro-Diez et al. (1998) also suggests that fast-growering plants require a xylem with wide conduits to achieve high hydraulic conductivity and that they efficiently construct stems to maximize allocation to leaves. These plants have a higher proportion of transpiration surface and, therefore, a higher potential for loosing water per unit of plant biomass. As they allocate little matter to transport organs (stems and roots), their xylem transports the water more efficiently to meet the foliage demands for transpiration. High hydraulic conductance can be achieved by developing wide diameters among a fraction of the xylem conduits and/or by increasing the relative amount of xylem and thus the total number of conduits (Shumway et al., 1993). However, the latter strategy could reduce LAR by reducing the proportion of biomass available to the foliage (leaf weight fraction), which is a correlate of LAR (Cornelissen

et al., 1996). It thus appears that the most reliable strategy to simultaneously maximize the hydraulic conductance, LAR, and therefore also RGR is the development of xylems with widexylem conduits.

6.5.5 Growth response to light regime

Moderately shaded and irrigated seedlings had significantly higher LMR, which indicates the higher biomass allocation to the leaves than to the other parts. This is in contrast to most other variables, which showed no significant variations neither due to single nor interaction effects. However, seedlings exposed to direct sunlight had relatively higher RMR, SMR, CA and LAI, suggesting that full light does not have a strong influence on plant morphology. The possible explanation for this might be that seedlings in full light may suffer from water limitations or high soil temperatures. This contrasts with the response of seedlings on the shaded and irrigated plots, where SLA, LAR, LARMR and SSL tended to increase. According to Fahl et al. (1994), shade-grown coffee plants can develop thinner leaves with more thylakoids per granum and more grana per chloroplast, higher chlorophyll content and larger individual leaf area, which allow a more efficient capture of available light energy. Reduced CO_2 assimilation rates in coffee leaves subjected to full sun have been associated with leaf temperatures above 25°C and with consequent stomatal closure (Kumar and Tieszen, 1980). The authors observed that the photosynthesis of shade-grown plants with increasing irradiance levels was substantially higher than those grown in full sunlight, even when the leaf temperature was around 25°C. On the other hand, Fahl et al. (1994) reported that high irradiance did not decrease net photosynthesis of coffee leaves when the temperature in the CO_2 assimilation chamber was maintained at 25°C.

Well-irrigated seedlings in full sunlight showed considerable reductions in growth, especially in LMR, compared to shaded seedlings. This could be related to the three possible reasons mentioned by Poorter (1999). First, very high irradiance levels may lead to irreversible damage to the photosynthetic system. Second, high irradiance around midday leads to stomatal closure and some times even to turgor loss and wilting of the leaves (Chiariello et al., 1987). This may have such an impact, even late in the afternoon; light-saturated photosynthetic rates can be considerably lower compared to the morning (Poorter and Oberbauer, 1993). Third, high radiation loads require a larger

biomass allocation to the roots for water uptake to compensate for transpiration losses. Less biomass can, therefore, be invested in leaf material, which strongly reduces photosynthetic gain and growth potential rate (Körner, 1991). Veenendaal et al. (1996) compared seedling growth of tree species at various light levels. It was found that shade-tolerant species showed highest RGR at 16 or 27%, above which it declined, whereas for the pioneer species optima were between 26 and 100%. In contrast to shaded seedlings, RMR was negatively related to SDW, CA and LAI of the sun plots, but the correlations were weak. The results indicate that plant responses to light are governed by different resource constraints at each end of the light gradient. At low light, plants enhance light interception by means of a high biomass allocation to leaves and the formation of thin leaves with a high SLA, leading to a high LAR.

The accessions in Bonga had the greatest SLA and LAR as opposed to the lowest SLA and LAR in Yayu and Harenna, respectively. This demonstrates the increased leaf thickness of these accessions as compared to the others and may be related to relative growth and net assimilation rates in coffee seedlings as found for other tropical tree species (Poorter, 1999). This underscores the importance of SLA in explaining difference in accession performance in contrasting light environments. As the energy provided by sunlight plays a central role in the metabolism of green plants, plant production is thus limited by the availability of light.The increased SLA and higher carbon storage in low light reflects the adaptive phenotypic plastic plant structural characteristics of coffee seedlings, which enable them to tolerate shade environments under the natural forest canopy. The results were in consistence with the work done by Yacob et al. (1998), who found extremely variable leaf responses within crowns of Arabica coffee trees in Ethiopia due to tree and foliage age, location in the crown and direction of exposure to light. A positive correlation between seedling growth in high and low light is also found in a number of other species (Kitajima, 1994; Osunkoya et al., 1994).

In Ghana, tree species showed a reversal in seedling performance in high irradiance compared to low, whilst pioneer species realized highest growth rates in full sun light, they showed negative growth rates in low light, whereas the shade-tolerant species maintained positive growth rates. It was suggested that realized growth in the field is the result of two components: biomass production through growth and biomass

loss as a result of herbivory, mechanical disturbance and shedding (Givnish, 1988), and their relative importance differs between habitats. Accordingly, in this study, more insect and rust-damaged leaves were observed during the wet and dry seasons in shaded coffee seedlings. This indicates that the second component can override in importance in low light environments. Biomass loss can be minimized by a low leaf turnover (King, 1994) and by allowing resources to be stored in the stem and roots. Furthermore, thick, lignified leaves with low SLA at the expense of reduced potential growth can reduce risk of herbivores. It has been found that tree species that are less prone to herbivory are characterized by a high leaf roughness and low inherent growth rates.

The findings of this study also demonstrate the same responses in SLA and LAI with varying light levels, suggesting the more stable and accession-specific nature of these traits. These traits indicate resource-use aspects, as Meinzer et al. (1991) reported that leaf change was strongly correlated with inherent water-use efficiency, hydraulic conductivity, and grain yield of diverse coffee cultivars. There were differences in the magnitude of association between seedling variables due to shade levels. At high light intensity, plants reduce transpiration losses and increase carbon gain by making small-sized thick leaves with a low SLA. This may be related to the formation of several photo-synthetically active parenchyma layers that can enhance their photosynthetic capacity. Furthermore, such leaves have a thin boundary layer and better heat loss to the environment, and less transpiration is needed for cooling the leaf in a high light environment (Givnish, 1988; Larcher, 2003). Similar patterns have been observed for leaves of seedlings along a light gradient and for leaves of trees along a height gradient in the forest canopy (Poorter et al., 1995). The increased SSL for the shaded, irrigated accessions from Bonga and Berhane-Kontir reveal the weak investment in stem and suggest the relative light demands of the seedlings. This is because an increased interception of light through a plastic response in height may lead to only low growth or put the seedling above its whole-light compensation point (Kohyama, 1991). The LAI varies with species, cultivars, stage of development, nutrition, availability of moisture and plant population. Below the critical LAI, maximum light interception is not achieved; above the critical LAI, yield may even tend to decline due to shading and competition for water and nutrients. According to

Gathaara and Kiara (1985), the downward flux of PAR is the major factor affecting yield in coffee.

The relationships between morpho-physiological characteristics in the sun and shade were related to the extension growth attributes. This, therefore, suggests the tight relationships among the parameters such as morphology, allocation and architecture of coffee seedlings. It supports the fact that the direct and diffuse solar radiation output properties of the light are the two main driving variable inputs into the canopy microclimate and photosynthetic assimilations. They largely determine the energy available to the plant canopy for photosynthesis and are vital for driving plant evapotranspiration, soil evaporation and heat fluxes. The findings of this study agree with others (Agyeman et al., 1999; Niinemets, 2006; Poorter, 2001). Walters et al. (1993b) also reported reduced LMR and LAR with plant size. Further, the declined SSL in full sun may be associated with the inhibited stem elongation and enhanced total dry matter partitioned to stems. Such seedlings were found to have thicker stems, which may facilitate hydraulic conductance and photosynthesis. This is in agreement with Sack et al. (2005), who reported that sun species had a higher proportion of leaf resistance in the xylem.

The work done by Poorter (1999) shows that plants shaded by other trees produce larger, thinner and wider leaves, and have higher LAR, LWR and SLA, and lower allocation to the roots. This can result in a decrease in net photosynthesis and stomatal conductance. However, plant responses to light vary with position along the light gradient and those at the lower light gradient enhance their light interception. Several authors (Christopher, 2002; Larcher, 2003; Osunkoy et al., 1994) have shown that shaded plants have a higher biomass allocation to leaves LMR, a higher leaf area per unit leaf mass (SLA), resulting in a higher leaf area per unit plant mass (LAR). There is a reduction in leaf-level light compensation point. Kohyama (1991) also found that wide crowns with a low leaf area index can reduce mutual shading. Such traits would increase net carbon gain at the leaf and whole-plant level by plants growing in the shade, as would mechanisms that enable understorey plants to take advantage of brief sun flecks (Chazdon, 1988). However, reviews on seedlings grown in artificial environments (Sterck et al., 2006; Walters and Reich, 1999) concluded that biomass distribution patterns of shade-tolerant species showed the opposite trends to those

predicted by Givnish (1988). When grown in low light, small seedlings of shade-tolerant plant species generally had lower LAR than light-demanding associates. The assimilation rate at which arable crops accumulate dry matter during early growth is proportional to the rate at which radiant energy is absorbed by the canopy. The evidence so far reviewed suggests that light does not limit yield by net assimilation rate, but that the growth of a crop is almost proportional to the radiation intercepted by its canopy, and the rate of photosynthesis increases with irradiance upto saturating irradiance beyond which it is constant.

Similarly, Walters and Reich (1999) did not find support for the widely held beliefe that light compensation points in low light are pivotal for shade tolerance differences, as the plasticity of some light-demanding species enables them to maintain lower leaf-level compensation points by greatly increasing SLA in low light. Defense and storage, rather than carbon gain and growth, have therefore been emphasised as key priorities in shaded habitats (Kitajima, 1994). The author has indicated that some traits that maximize net energy capture, while important for competitive ability in well-lit habitats, might increase the risk of mortality in low light. For example, high SLA increases palatability and fragility of leaves, increasing the risk of premature tissue losses. Similarly, heavy commitment of resources to foliage production would reduce the scope for storage, which is important for surviving during resource shortage periods and for recovery from damage.

Growth efficiency, stem wood carbon production per unit leaf area per year (Waring et al., 1980) was comparable and did not depict significant variations between shade, irrigation and among coffee seedlings. Growth efficiency did not differ between shade levels, though it decreased with reduced light intensity. Average growth efficiency values were slightly higher for the Harenna and Yayu accessions as opposed to Bonga and Berhane-Kontir. This is in consistence with SMR, but reciprocal to LMR. This could be due to size-related compensation mechanisms and potential changes to increase the water transport capacity of the seedlings to the relative total leaf area (Becker et al., 2000), increased sapwood area (McDowell et al., 2002), increased driving force between soil and leaf (Hacke et al., 2000b), and increased root surface (Magnani et al., 2000; Sperry et al., 1998). Hence, growth efficiency is a useful measure, as it standardizes stem wood growth to the amount of leaf area held by each

tree and thus, allows comparisons of different sizes with different leaf areas (McDowell et al., 2002; Ryan et al., 1997; Waring et al., 1980). This is similar to that of the large and small seedling sizes in groups 1 and 4, respectively. In general, the Bonga and Berhane-Kontir seedlings showed the farthest similarity. Cognizant of the negative effects of low light interception in forest strata, morphological components related to architecture, leaf area and leaf display deserve closer attention. A large area appears to be of prime importance, as it was not so much attained by biomass allocation to leaves as by the formation of thin leaves with a high SLA. On the other hand, low foliage allocation in high light is clearly an adaptive mechanism in such habitat. The results, therefore, suggest the importance of seedling growth stages in evaluating accessions under varying resource gradients. The extremely heterogeneous environments may contribute to the patterns of trade-offs in the various adaptation strategies of coffee seedlings. Therefore, the findings presented provide insights into the influence of light gradients and irrigation levels on growth of different wild Arabica coffee accessions. Nevertheless, in-depth *in-situ* investigations on regeneration patterns and adaptive strategies of coffee trees under natural shade conditions are necessary and should take into account, among others, resource gradients, plant ontogeny and climatic variations.

7   WATER RELATIONS AND HYDRAULIC CHARACTERISTICS OF COFFEE SEEDLINGS

7.1   Introduction

There is no other single component that affects plant processes, including photosynthesis, more than water. 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 (Hopkins, 1995; Larcher, 2003). Plant growth is controlled directly by drought stress and only indirectly by soil and atmospheric drought stress. Roots are the organs that are stressed owing to the time lag in transpiration of water from leaves and their proximity to the source of water. However, drought slows root growth and decreases water absorption (Hale and Orcutt, 1987; Kramer, 1983). In general, roots are less sensitive than shoots to drought stress and the growth of leaves is more sensitive than root growth (Hopkins, 1995). 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). 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.).

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

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wind. The plant regulates drought stress by opening and closing the stomata, leaf flagging, rolling and shedding (Hale and Orcutt, 1987).

Investigation on the adaptation mechanisms of plants species is important to understand their ecological success and growth conditions (Sobrado, 1986). 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). 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 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). At predawn, reduced atmospheric demand for water slows down the water loss from the plant (Hopkins, 1995).

Although coffee appears to be a fairly drought-tolerant plant, its performance during the dry period may be increased by providing the trees with extra nitrogen (N) before the onset of this period. Again, potassium (K) appears to be a major osmotically active substance for stomatal opening, whereas the divalent cations calcium (Ca) and magnisium (Mg) are inhibitory, which reduces stomatal pore size. Nitrogen acts as a regulatory element in the sense that when water supply is plentiful, stomata are wide open and transpire freely. However, under a limiting water supply, N-rich plants transpire less and conserve more water during a dry period than N-poor plants (Wrigley, 1988). This study, therefore, was undertaken with the aim to explore whether or not osmotic adjustments are involved in the drought-resistance stagies of coffee seedlings. In this regard, the accumulation of selected inorganic ions was assessed in seedlings of wild coffee accessions subjected to environmental stresses (soil moisture and irradiance) in controlled nursery conditions.

A practical measure of the hydraulic supply capacity of the xylem is leaf-specific conductivity (Zimmermann, 1978). For example, the specific leaf conductivity of a stem segment can be used to relate the average transpiration water loss from leaves supported by the segment to the decline in water potential per unit path length within the segment. Thus, the distribution of leaf-specific conductivity within a tree influences patterns of water potential throughout the crown and can impose constraints on such

physiological processes as transpiration and photosynthesis (Shumway et al., 1993; Yang and Tyree, 1993).

Plants generally respond to acute water deficits by closing their stomata in order to match transpirational water loss through the leaf surfaces with the rate at which water can be resupplied by the roots. Stomatal frequency or density (the number of stomata per unit area of one leaf surface) can vary significantly within leaves, plants or individuals of a single species within a community and can be modified by environmental factors, leaf morphology and genetic composition. Stomatal frequencies often vary according to cell size, and smaller guard cells are usually associated with higher stomatal frequencies. Given the pressure regulator mode of stomatal function, it is inevitable that changes in the hydraulic conductance of the soil-leaf pathway, soil moisture, and evaporative demand will indirectly drive changes in stomatal conductance and transpiration (Comstock and Mencuccini, 1998; Fuchs and Livingston, 1996; Hubbard et al., 2001; Saliendra et al., 1995). Thus, the analysis of soil-plant hydraulics can be used to explain and predict patterns of plant water use with respect to the soil and atmospheric environment, and the large differences between species and cultivars. Earlier work tended to emphasize soil hydraulics, because flow in the soil is a physical process and can be readily quantified, whereas plant hydraulics were less well understood. The incorporation of soil and xylem dynamics can improve the treatment of plant hydraulics and set a physical constraint on the stomatal regulation of transpiration and water potential (Sperry et al., 2002).

In Ethiopia, information on relationships between growth architecture and hydraulic properties in coffee plants is insufficient. The study was, therefore, designed to examine the hydraulic characteristics of wild coffee accessions under contrasting shade and irrigation regimes. From the correlation analysis, stem size and leaf growth were the strongest parameters related to hydraulic efficiency of coffee seedlings. Consequently, leaf- and stem- specific hydraulic conductivities were calculated to describe the diversity in wild coffee accessions with regard to water properties and biomass production under contrasting light and soil water regimes. This chapter focuses on the detailed analysis of the physiological basis of survival, dry matter production, ability to cope with drought-stress and the growth responses of wild coffee accessions along the simulated light and drought stress gradients. Plant growth, however, depends

on plant and environmental factors and hence, information on the relative loss in xylem hydraulic conductance in seedlings of wild coffee populations subjected to varying amplitudes of drought stress conditions was the focus of this study. In addition, attention was given to determine stomatal characteristics and compare the variability among seedlings of wild coffee accessions in open sun and partial shade conditions.

7.2 Material and methods

7.2.1 Determination of moisture content

Soil moisture content (SMC, % vol.) was measured with a Theta probe type ML2 (Delta-T Devices Ltd., Cambridge, UK). This was done in plastic pots planted with seedlings of different wild coffee accessions, which were subjected to two levels of irrigation (drought-stressed and well-watered) and two shade regimes (full sun and moderate shade). The temporal dynamics in moisture status of the potting soil were recorded between the first (0 DAI) and last day after irrigation (16 DAI) after which the 16-day drying treatment was conducted. At the same time, leaf water potential (LWP) and relative water contents (RLWC) were measured for the treatments. The measurements were performed twice a day: predawn (05:30-06:30 h) and midday (12:00-13:00 h) at 4-day intervals. Mature and healthy leaf samples were taken from the same node position and direction on primary branches. A pump-up pressure chamber (PMS Instrument Co., Corvallis, USA) was used to measure leaf water potentials. Seedlings exposed to drought stress in full sun conditions exhibited minimum LWP on 8 DAI and the pressure chamber exceeded its maximum capacity (-2.1 MPa) for most coffee accessions, particularly those from Harenna wild coffee population.

Relative leaf water content (RLWC) was then measured to determine the water retention capacity and thus drought tolerance of the accessions under induced dehydration conditions. RLWC is an indicator of the moisture needed to bring the tissues to full turgor; it is the amount of water actually present in the tissue compared with the amount present in a turgid state (measure of internal drought stress). The parameter is useful because it expresses the absolute amount of water required for full saturation (Joly, 1985) and is therfore important for calculating the water requirements of a plant or stand. For this, leaf samples were weighed to obtain fresh weight (wf), floated on distilled water with the petiole intact and kept in a cooled incubator for 24 h

to eliminated any water deficit. After recording turgid weight (wt), the samples were finally oven dried at 105°C for 24 h for dry weight (wd). RLWC or relative turgidity was estimated using the equation described by Joly (1985): RLWC (%) = (wf-wd)/wt-wd)x100.

7.2.2 Percent loss of hydraulic conductance

The seedlings of the wild coffee populations were subjected to drought stress over a period of 16 days in full sun and partial shade conditions. Drought-stressed and well-irrigated seedlings of the same accessions were compared to estimate the extent of loss of hydraulic conductance and thus vulnerability to drought-induced xylem cavitation. This was computed starting a week after termination of irrigation. A transient method of the high-pressure flow meter was employed to measure the hydraulic conductance in root and shoot segments as described by Tyree et al. (1983) and Sperry et al. (1988). Percent loss of conductance (PLC) in root and various shoot segments were calculated according to Maherali and DeLucia (2000a) as: PLC = $100((K_{max}-K_{min})/K_{max})$, where K_{max} and K_{min} represent maximum and minimum hydraulic conductance in hydrated and dehydrated segments, respectively.

7.2.3 Recovery from drought stress

Ten potted coffee seedlings were selected and arranged in sun and moderate shade plots. The seedlings were 9 months old and had attained the desired stage of 50 cm tall with 6-9 pairs of true leaves and 1-4 pairs of primary branches. Drought stress was induced by withholding irrigation for 20 days (February 11-March 02, 2005). On the second day after re-watering, the number of wilted seedlings was counted at predawn for shade treatment and coffee accession and the percent of wilted seedlings was estimated. Then, the seedlings were divided into equal halves and relatively older leaves from the bottom part were removed on March 03, 2005, i.e., two levels of defoliation (50% defoliation and control, i.e., 100% leaves intact) were applied on an equal number of seedlings per accession.

Subsequently, the recovery rate of the wilted seedlings was examined. For this, percents of fully turgid, wilted, dried and new leaves were recorded starting 14 days after defoliation. The degree of incipient leaf wilting was recorded at predawn (06:00-

07:00 h). Most seedlings, particularly the bigger ones in full sun showed leaf wilting and drying symptoms within the 16-day of drought stress. On the last day, soil and leaf samples were collected and oven-dried at 105°C for 24 h, weighed and their moisture content was determined using the equation: water content (% dry weight basis) = [(fresh weight-dry weight)/dry weight]x100. Then, the seedlings were re-watered up to full saturation of the potting medium and the droughted seedlings were no more covered with the white plastic shelter. The leaves of moderately drought stressed seedlings showed immediate leaf turgidity and the leaves remain pale green or brownish. Two days after termination of the drought treatment, the moisture content was measured using the Theta probe for soil and on a dry weight basis for leaf samples. Then, conventional nursery practices were applied for 10 months (between March and December 2005) after the first day of re-watering.

The experiment was repeated on another set of drying experiment with the aim to assess the consistency of the responses of the wild coffee accessions to drought stress treatment. In this case, the drying period lasted for 24 days between June 02 and 25, 2005. Severe drying was observed and most seedlings of all accessions were irreversibly dried due to the severity of the extended dehydration beyond the threshold level. Five seedlings of the same coffee accessions were selected and re-watered after 20 DAI in the two shade treatments. At the end of the drying experiment 16 DAI, the status of soil-plant moisture was determined. Ten days after irrigation, visual score on the magnitude of leaf wilting, extent of leaf folding and thus, reduction in leaf area were determined for the shade treatment and coffee accessions.

Finally, survival rate of the seedlings and sprouting (new leaf flush) were assessed after 7 months of re-watering in December 2005, and leaf turnover (LTO) rate was estimated. For this, leaf fall and new leaf sprouts were recorded at a monthly interval and the extent of leaf growth and rate of recovery were calculated as: $(n_i-n_f)+n_m)x100$ where n_i and n_f are initial and final number of leaves, respectively; n_m = leaf mortality rate. Moreover, the seedlings were visually assessed for drought tolerance using scores ranging from 1 to 4. These represent increased magnitudes of drought stress symptoms on the leaves (1= all leaves are fully green; 2 = most older leaves are turgid and youngest leaves show partial wilting at midday; 3 = all leaves show leaf wilting and folding at predawn, and 4 = leaves become pale green or

brownish and do not recover during predawn. In addition, percent leaf rolling was calculated as: $(1-w_1/w_2) \times 100$ where w_1 and w_2 are maximum diameter of folded and unfolded leaves at the center.

7.2.4   Soil-plant chemical compositions

After the first drying cycle (24 DAI), soil and leaf tissue were collected from the same pots. To examine the influence of drought stress on soil and leaf chemical compositions including soluble ions, the samples were air-dried and labelled for laboratory analyses on chemical compositions. All analyses were carried out at the International Livestock Research Institute, Ethiopia, analytical service laboratory using the procedures described for soil and plant analysis (Tekalign et al., 1991).

7.2.5   Hydraulic measurements

Hydraulic measurements were performed on seedlings of 12 wild coffee accessions manganed under controlled nursery conditions between March 29, 2004 and May 31, 2005 (428 days). The seedlings were arranged in two shade treatments (full sun and moderate shade) for a 3-month period between June and August 2005. All nursery practices were applied according to the recommendations (IAR, 1996). Full sun seedlings were acclimatized to maximum light conditions through gradual reduction of the shade cover so as to minimize the possible risks associated with a sudden change to a new and stressful environment. The seedlings were well-watered to field capacity of the potting medium at 4-day intervals. Shoot extension growth parameters were recorded in a month intervals. Soil moisture was maintained by applying water to each pot in the late afternoon of the day before the hydraulic measurements.

Root and shoot hydraulic resistance was measured for the same central seedlings to determine the relationship between seedling growth and hydraulic characteristics. Hydraulic data were measured using a high-pressure flow meter (HPFM, Dynamax Inc, Houston, TX, USA). In this study, the red flow range was determined to be the most suitable and used for the hydraulic measurements in coffee seedlings as described in Tyree et al. (1995) and Tausend et al. (2000b). First, the HPFM was connected to the base of the debarked main stem cut at about 5 cm above the soil surface. The initial pressure was set and increased at 5 kPa s^{-1} and flow rates were

recorded at 2 seconds intervals. Root hydraulic conductance (reciprocal of hydraulic resistance) was measured by the transient method and hydraulic conductance was calculated from the slope of the change in the amount of water flow and applied pressure. Next, the seedling was saturated by immersing and flushing with clean water and the main stem was cut again under water, debarked and attached to the HFPM to measure hydraulic resistances in the whole shoot and different shoot parts (leaf, petiole and primary branch). This was measured using a steady state flow meter method of the HPFM. The resistance of the seedling segments was determined by the consecutive removal of each part. The hydraulic resistance was recorded whenever the steady state flow meter attained a constant flow rate. The initial result with all above-ground shoot parts was recorded as whole-shoot resistance and then, leaves, petioles and primary branches were sequentially removed. The straight main stem axis was cut to a 20-cm length. Finally, the contribution to whole-plant and whole-shoot resistance was calculated from the difference in resistance before and after removal of each segment. The whole-plant resistance included root and whole-shoot resistance.

The hydraulic conductance in root and shoot parts as well as leaf and stem hydraulic conductivity were examined in wild coffee accessions exposed to contrasting shade and irrigation treatments. Water was withheld from 50% of the seedlings (drought stressed, W0), while the other 50% received water (well-watered, WW) at 4-day intervals. This was performed under full sun (S0) and moderate shade (S1) conditions. In the drying treatments, the seedlings were covered by a white plastic sheet at night and whenever there were clouds (rain) in the daytime. In this way, they were progressively subjected to soil drying for 16 days after irrigation (DAI). Root and shoot hydraulic conductance was measured using the transient method of the HPFM at 4-day intervals (4, 8, 12 and 16 DAI). The first day after irrigation (0 DAI) was also included and maximum care was taken to keep the seedlings remain dehydrated during the hydraulic measurements. Hydraulic conductance in root, whole shoot and shoot parts were recorded separately.

The diameter of the debarked main stem axis was measured with a calliper and the cross-sectional area was calculated. The water flow through a 20-cm long main stem was measured using a high-pressure flow meter as described by Tyree et al. (1983) and Sperry et al. (1988). The amount of water was divided to the total leaf area supported by

the main stem and to the basal area of the debarked main stem to obtain leaf- and stem - specific hydraulic conductivity of the seedlings, respectively. After the hydraulic measurements, each part of the seedling was divided into leaves, main stem, lateral branches and roots. The roots were separated from the soil by careful washing. After recording the fresh weight, the samples were oven-dried for 24 h at 105°C and immediately weighed using a Sartorius analytic sensitive balance. The relationships between growth and hydraulic characteristics were assessed in seedlings of wild coffee accessions.

7.2.6   Stomatal characteristics

Coffee seedlings of the 12 accessions were maintained in full sun and moderate shade environments at the Jimma Agricultural Research Center nursery site for a period of 8 months (between May 2005 and January 2006). Irrigation was applied to maintain full leaf turgidity and stomatal measurements were undertaken in the morning when the leaf stomata were expected to remain open. Fully mature and healthy leaf samples were used from the third to fourth nodes of the primary branches of the middle crown position. The samples were stored in a plastic bag and immediately brought to laboratory for measurement. The leaves were cleaned and a small part of the leaf surface from the lower (abaxial) and upper (adaxial) epidermis was sampled using a thin layer of transparent nail polish. The so-prepared sample was left for about 10 minutes to dry and the nail polish impression was swiftly removed using a transparent adhesive tape. This was placed on an object slide and observed under a light microscope at 400 times magnification. The diameter of field of vision for the binocular was measured by stage micrometer at 40 objectives and the area was calculated as πr^2.

The density of stomata and dimension of guard cells were recorded within a small field of view (0.15 mm^2) as described by Weyers and Meidner (1990) and Van Duren et al. (1996). The density of stomata was determined in the wet (August/September) and dry (December/January) seasons of the year 2005/06 (Figure 3.3). There were no clearly differentiated cells around the two guard cells for measurement. Hence, the width of guard cell pair was measured along with its maximum length and used in the estimation of the other stomatal characteristics. Hence, it was not possible to estimate the frequency of stomata relative to the other types of

cells on the epidermis (stomatal area index). However, stomatal area index (SAI), stomatal area (SA) and total number of stomata on a leaf area basis were estimated for shade treatment and coffee accession. The SAI was calculated as SAI = stomatal density multiplied by guard cell length. The total number of stomata on a leaf surface was estimated from the product of stomatal frequency by leaf area (Weyers and Meidner, 1990).

7.3 Statistical analysis

Two-way analysis of variance (ANOVA) was carried out to examine the differences between shade levels, irrigation regimes, coffee accessions and interactions on soil moisture status, diurnal leaf water potentials and relative leaf water contents. In the case of hydraulic conductance, the main independent variables (shade, irrigation and plant part) and interaction effects (shade-irrigation, shade-plant part and irrigation-plant part) were assessed at 4-day intervals between the first day after irrigation (0 DAI) and subsequent soil drying period (4, 8, 12 and 16 days). Pearson correlations, principal component and cluster analyses were carried out for the parameters considered. All statistical analyses were performed using the SAS system for Windows 8 software (SAS Institute, Cary, NC). Treatment means were ranked according to Tukey test at P = 0.05 whenever the F-test showed significant differences.

7.4 Results

7.4.1 Soil moisture content

The moisture content in the potting medium showed significant (P<0.001) differences due to shade, irrigation and interaction between shade and irrigation treatments. In contrast, coffee accessions did not exhibit a significant impact on soil moisture content, singly or in combination with shade treatment. Accordingly, shaded (27.4% vol.) and irrigated (35.4% vol.) plots showed a higher soil moisture content with the respective increment of 15 and 57% over sun (23.4%vol.) and water withheld (15.4% vol.) pots. Moreover, soil moisture content in pots with different coffee accessions ranged from 25.4 to 26.3% vol. for Berhane-Kontir (III-3) and Yayu (IV-3) seedlings, respectively. The accessions were comparable in soil moisture content and showed a minimum coefficient of variations with an overall average value of 24.3%vol. With regard to

temporal dynamics in soil moisture, significantly (P<0.01) reduced soil moisture content due to shade and irrigation treatments was observed, except in the well-irrigated pots in full sun conditions. For instance, there was a drop in soil moisture content from 29.1 to 3.7% vol. and 33.7 to 4.0% vol. between the 0 DAI and 16 DAI in sun and shade plots, respectively (Table 7.1; Figure 7.1). In other words, soil moisture content decreased more during the early periods of drought stress (0-8 DAI), when the soil moisture loss was almost double than that of the plots in moderate shade. However, the highest difference (13.1% vol.) with a 61% increment was recorded on 8 DAI, while the difference was minimal thereafter both in sun and shade plots. This was when shade plots showed significantly higher soil moisture (3 times higher than in full sun plots).

Table 7.1   Soil moisture content (means±SD %vol.) in coffee seedlings under two shade and irrigation treatments. Drought stress period was between 0 and 16 days after irrigation (DAI)

Treatment	Sun		Shade	
Drought period (DAI)	Drought stressed ***	Well-watered Ns	Drought stressed ***	Well-watered ***
0	29.08±2.65a	34.23±1.94	33.71±2.16a	36.42±2.05b
4	14.05±1.82b	34.05±2.83	25.50±3.28b	35.85±1.52b
8	8.35±1.67 c	34.48±1.83	21.46±4.06 c	35.27±1.83bc
12	5.17±1.28d	33.71±3.52	8.55±0.88de	39.71±1.46a
16	3.68±0.62d	36.78±4.35	3.98±0.65e	33.51±2.53c
Accession	Ns	*	Ns	**
I-1	12.67±12.84	36.18±2.46ab	17.83±12.46	34.42±3.15b
I-2	12.26±10.80	33.68±1.82ab	19.45±12.81	36.38±3.46ab
I-3	10.50±9.56	35.95±2.99ab	19.43±13.80	34.39±2.99b
II-1	12.11±8.93	36.01±2.42ab	15.66±11.16	36.82±2.96ab
II-2	11.47±9.67	34.65±2.60ab	18.22±12.42	38.67±1.55a
II-3	13.69±11.40	34.39±2.93ab	16.83±12.01	36.80±2.38ab
III-1	13.03±11.60	33.65±2.76ab	20.28±13.01	36.33±2.09ab
III-2	12.35±10.18	35.37±2.11ab	17.51±11.11	36.75±3.30ab
III-3	11.83±10.80	30.25±5.25b	20.69±13.23	34.55±4.66b
IV-1	11.05±8.86	35.96±3.50ab	19.46±12.85	35.18±0.91b
IV-2	11.23±9.45	33.24±2.60ab	18.84±11.17	36.84±1.18ab
IV-3	12.60±10.38	36.45±2.00a	19.49±12.89	36.72±1.74ab
Mean	12.07	34.65	18.64	36.15
CV (%)	13.81	7.99	12.65	4.42

*Ns = Not significant; *, **, *** = Significant at P<0.05, P<0.01 and P<0.001, respectively. Means with the same letter in a column are not significantly different (Tukey test at P = 0.05).*
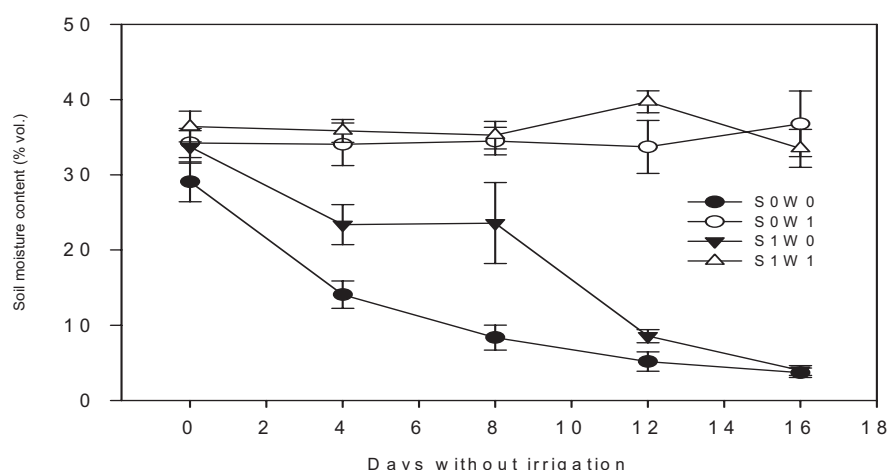
Figure 7.1   Influence of two shade and irrigation levels on soil moisture content of coffee seedlings. S0W0 = no shade not watered, S0W1 = no shade watered, S1W0 = with shade not watered and S1W1 = with shade watered

7.4.2   Leaf water potential

Diurnal leaf water potential was significantly (P<0.001) changed due to shade and irrigation treatments (Appendix 7). Shade treatments showed highly significant differences on 4 and 8 DAI. This gradually declined and a significant (P<0.05) effect was observed 12 and 16 DAI. The results show maximum predawn (-0.66±0.43 MPa) and midday (-1.35±0.24 MPa) leaf water potential (LWP) in shaded seedlings as compared to those in full sun with mean predawn and midday values of -0.95±0.70 and -1.52±0.36 MPa, respectively. However, the diurnal change in LWP was significantly lower (-0.70±0.22 MPa) for shaded leaves as opposed to the sun exposed leaves (Table 7.2). This could be attributed to an increased moisture gradient between soil-leaf pathways and thus demonstrates the advantage of moderate shading before severe drought occurs.

On the other hand, irrigation showed highly significant variations throughout the drying periods, except on predawn LWP at the beginning of the drought treatment. Hence, drought-stressed seedlings had significantly higher predawn (-0.26±0.02 MPa) and midday (-1.16±0.12 MPa) LWP as compared to well-watered seedlings with a significantly lower change in diurnal leaf moisture potential (-0.89±0.12 MPa). On the other hand, drought-stressed seedlings showed significantly lower LWP in sun (predawn = -1.62±0.23 and midday = -1.90±0.27) and shade (predawn = -0.77±0.45 and

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midday = -1.53±0.29 MPa) conditions 4 and 8 DAI, respectively (Figure 7.2). This shows a two-fold reduced irrigation interval in shaded seedlings as opposed to those in full sun. This could, therefore, serve as a threshold soil moisture deficit level to apply irrigation at the above intervals for the sun and shade conditions.

In contrast, except the significant (P<0.05) variation in midday LWP on 4 DAI, there was no significant difference among accessions and their interactions with shade and irrigation levels. The lowest (-1.54 MPa) and highest (-1.32 MPa) midday LWP were recorded for the Bonga and Berhane-Kontir accessions, respectively. Similarly, relatively low (-0.87 MPa) and high (-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 LWP with averages of -0.81, -1.44 and -0.63 MPa determined for predawn, midday and change in LWP, respectively (Table 7.2). Although insignificant, the accessions from Harenna (I-1 = -0.89 MPa) and Berhane-Kontir (III-1 = -0.90 MPa) showed the lowest LWP at 4 DAI. This, however, declined after 8 DAI to the respective low LWP of -1.28 and -1.75 MPa. This is in consistence with the high percent loss of hydraulic conductance in the same coffee accessions (section 7.2.3), whereas the Bonga and Yayu accessions showed reduced LWP from -0.78 to -1.98 MPa and from -0.63 to -1.98 MPa between 4 and 8 DAI, respectively. In addition, Harenna seedlings had substantially lower predawn LWP when drought stressed in full sun conditions. 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 significantly higher predawn LWP than the Bonga accessions when examined in drought-stressed plots in moderate shade conditions.

The two-way analysis of variance shows 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. Consequently, 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 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 drought stress in the sun with the lowest predawn (-1.64 MPa) and midday (-1.84 MPa) LWP values recorded early in the drought period. These values, however, declined as of 8 DAI. This was followed by low predawn (-1.06 MPa) and midday (-1.58 MPa) LWP due to the combined effect of drought stress and moderate shade, where the lowest values were observed after 8 DAI (Figure 7.3). In contrast, significantly high LWP were observed in well-irrigated seedlings both in the shade and sun with a significantly higher change in LWP. The results of the linear regression also demonstrate that the accessions from Bonga had low predawn and midday LWP values as opposed to Berhane-Kontir. The Harenna and Yayu accessions showed intermediate reductions in LWP (Figure 7.4). There was a significant ($r = 0.80^{**}$) and direct linear regression between soil moisture content and leaf water potential in seedlings subjected to drought stress for a period of 8 days (Figure 7.5). Accordingly, the Yayu accessions showed a higher LWP at maximum soil moisture when compared to the other accessions.

Table 7.2   Leaf water potential (MPa) of coffee seedlings as influenced by shade and irrigation treatments

Treatment	Predawn	Midday	Difference
	Shading		
Sun	-0.95±0.70b	-1.52±0.36b	-0.57±0.37a
Shade	-0.66±0.43a	-1.35±0.24a	-0.70±0.22b
	Irrigation		
Stressed	-1.35±0.32b	-1.72±0.16b	-0.37±0.18a
Watered	-0.26±0.02a	-1.16±0.12a	-0.89±0.12b
	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
	ANOVA (Pr>F)		
Shading	***	***	***
Irrigation	***	***	***
Accession	Ns	*	Ns
Shade*irr	***	***	***
Irr*acc	Ns	*	Ns
Shade*acc	Ns	Ns	Ns

Ns, *, *** = Not significant, significant at P<0.05 and P<0.001, respectively. Means with the same letter in a column are not significantly different (Tukey test at P = 0.05).
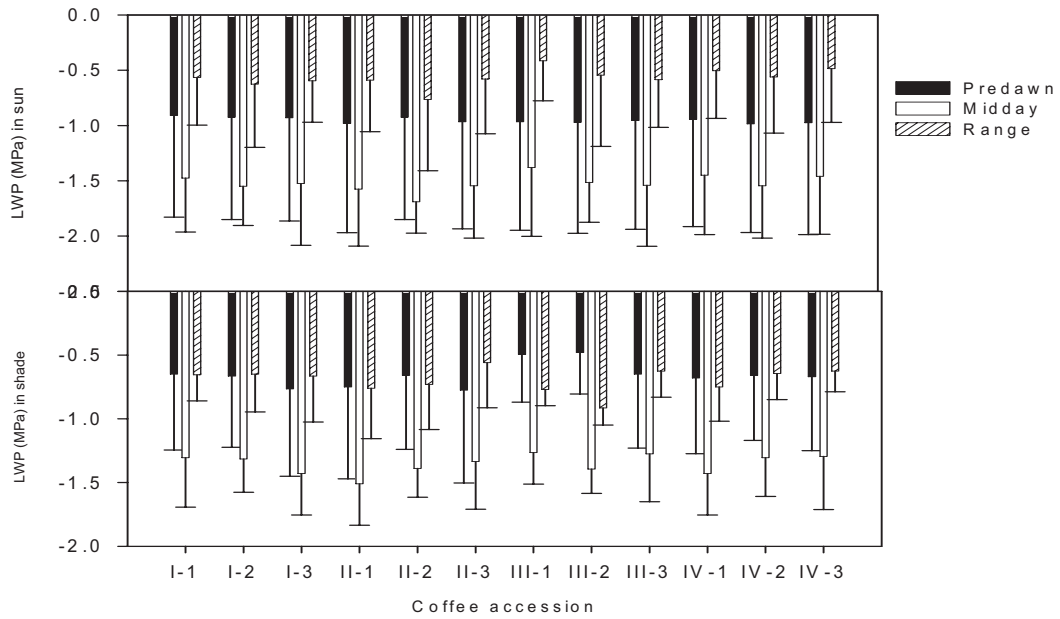
Figure 7.2   Diurnal changes of leaf water potential in seedlings of coffee accessions in sun and shade (capacity of the pressure chamber =-2.1 MPa)
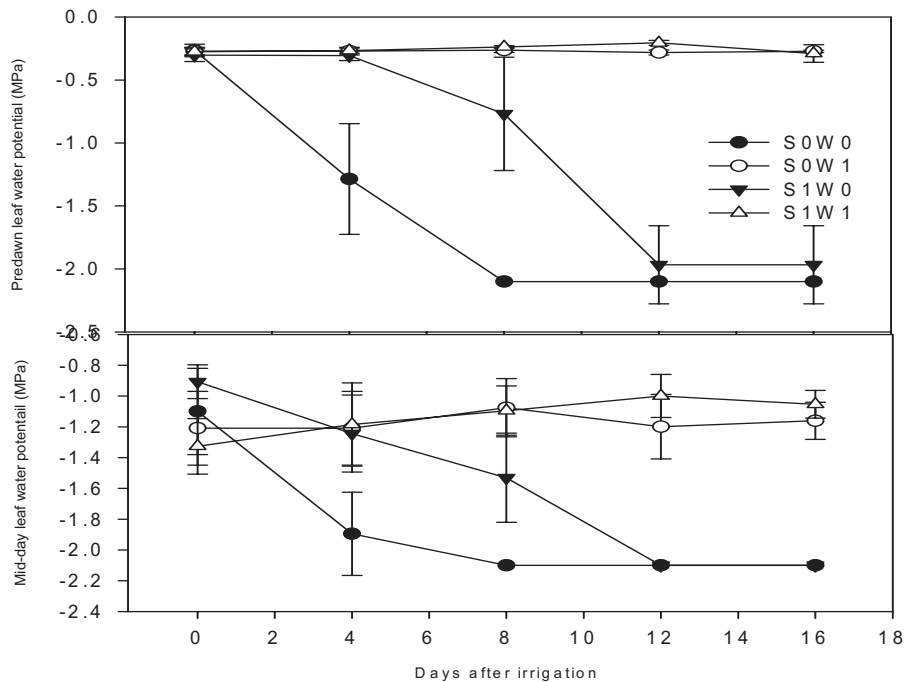
Figure 7.3   Diurnal leaf water potential in coffee seedlings as affected by shade and irrigation levels during drought stress periods. (S0W0 = no shade not watered; S0W1 = no shade watered; S1W0 = shaded not watered; S1W1 = shaded watered). Capacity of pressure chamber =-2.1 MPa
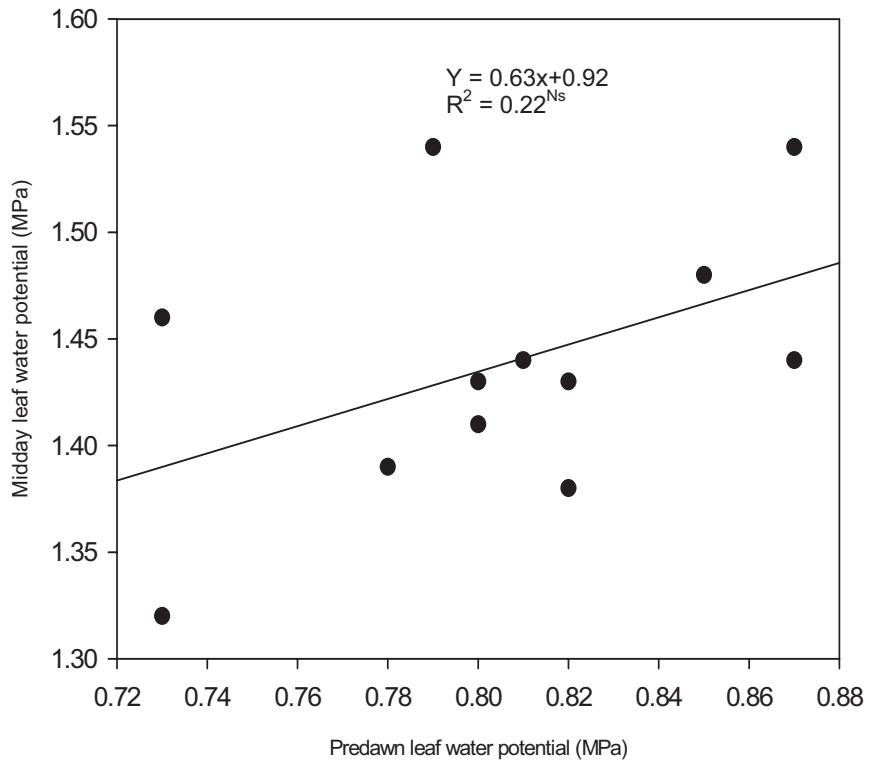
Figure 7.4   Relationships between predawn and midday leaf water potential in seedlings of wild coffee accessions
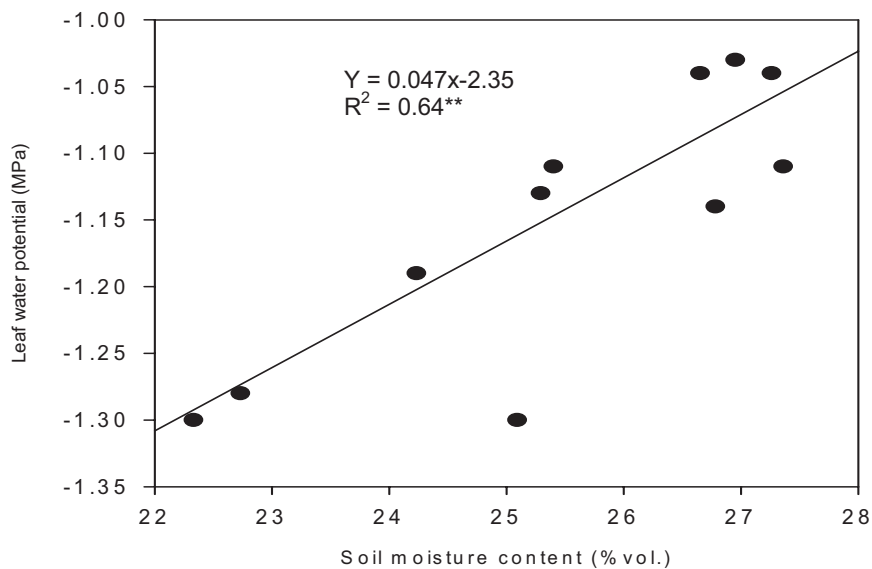
Figure 7.5   Relationships between leaf water potential and soil moisture content in drought-stressed coffee seedlings (8 days after irrigation)

7.4.3   Relative leaf water content

There were significant differences (P<0.001) in the diurnal relative leaf water contents (RLWC) of the coffee seedlings due to the main and interaction effects of shade and irrigation levels. Consequently, maximum predawn (76%) and midday (72%) average RLWC were recorded from shaded seedlings as compared to those in full sun (predawn = 58% and midday = 56%). At predawn, dew was observed on the surface of the coffee leaves of seedlings that were not covered by a white plastic sheet. This may contribute to the higher predawn leaf RLWC. Drought stressed seedlings had significantly lower RLWC at predawn (50%) and midday (47%). The RLCW did not significantly differ among coffee accessionsfor the two shade and irrigation treatments. However, high (IV-1 = 71%) and low (II-3 = 61%) predawn values were recorded for the Yayu and Bonga accessions, respectively. On the other hand, midday RLWC ranged from 59 to 69% for the Harenna and Yayu accessions, respectively (Figure 7.6). Similarly, the diurnal changes in RLWC were 61 and 69%, respectively for these accessions.

Although interactions were not significant, the most dried leaves were found on the not watered and sun-exposed Yayu and Harenna seedlings with the respective low RLWC of 39 and 23%. In addition, in drought-stressed plus shade conditions, the Yayu accessions showed the lowest RLWC. As a result, the values ranged from 26 to 45% for Bonga and Yayu seedlings, respectively. In other words, seedlings exposed to drought stress showed a significantly higher midday RLWC (47%) than well-watered seedlings. This is in consistence with the reduced leaf water potential and high of leaf wilting scores. Accordingly, the lowest predawn and midday RLWC was recorded from water deficit soils in full sun conditions (Figure 7.7), indicating the permanent wilting point of the potting soil. In contrast, not watered seedlings in shade environments revealed relatively higher fluctuations in RLWC. Hence, an increment of 54% and 52% in the predawn and midday relative leaf water contents respectively, were found compared to drought-stressed in full sun. In other words, leaf moisture contents declined to 22 and 43% in sun and shade conditions, respectively over 16 days period of soil drying (Figure 7.8). The contribution of shading was, however, more pronounced on 12 DAI when a maximum RLWC of 55% was observed as compared to the preceding and following days after irrigation.

The RLWC determined in water-withheld seedlings in full sun conditions for a week 8-day period showed that accessions from Harenna had minimum predawn and midday values with narrow ranges. This is in contrast to the Berhane-Kontir and Yayu accessions, suggesting their sensitivity to low availability of soil moisture. In addition, the overall average diurnal fluctuation in RLWC was high in the Berhane-Kontir accessions as compared to the Harenna accessions in particular. This indicates that the former accessions were more tolerant to varying levels of soil drying. The linear regression between predawn and midday RLWC showed significant (r = 0.55*) correlations. However, the pattern varied due to accessions, and maximum ranges were recorded for II-3, III-2, I-1, II-2, IV-1 and IV-2 in a descending order. This indicates that these accessions have a wider drought-stress tolerance range than the others (Figure 7.9). Most coffee accessions showed relatively severe drought-stress symptoms 8 and 12 DAI in full sun and shade conditions, respectively. This was when RLWC were about 50 and 57% in the sun and shade plots, respectively. The results of regression show that both predawn and middy RLWC tended to decrease with increased accumulation of potassium (K^+) in the coffee leaves, and the correlation was significant for the midday RLWC. This, however, differed among the wild coffee populations, where the Harenna accessions exhibited the lowest RLWC and highest accumulation of K^+. In contrast, the Yayu accessions showed a high RLWC at lower leaf K^+ contents. The values for the other accessions lie between the two populations (Figure 7.10).
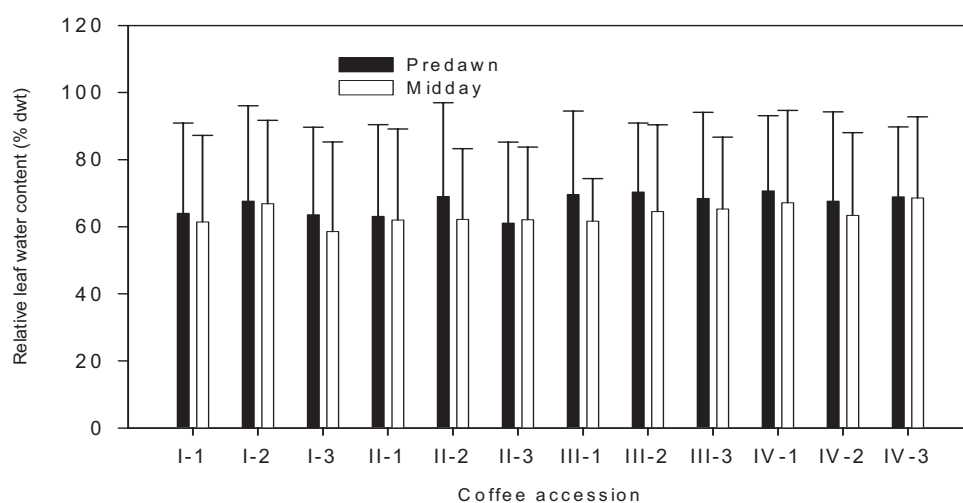
Figure 7.6   Average predawn and midday relative leaf water contents in drought-stressed seedlings of coffee accessions
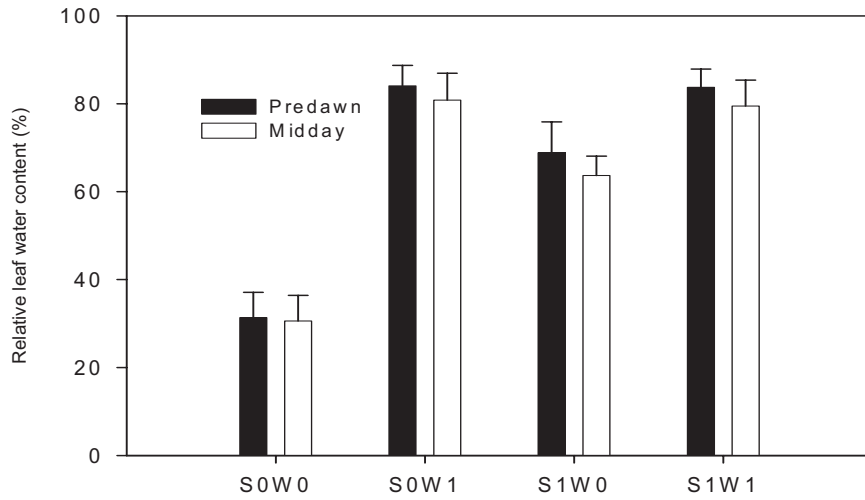
Figure 7.7   Diurnal relative leaf water contents in drought-stressed and irrigated coffee seedlings under sun and shade (S0W0 = not shaded not watered, S0W1, not shaded watered, S1W0, shaded not watered S1W1, shaded watered)
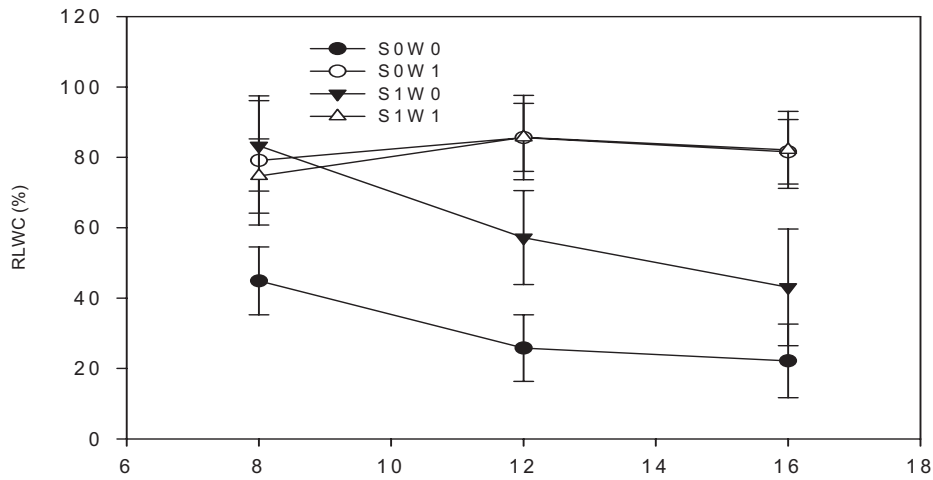
Figure 7.8   Average relative leaf water content in coffee seedlings exposed to two shade and watering treatments (S0W0 = not shaded not watered, S0W1, not shaded watered, S1W0, shaded not watered S1W1, shaded watered)
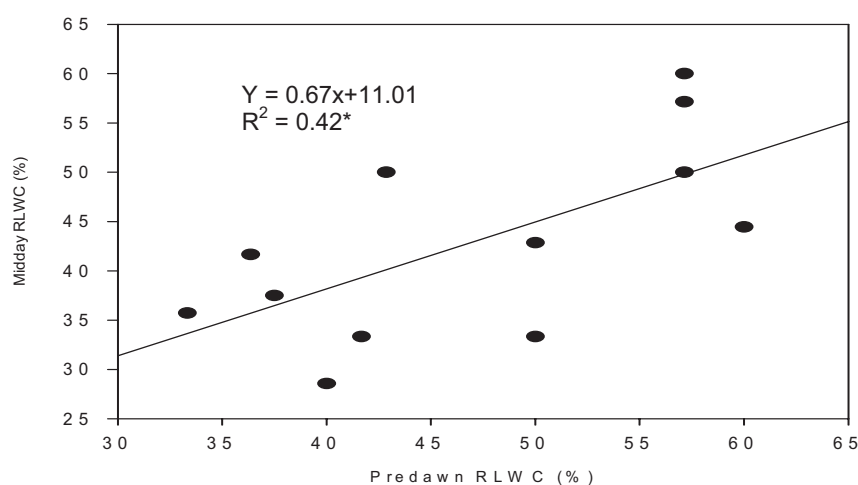
Figure 7.9   Predawn and midday values of relative leaf water content in seedlings of wild coffee accessions exposed to drought stress in full sun conditions
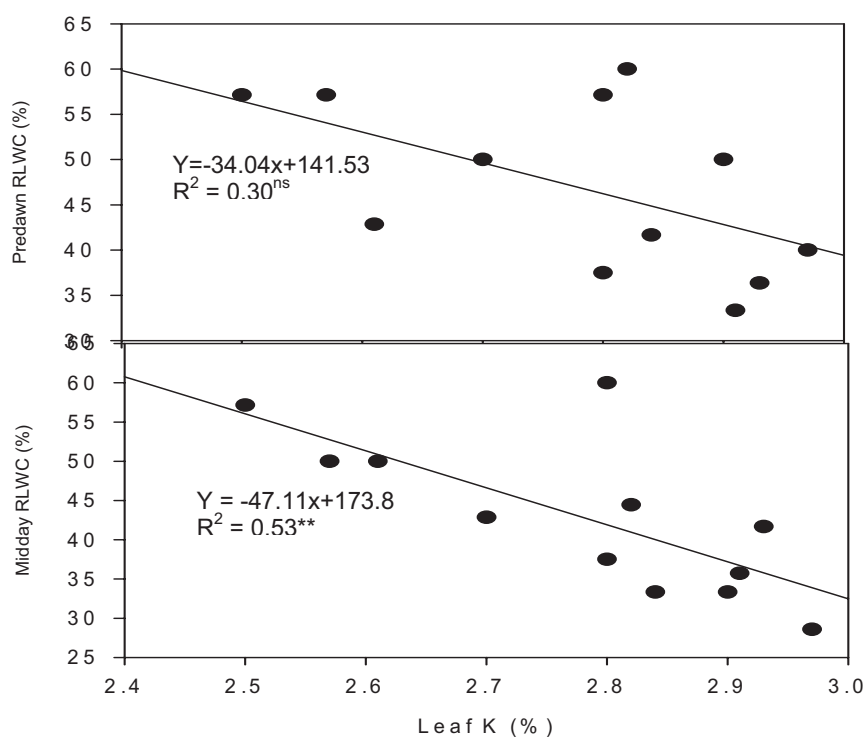
Figure 7.10   Relationships between leaf potassium (K) and predawn and midday relative leaf water contents (RLWC) in coffee seedlings of wild coffee accessions exposed to drought-stress in full sun conditions

7.4.4   Percent loss of conductance

There were significant variations among the seedlings in percent loss of conductance (PLC) in root and shoot systems due to the induced water deficits in full sun and shade

conditions. Although the results are inconsistent across drought periods and shade regimes, the Harenna and Yayu accessions showed significantly highest values of whole-plant PLC both in sun and shade plots. In contrast, most Bonga accessions revealed low PLC, particularly in shade environments. Low and high PLC respectively indicated that the xylem conduits were less and more dehydrated due to drought stress. As a result, in the shade, all shoot segments had significantly lowest PLC, indicating a gain in hydraulic conductance perhaps due to a higher water flow in drought-stressed than in hydrated plant segments. The overall average PLC throughout the drought period also varied among accessions and seedling parts in the two light regimes. In full sun, PLC in root part ranged from 33.3 to 82.1% in the Berhane-Kontir accessions. However, the lowest root PLC was calculated in shaded Yayu and Berhane-Kontir seedlings as opposed to the Bonga and Harenna accessions. On the other hand, the Berhane-Kontir and Bonga accessions displayed minimum and maximum whole-shoot PLC in full sun conditions, though average PLC values ranged from 3.4 to 55.1% in the Berhane-Kontir (III-1) and Yayu accessions (IV-2), respectively (Table 7.3).

PLC in the root and shoot systems of the coffee seedlings were also significantly different due to length of drought period in both full sun and shade plots. The highest root PLC (84.1%) and the lowest whole-shoot PLC (15.6%) were determined 8 DAI for seedlings in the sun. However, whole-shoot PLC was significantly high in the sun (62.2%) and shade (63.8%) 16 DAI. Overall, the results show significantly higher PLC in the root than in the shoot of the coffee seedlings. The average PLC was higher in the full sun than in the shade plots, indicating loss in turgor and water potential of leaves following cavitation. This supports the findings of Maherali and DeLucia (2000a). Whole-plant PLC had strong direct correlation with average leaf area and differed among coffee accessions. As a result, most Bonga accessions had small leaves and exhibited minimum PLC when compared to the others. In contrast, the broader Harenna accessions exhibited high PLC (Figure 7.11). In critically drought stressed-seedlings 8 and 12 DAI in the sun and shade, respectively, root PLC was 84% in the sun and 74% in the shade, while leaf PLC was 52% in sun and 40% in the shade.

Table 7.3   Percent loss of hydraulic conductance in root and shoot segments of coffee accessions exposed to drought-stress (between 8 and 16 DAI) in sun and shade conditions

Treatment	Sun			Shade		
	8	12	16	8	12	16
Accession	***	***	***	***	*	*
I-1	56.84a	50.31ab	17.55e	5.99ab	64.94ab	50.60ab
I-2	50.33abc	56.31ab	40.93cde	15.78ab	41.66ab	49.67ab
I-3	47.23abc	54.69ab	26.89de	26.67a	44.70ab	36.80ab
II-1	52.63abc	53.90ab	52.24abc	40.52a	33.81ab	60.93ab
II-2	12.89bc	70.69a	27.65de	4.18ab	5.20b	36.23b
II-3	52.83abc	40.36bc	49.75a-d	47.17b	22.75ab	55.79ab
III-1	9.37c	62.30ab	67.70ab	38.28a	12.18ab	56.49ab
III-2	76.81a	15.88c	69.76a	23.12a	13.35ab	47.78ab
III-3	53.03ab	65.30ab	58.14abc	20.28ab	31.54ab	48.32ab
IV-1	53.44ab	57.60ab	43.69cd	11.40ab	28.98ab	64.33ab
IV-2	41.48abc	70.79a	44.77bcd	11.02ab	0.18ab	66.36a
IV-3	54.59ab	71.51a	47.93a-d	14.96ab	85.63a	52.82ab
Seedling part	***	***	***	***	**	***
Root	84.05a	83.30a	83.81a	68.92a	74.01a	79.12a
Whole-shoot	15.63c	48.30bc	62.18b	40.18a	34.15ab	63.76ab
Leaf	51.90b	58.91b	48.92bc	1.35b	39.70ab	60.94ab
Petiole	48.75b	54.02bc	42.38cd	14.42b	0.34b	50.82bc
Branch	47.37b	48.92bc	29.40d	21.85b	27.03ab	34.99cd
Stem cut	33.03bc	41.35c	6.81e	28.40b	12.72b	23.42d

*$P<0.05$, **$P<0.01$, ***$P<0.0001$. Means followed by same letters in each column are not significantly different (Tukey at $P = 0.05$).*
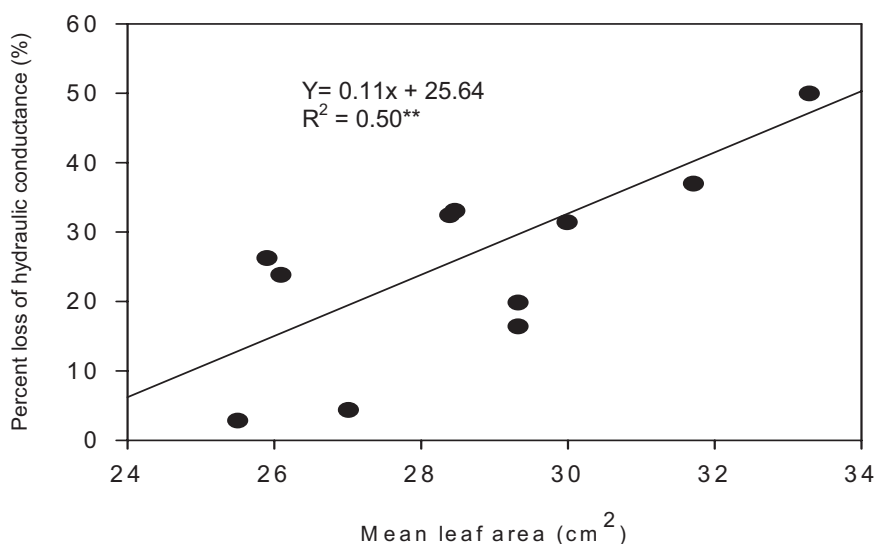
Figure 7.11   Average percent loss of whole-plant hydraulic conductance in drough-stressed coffee seedlings as influenced by leaf area

7.4.5   Recovery from drought stress

Extent of drough stress

Soil moisture content

Soil moisture content (SMC) was significantly (P<0.001) different between sun and shade plots with the respective values of 4.7 and 8.7% dry wt (Table 7.4). This is an increment of 46.0% in soil moisture status in shade over the open sun plots. Defoliation did not change the status of moisture in the soil and coffee leaf. However, the SMC was slightly higher in the pots of defoliated seedlings in sun and shade conditions. Similarly, defoliation resulted in higher SMC in pot-grown seedlings of all coffee accessions, except in the two accessions (I-1 and I-2) from the Harenna population. The reduction in foliage increased the SMC in the pots with Berhane-Kontir seedlings. These seedlings had high leaf water contents before and after re-watering. This was in contrast to the Harenna accessions where the leaf water content was significantly lowest due to the simulated drought, which was in contrast to the hypothesis mentioned earlier.

In addition, the moisture content of the potting media was not significantly influenced by coffee accessions. However, the average soil moisture ranged from 5.0 to 8.4% for pots with the Yayu accessions IV-3 and IV-1, respectively. The overall average SMC at the end of the drying cycle was 6.7% dry wt. In general, the change in soil-plant water status in the coffee seedlings was more pronounced due to variations in shade than to coffee accessions. The lowest and highest SMC were recorded in the Berhane-Kontir and Harenna populations, respectively. The Yayu accessions also showed a more rapid decline in SMC followed by Harenna seedlings. This result coincides with the net photosynthetic balance of the same coffee accessions under controlled nursery conditions (Beining, 2006).

On the second day after rewatering, the significant (P<0.001) difference in SMC between shade levels was determined. Accordingly, ahigher SMC (32.6%) was determined for shaded seedlings than for unshaded ones. The pots with the different coffee accessions did not differ in SMC. However, the average values ranged from 29.3 to 32.7%vol in the Bonga (II-3) and Harenna (I-1) accessions, respectively (Table 7.5). In general, the soil was relatively wet in the pots in the order Berhane-Kontir>Harenna>Bonga>Yayu accessions, indicating the variability in root and shoot growth characteristics. There was a positive significant (P<0.05) association between

soil and leaf moisture contents with minimum coefficient of variations among seedlings coffee accessions.

Leaf water content

Similarly, significant (P<0.001) variation in leaf moisture content (LMC) was displayed between shade levels, where a lower value was found for sun (13.9% dry wt) than the shade pots (46.5% dry wt), i.e., shaded seedlings showed an about 3-fold (70%) higher LMC over the unshaded seedlings. In contrast, the coffee accessions did not show significant variations in LMC as was the case with the SMC. The lowest LMC were determined for the Harenna (I-2 = 12.2%, I-1 = 18.4%) and Yayu (IV-3 = 20.2%) accessions. This is in contrast to the highest LMC in the Berhane-Kontir accessions (III-2 = 42.1% and III-3 = 47.2%) (Table 7.4).

Table 7.4   Means (±SD) soil moistute content (SMC) and leaf moisture content (LMC) at the termination of the first cycle of drying (16 days after irrigation, DAI) and 2 days after re-watering, DARW)

Variable	Moisture content (16 DAI)		SMC (% vol.), 16 DAI		2 DARW
	SMC (%dwt)	LMC (% dwt)	Defoliated	Undefoliated	LMC (% dwt)
Shading	***	***	***	***	***
Sun	4.72±0.87b	13.90±9.63b	4.59±0.99b	4.36±1.12b	33.79±15.60b
Shade	8.74±1.76a	46.53±13.92a	7.46±1.77a	7.36±1.16a	58.00±10.06a
Accession	Ns	Ns	Ns	Ns	*
I-1	6.10±3.17	18.40±15.14	4.41±3.35	4.87±3.89	30.00±31.11bc
I-2	5.94±1.73	12.16±5.30	4.29±0.83	5.07±2.42	23.51±17.60c
I-3	6.02±1.88	26.68±30.39	5.29±0.78	4.83±0.27	31.87±14.38abc
II-1	7.47±4.17	31.70±19.40	5.22±0.06	5.17±0.10	53.62±6.58abc
II-2	6.95±4.13	38.59±36.87	6.57±2.45	7.63±1.63	56.91±18.71ab
II-3	7.84±5.18	30.78±21.38	6.47±3.07	5.91±1.63	48.74±21.59abc
III-1	5.76±1.56	31.45±33.21	7.39±4.12	5.95±2.84	45.91±18.82abc
III-2	6.74±3.95	42.07±26.62	7.26±2.12	6.47±2.53	52.89±12.95abc
III-3	7.47±1.95	47.16±11.10	7.09±2.25	6.56±1.70	63.47±0.43a
IV-1	8.40±3.85	29.29±25.96	5.90±1.36	6.03±2.90	49.37±20.90abc
IV-2	7.06±0.95	34.02±30.30	5.09±1.15	5.54±3.11	50.40±22.58abc
IV-3	5.04±1.56	20.25±21.22	7.31±2.90	6.28±2.43	44.05±20.67abc
Mean	6.73	30.21	6.02	5.86	45.89
CV (%)	20.54	30.95	20.20	19.10	17.65

*Ns = Not significant; *P<0.05; **P<0.01 and ***P<0.001. Means with the same letter within a column are not significantly different (Tukey at P = 0.05).*

On the second day of re-watering, the coffee leaves attained turgidity, and the increase in LMC was significantly (P<0.01) higher in sun than in shade leaves. There was also a significant (P<0.05) difference among coffee accessions in LMC due to re-hydration of the potting soil, the results ranging from 23.51 to 63.47% for the

accessions from Harenna (I-2) and Berhane-Kontir (III-3), respectively. The accessions from Berhane-Kontir showed highest LMC with the results ranging from 45.91 to 63.47% (Table 7.4), indicating that these leaves were hydrologically more stable. On the second day of drought stress termination, the numbers of wilted seedlings were counted, and the average percent of wilted seedlings was highest in the Harenna accessions (I-1 = 70%, I-2 = 75%). This was in contrast to accessions from Berhane-Kontir (III-3 = 0%) and Bonga (5%), where no or only few seedlings exhibited predawn wilting symptoms (Figure 7.12).

There was a significant positive correlation between SMC and LMC (r = 0.78**). The low LMC and high degree of wilting for the Harenna and Yayu populations could be related to the faster seed germination rate and much more seedling vigor in the early growth stage. This was in contrast to the accessions from Berhane-Kontir and Bonga. A relationship between shoot water potential and symptoms of drought stress was apparent. The rapid decline in LMC in the drought-stressed Harenna seedlings may be due to their differences in xylem embolism and vulnerability ranges under drought stress situations.

With regard to interactions, the results show that incipient leaf wilting was significantly different due to the interaction effect between shade levels and coffee accessions. As a result, all accessions showed a higher wilting score in sun than in shade plots. The severity of the leaf-wilting symptom was, however, different among and within accessions of the same population (Figure 7.12). The scores were 2-fold higher in sun than in shaded seedlings from Harenna (I-1 and I-2) and Yayu (IV-1 and IV-2). In contrast, Bonga (II-2) and Berhane-Kontir (III-2 and III-3) seedlings were not specific to light conditions and revealed reduced difference between shade regimes.
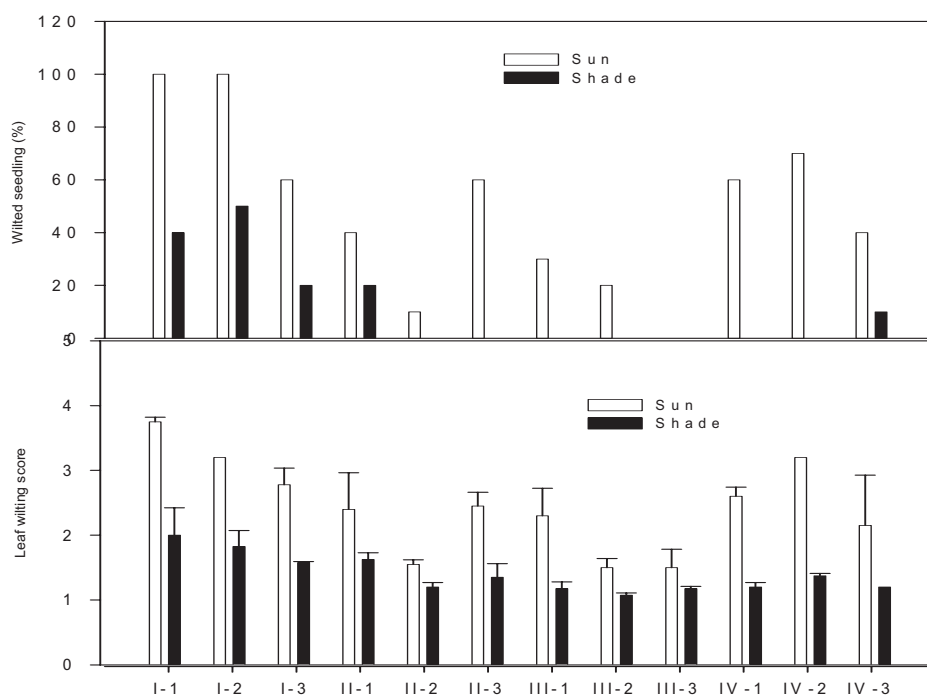
Figure 7.12   Percent of wilted seedlings and leaves in wild coffee accessions on the second day after rewatering the potting medium

The variation in daylight regimes had also significant effects on leaf water content (P<0.01), leaf turgid weight (P<0.05), leaf dry weight (P<0.01), relative leaf water content (P<0.01), specific leaf area and specific leaf mass (P<0.001). Consequently, most of these variables were higher in full sun than in shade seedlings, except leaf moisture content (68.42%) and specific leaf area (136.43 g cm^{-2}). The significantly (P<0.001) higher specific leaf mass (0.009 cm^{2}g^{-1}) could be among the possible reasons for the high RLWC (37.68%) determined in sun-exposed seedlings. According to the correlation results, leaf turgid weight tended to slightly decrease with increased soil and leaf moisture status. It also had an inverse, but insignificant relation with all the hydraulic resistance components of the seedlings. As a result, maximum leaf turgid mass (1.24 g) and dry mass (0.36 g) were recorded in full sun conditions. This corroborated with the extension growth response of the seedlings in contrasting light environments, where reduced seedling height, increased stem size and reduced mean leaf area were recorded for sun-exposed seedlings (Table 7.5), indicating the morphological adjustment between leaf area and sapwood area in maintaining the hydraulic homeostasis; main stem specific hydraulic resistance was significantly related

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to leaf water content (r = 0.64***) and relative leaf water content (r = -0.60**). These are some of the features of high hydraulic conductance to ensure increased photosynthetic responses in coffee seedlings if soil moisture is sufficient.

On the other hand, in well-watered coffee seedlings, leaf turgid weight was comparable among accessions of different wild coffee populations. Nevertheless, slightly high (1.31 g) and lowest (1.02 g) values were obtained from Harenna and Yayu accessions, respectively. This may suggest accession-specific variability in drought stress sensitivity and leaf tissue elasticity along varying shade environments. Seedlings from the Berhane-Kontir forests had a high mean leaf area (42 cm^2) and ultimately produced a high leaf dry mass (0.35 g) as compared to others, particularly Bonga accessions (II-1 and II-2), which had a low leaf dry mass (0.28-0.30 g) and lowest (24.62-40.66%) relative leaf water contents.

On the contrary, LMC was positively and significantly associated with the hydraulic resistance in the shoot and its various segments. However, with increased RLMC there were significant reductions (P<0.001) in root and shoot hydraulic resistance. As a result, these accessions showed low root and shoot growth in similar experimental conditions. This could be retalted to their high whole-plant hydraulic resistance and thus, low risk of the water potential falling below the threshold value at which cavitations occur. Conversely, accessions from the Berhane-Kontir and Harenna populations were found to produce maximum total biomass in well-watered and optimal environments, suggesting a response to increased high hydraulic conductance and water use at leaf level. Above all, the relationships between diameter of main stem with hydraulic resistance in root, shoot and whole plant was strong and negative (Table 7.14; Figure 7.17). Moreover, LWC (% dwt) was positively (r = 0.52, P>0.05) influenced by SMC (% dwt) in the pot, where low and high leaf water contents were determined for most Harenna and Berkane-Kontir accessions, respectively (Figure 7.13).

Table 7.5   Soil and plant moisture content (means±SD) in seedlings of wild coffee accessions subjected to drought-stress in sun and shade conditions

Treatment	SMC (%vol.)	LDW (g)	RLWC (%)	SLA (g cm^2)
Shade level	***	**	**	***
Sun	29.91±0.72b	0.36±0.03 a	37.68±7.84a	115.02±10.06b
Shade	32.57±2.01a	0.30±0.04b	26.97±5.27b	136.43±11.03a
Accession	NS	NS	NS	NS
I-1	32.67±3.23	0.34±0.13	38.06±9.03	123.11±27.10
I-2	31.52±1.39	0.33±0.07	32.99±2.45	114.70±10.83
I-3	30.16±0.67	0.33±0.07	31.64±11.66	122.99±34.00
II-1	30.73±1.45	0.32±0.05	40.66±9.17	121.99±11.26
II-2	33.02±3.63	0.28±0.07	36.25±22.99	141.71±32.12
II-3	29.27±0.52	0.30±0.00	24.62±0.93	134.99±0.17
III-1	32.23±2.05	0.33±0.00	26.33±6.09	130.90±6.51
III-2	31.83±3.89	0.35±0.00	29.98±7.27	124.24±9.97
III-3	32.08±2.83	0.35±0.00	27.99±7.38	124.89±16.55
IV-1	30.22±2.07	0.34±0.06	32.32±0.25	121.73±7.05
IV-2	30.70±1.84	0.32±0.02	35.12±6.90	118.25±16.28
IV-3	30.47±0.30	0.33±0.04	31.97±12.21	129.22±9.88
Mean	31.24	0.33	32.32	125.72
CV (%)	4.44	12.27	20.63	8.45

NS = Not significant (P>0.05), *P<0.05, **P<0.01 and ***P< 0.001 significance levels. Figures followed by different letters in a column are significantly different at P = 0.05. Abbreviations: SMC = soil moisture content, LDW = leaf dry weight, RLWC = relative leaf water content, SLA = specific leaf area.
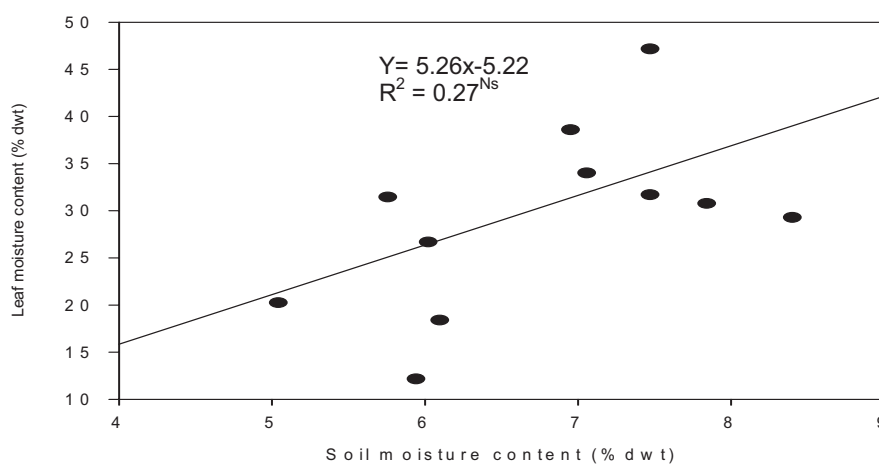
Figure 7.13   Linear regression between soil and leaf moisture contents in coffee seedlings subjected to drought-stress for 16 days

Leaf wilting and rate of recovery

The degree of leaf wilting and rate of recovery from drought stress significantly varied due to shade and accessions (Table 7.6). The severity of leaf wilting was high in the upper part of the seedlings, indicating an increased water potential along the soil-plant-

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atmosphere system. This was also observed between the tip and base of a leaf surface, indicating the decline in stomatal conductance and net photosynthetic rate due to increased drought stress. The degree of leaf wilting at the time of drought stress and rates of leaf growth and recovery after re-watering were significantly different due to shade, accession and their interactions. Consequently, sun seedlings showed a significantly (P<0.001) higher leaf wilting score (2.45) and higher rate of recovery than those in moderate shade conditions (Table 7.6). On the other hand, main and interaction effects of defoliation did not significantly affect rate of leaf wilting and growth rates, though the values were slightly higher for undefoliated seedlings with a large transpiration area. Significantly (P<0.001) high wilting was recorded for the Harenna as compared with the Berhane-Kontir accessions. As a whole, though there were intra-population variations, the results of visual scoring on leaf scorching due to induced drought stress was in the order Harenna>Yayu>Bonga>Berhane-Kontir populations.

At the end of the drying period, the same effect remained, and the coffee accessions showed significantly (P<0.05) different rates of leaf growth with a reversed sequence of order. The negative leaf growth rate for the Harenna accession (I-1) indicates the severity of drought stress causing leaf drying. This was evident from the early highest score (2.88) on leaf wilting. All other accessions, particularly Bonga (II-2) and Berhane-Kontir (III-2), were observed to produce and a maintain significantly highest photosynthetically active leaf area as opposed to the Harenna accession (I-1). In general, the seedlings produced a pair of true leaves and had recovery rate of 2 pairs of true leaves per month following re-watering at the end of the first drying cycle (Table 7.6). The extent of leaf fall at the end of the first cycle of soil drying and rate of recovery after re-watering was significantly different between shade (P<0.05) levels and coffee accessions (P<0.01). Accordingly, a higher leaf recovery was obtained under sun than shade conditions. Similarly, the induced water deficit for the 16-day period was severe enough to cause a wide range of leaf fall in the Harenna accessions with significantly low recovery rates as compared to the others. In contrast, all accessions from the wetter southwest areas maintained their initial leaves and produced new leaves after re-watering. Accordingly, maximum leaf growth changes were found in the Berhane-Kontir accessions with overall recovery rates ranging from 130 to 161%. The leaf recovery values were highest for the Bonga accession (II-2) (Table 7.6).

Table 7.6   Extent of leaf wilting and rate of recovery (%) in wild coffee seedlings as influenced by two light and defoliation levels after re-watering

Treatment	Wilting score	Overall recovery	Growth/month	Recovery rate /month
Shading				
Sun	2.45±0.74a	117±131a	2.60±3.04a	10.62±11.92a
Shade	1.40±0.31b	73±58b	1.54±1.14b	6.61±5.23b
Defoliation (Def)				
Undefolited	1.94±0.75	107±106	2.36±2.44	9.74±9.66
Defoliated	1.91±0.81	82±100	1.78±2.24	7.49±9.05
Accession (Acc)				
I-1	2.88±1.04a	-15±99b	-0.45±2.63b	-1.36±8.96b
I-2	2.51±0.81ab	37±123ab	0.66±2.73ab	3.34±11.15ab
I-3	2.18±0.71a-d	15±88ab	0.27±1.81ab	1.40±8.04ab
II-1	2.01±0.56b-e	110±110ab	2.71±2.53ab	9.97±9.96ab
II-2	1.38±0.21de	183±51a	3.64±1.14a	16.61±4.60a
II-3	1.90±0.66b-e	12±30ab	0.30±0.67ab	1.11±2.69ab
III-1	1.74±0.70b-e	130±120ab	2.95±2.95ab	11.86±10.87ab
III-2	1.29±0.26 e	161±107a	2.82±1.99ab	14.68±9.70a
III-3	1.34±0.25 e	157±92ab	3.41±2.08a	14.29±8.39ab
IV-1	1.90±0.81b-e	154±95ab	3.71±2.56a	14.01±8.65ab
IV-2	2.29±1.05abc	91±27ab	2.62±0.86ab	8.31±2.50ab
IV-3	1.68±0.71cde	101±82ab	2.25±1.89ab	9.15±7.47ab
ANOVA (Pr>F)				
Shade	***	*	*	*
Defoliation	Ns	Ns	Ns	Ns
Accession	***	**	**	**
ShadexDef	Ns	Ns	Ns	Ns
ShadexAcc	**	*	**	*
AccxDef	Ns	Ns	Ns	Ns

*Ns = Not significant P>0.05; *P<0.05; **P<0.01; ***P<0.0001. Figures followed by same letters within a column are not significantly different from each other (Tukey test, P = 0.05).*

The response of the seedlings to water deficit and subsequent rewatering was different among wild coffee accessions. Consequently, seedlings from the Harenna population showed early wilting symptoms and did not recover from the drought stress in full sun conditions, indicating the severity of a 16-day period drought stress of in such accessions. This was evident from the complete drying of the seedlings, indicative of the dysfunction of the xylem and phloem tissues above a certain threshold level. However, the dried leaves remained on the main stem and lateral branches, and no leaf fall was noticed in Harenna accessions. The drying symptom was quite similar to plant death in a waterlogged situation due to lack of oxygen. On the other hand, the Yayu seedlings shed their leaves and produced more leaf sprouts within 16 days after re-watering. The accessions from Bonga and Berhane-Kontir did not show early wilting

symptoms and thus maintained their healthy leaves. In addition, these seedlings had no sprouts, except the new leaf growth at the upper part of the seedlings (Table 7.7).

The rate of leaf recovery after artificial reduction of soil moisture deficits also significantly ($P<0.05$) varied among accessions. Consequently, all accessions, except Harenna, showed a higher rate of leaf recovery in sun than in shade plots. The seedlings from Berhane-Kontir had maximum average recovery values of 21.01 and 21.38% for III-2 and III-3, respectively. The accessions from Bonga (II-2 = 20.37%) and Yayu (IV-1 = 20.98%) also revealed high rates of leaf recovery. In contrast, seedlings from the Harenna population showed negative average monthly leaf recovery rates in the sun plots (Figure 7.14).
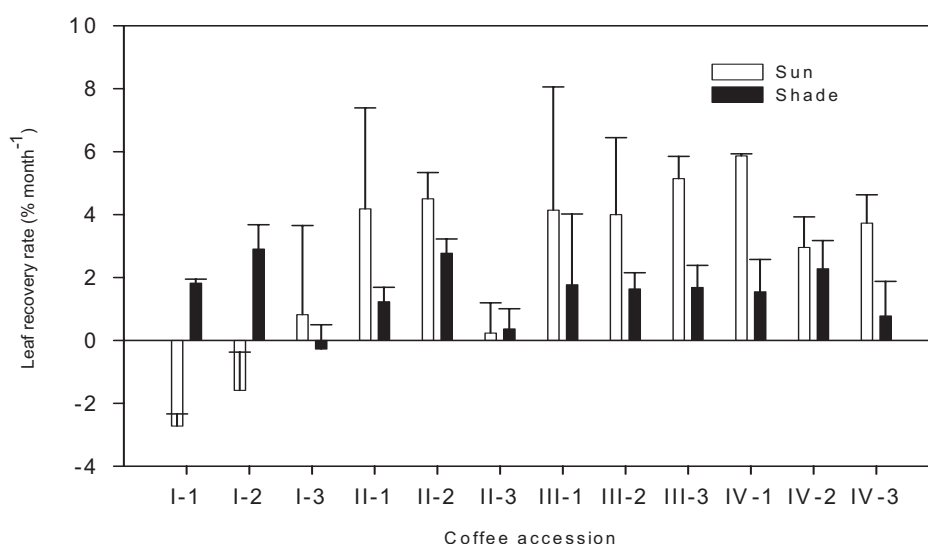
Figure 7.14   Monthly leaf turnover in seedlings of coffee accessions in sun and shade conditions

The status of leaf recovery (healthy, dried and new growth) from drought-stress-induced seedlings was significantly different between shade levels, where higher dried and new initiated leaves were recorded in sun seedlings. In contrast, more healthy leaves were maintanianed in shade conditions. The influence of defoloation was not significant, except the significantly ($P<0.05$) higher number of dried leaves on 50% defoliated seedlings. Neverthelss, defoliation was observed to enhance the retention of healthy leaves and encourage the production of new leaves. Similarly, coffee accessions significantly differed in response to drought stress. Consequently, the number of healthy leaves was significantly ($P<0.05$) highest in the Berhane-Kontir accession (III-3 =

78.5%) as opposed to the lowest value for Harenna (I-1 = 27.3%). On the other hand, the Harenna accessions exhibited significantly highest number of dried (P<0.01) and newly initiated (P<0.05) leaves as compared to the other accessions, particularly those accessions from Berhane-Kontir (Table 7.7; Figure 7.15). The results of the two-way analysis show no interaction effects, except shade by accsseion on dried and new leaves (P<0.05) as well as shade by defoliation (P<0.05) on the intensity of dried leaves. Accordingly, significantly higher proportions of dried and new initiated leaves were recorded from the Harenna and Bonga (II-1) accessions, both in the sun and shade plots, being higher in the sun. This is in contrast to the other southwest accessions with a significantly higher retention of healthy leaves and new leaf growth (Figure 7.15).

Table 7.7   Percent of healthy, dried and new leaves in defoliated and undefoliated seedlings of coffee accessions subjected to drought stress in sun and shade conditions

Treatment	Healthy	Dried	New
		Shading	
Sun	44.05±27.88b	53.88±22.53a	65.14±18.65a
Shade	72.12±11.19a	16.47±22.46b	33.87±40.76b
		Defoliation	
Defoliated	59.84±27.89	38.51±30.89a	53.33±34.12
Undefoliated	56.34±23.00	31.85±27.66b	45.69±36.39
		Accession	
I-1	27.30±32.66b	66.50±15.31a	74.19±17.55a
I-2	36.33±43.28ab	65.93±15.67a	74.41±6.70a
I-3	59.10±19.34ab	40.05±35.84abc	52.27±36.69ab
II-1	59.88±21.49ab	45.95±11.15ab	88.49±8.35a
II-2	60.61±15.81ab	25.36±24.02bc	39.83±47.38ab
II-3	60.02±18.18ab	38.14±44.07abc	37.89±43.95ab
III-1	63.31±21.28ab	17.58±30.58bc	58.65±29.23ab
III-2	69.94±10.79ab	28.46±32.71bc	42.40±29.22ab
III-3	78.49±10.59a	14.38±18.07c	13.92±17.90b
IV-1	62.07±33.01ab	26.10±25.60bc	39.93±46.58ab
IV-2	55.23±24.17ab	21.71±19.59bc	39.92±34.70ab
IV-3	64.76±23.95ab	32.01±35.62bc	32.21±38.41ab
		ANOVA	
Shading	***	***	***
Defoliation	Ns	*	Ns
Accession	*	***	*
Shade*Acc	Ns	*	*
Shade*Def	Ns	*	Ns
Acc*Def	Ns	Ns	Ns

*Ns = Not significant P>0.05; *P<0.05; **P<0.01; ***P<0.0001. Means followed by same letters within a column are not significantly different from each other (Tukey test, P = 0.05).*
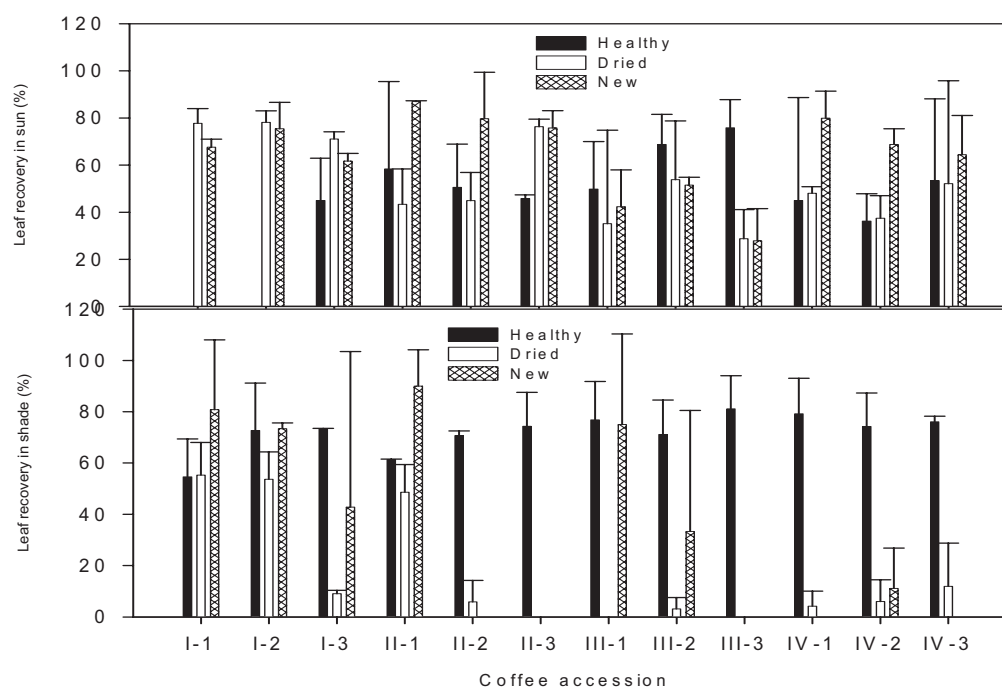
Figure 7.15   Percent leaf recovery in a 16 day drought-stressed seedlings of coffee accessions in sun and shade conditions

In the second set of drying experiments, within a 12-day drought stress period, most accessions showed severe drought stress symptoms with no significant differences in leaf wilting scores between sun (2.58) and shade (2.27) (Table 7.8). However, leaf rolling was significantly (P<0.01) higher in the sun (66.5%) than in the shade (39.1%) plot. Accordingly, the reduction in leaf area was 14.0 and 18.7% under shade and sun plots, respectively. Though not significant, sun seedlings showed higher leaf senescence with a higher number of brownish colored dried leaves, while shade leaves were still pale green and slightly wilted.

The results show no significant variations among coffee accessions in the extent of leaf wilting, leaf folding and reduction in leaf area. However, a significant difference (P<0.05) was noted in the severity of dried leaves, with the lowest and highest average of brownish leaves recorded in the Yayu (IV-2 = 3.35) and Bonga (II-1 = 44.24) accessions. Seedlings from Berhane-Kontir also had a low degree of dried leaves. In addition, the extent of leaf folding ranged from 41.2 to 84.5% in the Harenna and Yayu accessions, respectively (Table 7.8). Similarly, the lowest (6.4%) and highest (26.5%) reductions in leaf area were determined in Harenna and Yayu accessions,

respectively, which was more related to leaf size. The findings are similar to the response of the seedlings to the imposed drought stress for a 16-day drought period (first drying experiment).

Table 7.8   Leaf wilting score, percent leaf rolling and reduction in leaf area (RLA) in seedlings of coffee accessions exposed to drought-stress in sun and shade conditions (10 days after re-watering)

Treatment	Leaf wilting	Leaf rolling (%)	RLA (cm^2)	Brown leaf
Shade level	Ns	**	Ns	Ns
Sun	2.58±0.70	66.46±10.36a	18.72±5.30	18.08±12.42
Shade	2.27±0.69	39.13±23.24b	14.04±8.07	14.66±13.07
Accession	Ns	Ns	Ns	*
I-1	2.50±0.71	47.94±12.06	15.16±2.05	10.53±8.08bc
I-2	1.63±0.53	41.16±42.49	6.42±4.66	9.02±2.27bc
I-3	2.63±0.18	46.29±34.71	12.57±7.89	33.24±1.70ab
II-1	3.50±0.00	59.84±23.13	19.76±7.44	44.24±1.56a
II-2	2.38±0.88	45.45±18.05	10.76±6.12	16.40±11.55bc
II-3	3.13±0.53	46.27±11.05	13.49±2.31	23.95±2.97abc
III-1	2.75±0.35	56.50±29.65	17.87±6.29	9.99±1.22bc
III-2	2.00±0.35	37.28±11.87	15.76±2.74	5.61±1.28c
III-3	2.75±0.35	38.49±41.57	15.15±14.11	14.60±13.29bc
IV-1	2.25±0.35	84.58±13.15	19.36±3.14	11.57±8.20bc
IV-2	1.50±1.06	66.37±2.93	23.75±6.10	3.35±4.74c
IV-3	2.13±0.53	63.37±17.52	26.50±2.23	13.94±5.59bc
Mean	2.43	52.79	16.38	16.37
CV (%)	22.21	30.72	34.60	39.01

*Ns = Not significant P>0.05; *P<0.05; *P<0.01. Means with the same letter are not significantly different at P = 0.05 (Tukey test).*

7.4.6   Soil-plant chemical compositions

Soil composition

An analysis of varainace for soil chemical composition based on shade, irrigation and coffee accessions was computed (Table 7.9). The results show that withholding water in the shade plots significantly increased soil TN (P<0.01), available Ca (P<0.05), soil organic matter (P<0.001), pH (P<0.05) and C:Nratio (P < 0.05). This was in contrast to the significantly increased available K (P<0.05), electrical conductivity (P<0.001) and cation exchange capacity (P>0.05) in well-watered seedlings in the shade. Similarly, there were great changes in soil chemical composition, except for Mg, CEC and base saturation, due to variations in irrigation levels in full sun condition. Consequently, significantly higher total nitrogen (P<0.001), available phosphorus (P<0.001), exchangeable K (P<0.01) and Ca (P<0.001), organic matter (P<0.001) and electrical

conductivity (P<0.01) were determined for drought-stressed than well-watered pots. However, soil pH was significantly (P<0.0001) higher (5.86) in wet soil than in dry soil (5.72). In addition, C:N ratio was insignificantly lower (11.05) in dry soil, indicating the reduced chemical reactions and activities of soil microorganisms. Contrary to the well-watered plots, the effect of shading was more pronounced in the drought-stressed plots. Accordingly, when soil moisture was low, significant (P<0.001) variations in total nitrogen were observed between shade and sun, with a higher value in the sun. This was, however, not significant in the well-watered plots, where the total nitrogen content of the soil was almost equal. Further, significant differences in available P, K, Ca, organic matter, electrical conductivity, soil pH and carbon to nitrogen ration were found between shade levels both in drought-stressed and irrigated plots. Thus, most soil variables were higher in the sun, except available P and K. There was an inverse pattern in EC and soil pH between sun and shade compared along varying irrigation levels. The results indicate great variations in soil conditions in drought-stressed and sun-exposed plant pots as compared to the irrigated and shaded pots. Soil conditions, however, did not alter due to coffee accessions exposed to varying irrigation levels both in shade and sun environments. This was also observed when the effects of shade regimes and coffee accessions were examined in dry and sufficiently moist soil conditions. This illustrates the relatively similar growth of the coffee seedlings causing considerable changes in soil chemical conditions within the short experimental periods.

An overall treatment analysis (Table 7.9) shows significant differences in total nitrogen (P<0.001), exchangeable bases (K and Ca, P<0.001), organic matter (P<0.001) and carbon to nitrogen ratio (P<0.05) of the soil according to shade levels. Consequently, except for the higher available P (7.17±1.16 ppm) and K (6.06±0.36 meq/100g) levels in shaded pots, all other soil parameters were higher for the sun pots. Similarly, Mg, CEC, pH and base saturation were also higher for the sun pots, though the values were not significantly different to those in the shade soil. Likewise, except for pH, all soil parameters were higher in the dry than in the moist soil. Consequently, significantly higher total nitrogen (0.42±0.04%, P<0.001), available phosphorus (6.58±1.20 ppm, P<0.01), Ca (13.62±1.37 meq/100g, P<0.001) and organic matter (8.00±0.65%, P<0.001) were measured in the dry soil. In contrast, soil pH ranged between 5.77±0.07 and 5.81±0.07 for dry and irrigated soils, respectively. On the other

hand, coffee accessions did not significantly change the chemical conditions of the soil. Total nitrogen was, however, low for the Bonga and Berhane-Kontir accessions in contrast to the slightly higher values for the Yayu and Harenna coffee accessions. This could be related to the variations in growth stages and thus, nitrogen uptake by the seedlings, which be partly due to variations in soil organic matter and carbon to nitrogen ratio in contrasting shade and moisture regimes. According to Tekalign et al. (1991), the soil had high ratings for TN, OC and K, medium for Mg and low for Ca.

The interactive effect between shade and irrigation was significant on pH, total nitrogen, electric conductivity, K and Ca status of the soil. The other soil results, however, do not display significant differences. In addition, the interaction between shade and accessions was not significant on all soil chemical properties considered. Hence, in well-watered pots, pH was higher in the sun than in the shade. In drought-stressed plot, however, pH was lower in the sun than in the shade. In the sun, both well-watered and dried soils had significantly higher total nitrogen as compared to the reduced values in the shade, particularly in drought-stressed pots. Similarly, drought-stressed and irrigated soils had significantly higher EC in sun and shade conditions, respectively. This was in consistence with the patter of total nitrogen in drought-stressed pots. EC and pH, on the other hand, showed inverse relationships due to the combined effects of shade and irrigation treatments. Available K was higher in the shaded pots with and without irrigation, though it was slightly higher for the latter. Unlike this, the Ca content of the soil was significantly higher in the sun for both irrigation levels and was higher in the dry soil. The results reveal the benefits of shade to reduce differences in the K contents of dry and moist soils.

The soils of the Harenna and Bonga seedlings had a relatively high pH in the shade as opposed to the high values for the Berhane-Kontir and Yayu seedlings in shade plots. The lowest values were obtained for I-1 and III-3 seedlings in the sun and shade plots, respectively. The base saturation showed inconsistent patterns for the coffee accessions in contrasting shade levels;the sun-exposed pots with I-1, II-2, III-1 and III-3 showed maximum values, which is in contrast to the highest values for the Yayu accessions in shade environments. Shaded Berhane-Kontir and Yayu seedlings showed increased soil available P compared with the sun pots. Unlike most soil parameters, available K was highest for the III-1 accession in the shade condition.

Water relations and hydraulic characteristics of coffee seedlings

Table 7.9   Chemical properties (means ± SD) of the soil according to shade, irrigation and coffee accessions

Treatment	pH-H₂O (1:2)	Available P (ppm)	Exchangeable base (meq/100g)			CEC (meq/100g)	EC (mmhos/cm)	Base satu. (%)	Organic matter (%)	Total N (%)	C:N
			K	Ca	Mg						
Shade level	Ns	***	***	***	Ns	Ns	Ns	Ns	***	**	*
Sun	5.79±0.09	5.13±0.99	5.32±0.31	13.89±1.19	5.51±0.28	32.12±1.97	0.13±0.02	77.20±5.45	7.81±0.81	0.41±0.05	11.17±0.62
Shade	5.79±0.06	7.17±1.16	6.06±0.36	12.17±0.87	5.43±0.30	31.09±1.85	0.14±0.01	76.26±4.68	7.09±0.64	0.38±0.03	10.70±0.56
Irrigation	*	**	Ns	***	Ns	Ns	Ns	Ns	***	***	Ns
Stressed	5.77±0.07	6.58±1.20	5.70±0.33	13.62±1.37	5.50±0.28	31.97±1.72	0.14±0.02	77.75±4.21	8.00±0.65	0.42±0.04	11.00±0.63
Watered	5.81±0.07	5.71±1.64	5.68±0.63	12.44±1.06	5.44±0.30	31.25±2.15	0.13±0.02	75.71±5.68	6.90±0.52	0.37±0.02	10.87±0.64
Accession	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns
I-1	5.76±0.14	5.37±1.47	5.53±0.41	13.54±1.29	5.62±0.30	30.39±1.13	0.14±0.02	81.23±1.37	7.62±0.91	0.42±0.08	10.64±1.32
I-2	5.81±0.12	5.79±1.25	5.73±0.70	13.48±1.44	5.60±0.24	31.56±2.06	0.14±0.03	78.72±3.33	7.61±0.70	0.40±0.05	11.07±0.65
I-3	5.80±0.08	6.03±0.85	5.48±0.49	13.55±1.45	5.59±0.22	32.31±1.43	0.13±0.02	76.31±4.98	7.54±0.94	0.40±0.04	10.86±0.70
II-1	5.82±0.09	5.99±1.13	5.86±0.87	12.69±1.81	5.33±0.20	30.74±2.09	0.13±0.02	77.92±6.21	7.26±0.79	0.38±0.06	11.12±0.43
II-2	5.80±0.03	5.92±2.08	5.62±0.50	12.59±1.16	5.33±0.13	31.65±2.33	0.14±0.01	74.61±4.97	7.00±0.90	0.38±0.04	10.59±0.45
II-3	5.81±0.04	5.89±0.79	5.85±0.26	12.29±0.56	5.17±0.25	31.52±0.94	0.13±0.02	74.02±3.36	7.16±0.71	0.38±0.02	10.84±0.57
III-1	5.77±0.09	5.90±0.92	6.02±0.66	12.32±2.45	5.18±0.52	31.15±3.34	0.13±0.02	75.77±7.17	7.29±1.38	0.37±0.04	11.28±0.87
III-2	5.79±0.10	6.26±2.16	5.76±0.43	12.66±0.42	5.46±0.24	32.95±2.95	0.12±0.03	72.91±6.56	7.27±0.46	0.38±0.02	11.10±0.23
III-3	5.75±0.07	6.43±2.42	5.44±0.44	13.75±1.87	5.63±0.23	30.83±1.51	0.14±0.01	80.47±3.82	7.82±0.91	0.40±0.04	11.27±0.47
IV-1	5.78±0.07	6.03±1.90	5.70±0.45	12.88±1.58	5.40±0.23	32.60±1.61	0.13±0.03	73.71±6.25	7.70±1.14	0.41±0.04	11.00±0.60
IV-2	5.78±0.05	6.51±1.38	5.60±0.60	13.18±0.78	5.64±0.14	32.03±0.78	0.14±0.02	76.28±3.00	7.77±0.54	0.42±0.03	10.79±0.30
IV-3	5.82±0.04	7.66±1.54	5.70±0.37	13.42±1.05	5.67±0.25	31.56±2.79	0.13±0.01	78.82±4.70	7.39±0.78	0.40±0.03	10.64±0.73
Mean	5.79	6.15	5.69	13.03	5.47	31.61	0.13	76.73	7.45	0.40	10.93
CV (%)	0.85	11.69	4.56	4.87	4.79	6.19	12.41	7.40	5.69	4.58	6.68
Shade*irr	***	*	***	*	Ns	Ns	***	Ns	Ns	***	Ns
Shade*acc	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns
Irr*acc	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns

Ns = Not significant; *P<0.05 significance level; **P<0.01 significance level and ***P<0.001 significance level. Means with the same letter(s) within a row are not significantly different at P = 0.05 significance levelLeaf composition

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The results of the irrigation treatment analysis show no significant differences for most leaf compositions when independently analysed for moderate shade conditions, whereas Ca, Mg (P<0.0001) and P (P<0.01) were significantly higher in drought stressed seedlings than in well-watered ones. The level of shade modified the type and degree of correlation between soil and leaf parameters of the same coffee accession. Accordingly, most leaf compositions were more related to soil chemical conditions in the full sun plots, indicating enhanced physiological processes and increased dependency on soil conditions. The overall one- and two-way analyses of variances for shade, irrigation and coffee accession are presented in Table 7.10. Accordingly, shade and sun leaves showed significant variations in leaf OM (P<0.05), K (P<0.01) and N (P<0.01). As a consequence, higher leaf OM (8.41±0.47%), K (2.82±0.29%) and N (2.04±0.14%) were determined for sun than for shade leaves. Although the results are not statistically significant, a slightly higher Mg (0.23±0.04%g) content was found in shade than in sun leaves (0.22±0.04%). In contrast to most leaf compositions, higher Ca (0.74±0.17%) and P (0.57±0.13%) were determined in sun leaves, but this was not significant in shade leaves.

The uptake of the major nutrients by the coffee seedlings and leaf carbon assimilation were significantly higher with increased light intensity. In open sun, soil pH were negatively correlated with other soil chemical attributes. However, soil pH had significant and indirect influence on the concentration of the analyzed elements in sun-exposed seedlings. Leaf K was positively correlated with TN (r = 0.50*), available K (r = 0.052**) and EC (r = 0.43*), though it was negatively correlated to soil pH (r = -0.61**). In most cases, the correlations of leaf Ca and Mg with most soil parameters followed the same trend in both light regimes. In contrast, leaf P was negatively correlated to available soil P (r = -0.41*) and EC (r = -0.52**) of the potting medium in shade conditions (Table 7.11a). In the shade plot, the reverse was true and increased leaf phosphorus was measured with increased pH, which was consistent with the increased soil N contents.

On the other hand, the seedlings did not show significant variations for most leaf compositions, except K and phosphorus. However, relatively maximum average leaf dry matter was recorded in the Harenna, Bonga, Berhane-Kontir and Yayu accessions in that order. Accordingly, the lowest (7.39±0.75%) and highest

(8.54±0.97%) values were obtained from the Yayu and Harenna accessions, respectively. In addition, the concentration of K was significantly (P<0.01) different among accessions. Consequently, the lowest (2.37±0.18%) and highest (3.01±0.25%) values were determined for the accessions of Yayu and Bonga populations, respectively. The concentration of leaf K was higher than the optimum range of 1.5-2.5% (Clowes and Hill; 1981), although leaf Ca was inconsistent for accessions of the same or different populations; the highest (0.81±0.08%) and lowest (0.66±0.11%) values were obtained from the Yayu and Bonga seedlings. Accordingly, some accessions from each population revealed low leaf Ca below the reported optimum range of 0.7-1.5%. The results show relatively low Mg in the Harenna coffee accessions with mean values that range between 0.20±0.05 and 0.22±0.04% for I-1 and I-3, respectively. This is followed by the Bonga accessions as compared to the Berhane-Kontir and Yayu accessions. The concentration of leaf Mg was found to be within the optimum range (0.20-0.40%). Leaf N was inconsistent among accessions, the results ranging from 1.78±0.25 to 2.17±0.23% for Bonga (II-1) and Yayu (IV-4) seedlings, respectively. In all cases, leaf nitrogen was below the reported optimum range (2.5-3.0%). The other accessions showed intermediate results, thus their tolerance to drought stress could vary accordingly.

In addition, the interactive effect between shade and irrigation was significant for leaf organic matter contents, but not for other parameters. As a result, well-watered seedlings in sun-exposed plots showed great variations in leaf organic matter with 17.4% reductions over drought-stressed seedlings. This was in contrast to well-watered seedlings, which exhibited an increment of 16.0% in leaf organic matter for shade over sun plots. The effect of irrigation regimes was minimal in shaded seedlings, with little variation (1.4-2.8%) in leaf organic matter content.

On the other hand, there were no significant interactions between coffee accession and shade or accession and irrigation. However, most accessions accumulated higher dry mass in full sun and drought stressed conditions, except the higher results obtained from well-watered II-2 and IV-1 seedlings. Unlike the lowest value for the irrigated I-3, seedlings of III-2 and IV-3 accessions assimilated almost the same amount of dry matter both with and without irrigation. Similar to dry matter, leaf organic matter was relatively higher for drought stressed seedlings as compared to the irrigated

seedlings of all coffee accessions. In this case, the lowest organic matter (highest ash content) was obtained from irrigated I-3 seedlings as opposed to IV-2 and IV-3, which could probably be attributed to the variations in shoot and root characteristics and thus differing water consumption rates.

The concentrations of the major nutrients in the coffee leaves were slightly affected by irrigation treatments. Accordingly, relatively more K was measured in drought-stressed seedlings for all accessions, except in III-1, where the seedlings had higher K when irrigated. In all accessions, the concentrations of Mg and Ca followed the same pattern, and drought- stressed seedlings showed higher values, except IV-3 with about the same values with and without irrigation. In addition, drought stressed seedlings of most accessions, especially those from Harenna and Berhane-Kontir, revealed higher leaf nitrogen contents. In contrast, in the other accessions, particularly II-3 and III-3, seedlings showed minimum differences due to variations in the irrigation regimes.

Table 7.10   Leaf composition (%) (means±SD) in seedlings of coffee accessions according to shade and irrigation treatments

Water relations and hydraulic characteristics of coffee seedlings

Treatment	Dry mass	Organic matter	Potassium	Calcium	Magnesium	Nitrogen	Phosphorus
Shading	Ns	*	**	Ns	Ns	**	Ns
Sun	89.59±0.69	7.90±1.01b	2.66±0.19b	0.74±0.17	0.22±0.04	1.85±0.23b	0.57±0.13
Shade	89.23±0.58	8.41±0.47a	2.82±0.29a	0.69±0.11	0.23±0.04	2.04±0.14a	0.56±0.13
Irrigation	Ns	***	**	***	***	*	**
Stressed	89.55±0.63	8.59±0.48a	2.82±0.19a	0.82±0.11a	0.26±0.03a	2.00±0.21a	0.61±0.13a
Watered	89.27±0.66	7.71±0.86b	2.66±0.29b	0.61±0.09b	0.20±0.03b	1.88±0.20b	0.52±0.11b
Accession	Ns	Ns	*	Ns	Ns	Ns	*
I-1	89.80±0.38	8.54±0.97	2.89±0.21ab	0.72±0.27	0.20±0.05	1.89±0.19	0.64±0.08ab
I-2	89.70±0.39	8.45±0.93	2.93±0.19ab	0.72±0.18	0.21±0.05	2.04±0.32	0.74±0.09a
I-3	88.60±1.21	7.87±1.60	2.78±0.19ab	0.68±0.22	0.22±0.04	1.96±0.28	0.67±0.10ab
II-1	89.42±0.32	8.35±0.74	2.77±0.14abc	0.71±0.19	0.23±0.05	1.78±0.25	0.54±0.17ab
II-2	89.23±0.45	8.42±0.68	3.01±0.25 a	0.66±0.11	0.24±0.05	1.93±0.23	0.57±0.03ab
II-3	89.21±0.74	8.49±0.50	2.77±0.15abc	0.70±0.14	0.23±0.05	1.92±0.18	0.58±0.08ab
III-1	89.48±0.18	8.40±0.75	2.91±0.37ab	0.74±0.16	0.25±0.05	2.01±0.26	0.59±0.09ab
III-2	88.99±0.77	8.22±0.41	2.75±0.18abc	0.67±0.12	0.22±0.04	1.88±0.20	0.59±0.14ab
III-3	89.80±0.57	8.05±0.74	2.62±0.19abc	0.75±0.10	0.24±0.04	1.98±0.20	0.41±0.09b
IV-1	89.62±0.77	8.08±0.56	2.58±0.17bc	0.74±0.14	0.26±0.04	1.94±0.18	0.53±0.12ab
IV-2	89.51±0.45	7.39±0.75	2.37±0.18c	0.69±0.06	0.24±0.03	1.93±0.18	0.47±0.09b
IV-3	89.61±0.72	7.58±0.85	2.57±0.15bc	0.81±0.08	0.23±0.05	2.07±0.23	0.50±0.15ab
Mean	89.41	8.15	2.74	0.71	0.23	1.94	0.57
CV (%)	0.68	8.00	6.35	15.09	11.08	10.00	16.73
Shade*irr	Ns	**	Ns	Ns	Ns	Ns	Ns
Shade*acc	Ns	Ns	Ns	Ns	Ns	Ns	Ns
Irr*acc	Ns	Ns	Ns	Ns	Ns	Ns	Ns

Ns = not significant; *P<0.05; **P<0.01 and ***P<0.001 significance levels. Means with the same letter(s) within a column are not significantly different at P = 0.05 (Tukey test).

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In the sun plots, leaf nutrient composition was positively correlated with the concentration of the corresponding nutrient in the soil, i.e., TN (r = 60*), P (r = 0.05), K (r = 0.52**) and Ca (r = 0.74**). The status of nitrogen and phosphorous in the soil-plant system, however, was negatively correlated in the shade plots where the correlation was significant for P (r = -0.41*). Soil-plant Mg content was negatively correlated in both shade and sun plots, but not significantly.

Table 7.11   Pearson correlation value (r) between soil and leaf composition in coffee seedlings as influenced by (a) shade and (b) irrigation treatments

a)   Shade level

Shade regime	Soil variable	Leaf composition							
		DM	OM	Ash	K	Ca	Mg	N	P
Sun	TN	0.31	0.64**	-0.64**	0.50*	0.84**	0.64**	0.60**	0.21
Shade		0.16	-0.12	0.12	-0.31	0.46*	0.46*	-0.08	-0.04
Sun	AP	0.19	0.42*	-0.42*	0.40	0.62**	0.51*	0.51*	0.05
Shade		-0.01	-0.31	0.31	-0.27	0.29	0.29	0.39	-0.41*
Sun	K	0.19	0.53**	-0.53**	0.52**	0.32	0.48*	0.41*	0.20
Shade		0.15	0.04	-0.04	0.02	-0.46*	-0.37	0.12	0.00
Sun	Ca	0.26	0.49*	-0.49*	0.34	0.74**	0.53**	0.47*	0.19
Shade		0.01	-0.19	0.19	-0.34	0.38	0.26	-0.18	0.03
Sun	Mg	-0.02	-0.23	0.23	-0.22	0.12	-0.13	0.05	-0.03
Shade		0.11	-0.20	0.20	-0.26	0.12	-0.04	-0.30	-0.16
Sun	OM	0.23	0.54**	-0.54**	0.36	0.72**	0.67**	0.46*	0.17
Shade		0.07	-0.09	0.09	-0.23	0.53**	0.54**	-0.13	0.11
Sun	CEC	0.34	0.29	-0.29	0.14	0.43*	0.42*	0.52**	0.16
Shade		-0.46*	-0.20	0.20	-0.18	-0.16	-0.13	-0.30	-0.11
Sun	EC	0.39	0.58**	-0.58**	0.43*	0.70**	0.65**	0.48*	0.14
Shade		0.08	-0.12	0.12	-0.08	-0.66**	-0.68**	-0.12	-0.52**
Sun	pH	-0.35	-0.77**	0.77**	-0.61**	-0.83**	-0.62**	-0.65**	-0.30
Shade		0.32	0.30	-0.30	0.13	0.22	0.22	-0.28	0.55**
Sun	BS	-0.09	0.13	-0.13	0.16	0.18	0.05	-0.07	0.01
Shade		0.46*	0.04	-0.04	-0.09	0.27	0.16	0.14	0.09
Sun	OC	0.23	0.54**	-0.54**	0.36	0.72**	0.67**	0.46*	0.17
Shade		0.07	-0.09	0.09	-0.23	0.53**	0.54**	-0.13	0.11
Sun	C:N	-0.22	-0.30	0.30	-0.32	-0.39	-0.15	-0.38	-0.08
Shade		-0.07	-0.01	0.01	-0.03	0.33	0.36	-0.10	0.24

*P<0.05; **P<0.01 significant levels (2-tailed). Abbreviations: DM = dry matter, OM = organic matter, CEC = cation exchange capacity, EC = electrical conductivity, OC = organic carbon, TN = total nitrogen, .AP = available P, BS = base saturation, C:N = carbon to nitrogen ratio.

b)   Irrigation level

Irrigation	Soil variable	Leaf composition						
		DM	OM	K	Ca	Mg	N	P
Stressed	TN	0.48*	0.24	-0.09	0.69**	-0.22	0.02	-0.12
Watered		-0.03	-0.30	-0.32	0.02	-0.22	-0.02	0.12
Stressed	AP	-0.08	-0.14	0.19	-0.24	0.18	0.33	-0.20
Watered		-0.48*	-0.20	0.01	-0.31	0.07	0.18	0.26
Stressed	K	-0.22	-0.26	-0.15	-0.44*	0.27	0.24	0.20
Watered		-0.31	0.03	0.35	-0.40	0.14	0.04	0.20
Stressed	Ca	0.45*	0.21	-0.12	0.59**	-0.23	-0.12	-0.12
Watered		0.25	0.03	-0.27	0.39	-0.42*	0.08	-0.01
Stressed	Mg	0.36	-0.18	0.11	0.14	-0.39	-0.13	-0.19
Watered		-0.13	0.04	-0.13	0.21	-0.31	0.30	0.27
Stressed	M	0.43*	0.03	-0.26	0.41*	-0.18	-0.30	-0.21
Watered		0.42*	-0.00	-0.29	0.49*	-0.39	0.05	0.08
Stressed	CEC	0.10	0.03	-0.20	0.09	-0.35	-0.11	0.13
Watered		-0.21	-0.55**	-0.28	-0.18	-0.17	-0.22	0.15
Stressed	EC	0.47*	0.22	-0.11	0.50*	0.07	0.05	-0.05
Watered		-0.35	-0.30	0.14	-0.44*	0.07	-0.03	0.13
Stressed	pH	-0.24	-0.46*	0.13	-0.78**	0.01	-0.25	-0.08
Watered		0.28	0.20	0.04	0.30	-0.30	-0.14	-0.07
Stressed	BS	0.37	0.09	0.06	0.43*	0.10	0.02	-0.24
Watered		0.19	0.54**	0.19	0.31	-0.10	0.29	-0.02
Stressed	OC	0.43*	0.03	-0.26	0.41*	-0.18	-0.30	-0.21
Watered		0.42*	-0.00	-0.29	0.49*	-0.39	0.05	0.08
Stressed	C:N	-0.08	-0.24	-0.20	-0.38	0.03	-0.43*	-0.08
Watered		0.57**	0.31	-0.07	0.63**	-0.29	0.08	-0.02

*P<0.05; **P<0.01 significant levels (2- tailed).*

From the nutrient relationships between soil and leaves, not only the status of nutrients in the soil, butt also the availability of moisture was found to influence the uptake and accumulation pattern of plant nutrients. Except N and Ca, the other nutrients (P, K, Mg) in the soil-plant systems were negatively correlated due to soil drying, indicating the role of water in the nutrient uptake of plants. For instance, the C:N ratio was negatively and significantly (r = -0.43*) correlated with leaf N, indicating that soil N can be taken up in the form of dissolved ions. This could be evidenced from the direct and positive relations between C:N ratio and leaf Ca content and dry mass accumulation in the irrigated seedlings. There was a slightly positive relation between soil and leaf nitrogen (r = -0.02) in drought-stressed seedlings as opposed to the trend in the irrigated pots (r = 0.02). Similarly, leaf Ca was significantly (r = 0.59**) increased in drought stressed plots. This corresponds with the correlation between base saturation and SOM in the pots. In the dried soils, pH was found to indirectly affect all leaf compositions,

except K and Mg; correlations were significant for leaf Ca (r = -0.78**) and leaf organic matter (r = -0.46*). In wet soil, base saturation was highly positively (r = 0.54**) correlated with leaf OM (Table 7.11b).

7.4.7   Hydraulic measurements

Hydraulic resistance

The results reveal that shade regimes significantly (P<0.01) influenced the hydraulic resistances in the whole shoot and in its various parts, but not in the root and whole plant. However, maximum root values were recorded for sun seedlings as compared with those in shade environments. Whole-plant and shoot resistances were higher in seedlings maintained in moderate shade than those in full sun. Hence, sun and shade seedlings exhibited the respective reductions in shoot hydraulic resistances from 8.12×10^4 MPa m^2 s kg^{-1} to 2.32×10^4 MPa m^2 s kg^{-1} and 9.61×10^4 MPa m^2 s kg^{-1} to 3.09×10^4 MPa m^2 s kg^{-1} due to the removal of leaves, petioles and primary branches (Table 7.12). This could be attributed to the significantly (P<0.001) maximum main stem diameter, thick leaves and high dry mass in the sun-exposed seedlings.

The lowest hydraulic resistances (highest conductances) were recorded for the reduced main stem length (20 cm), and the results are significantly (P< 0.01) different according to shade level. Hence, the respective values of 1.64×10^4 MPa m^2 s kg^{-1} and 2.24×10^4 MPa m^2 s kg^{-1} were measured for sun and shade seedlings. Likewise, significantly (P<0.01) minimum (2.43×10^4 MPa m^2 s kg^{-1}) and maximum (4.45×10^4 MPa m^2 s kg^{-1}) main stem specific hydraulic resistances were determined for sun and shade seedlings, respectively. This is in line with the variation in stem diameter. In the contrast, root hydraulic resistance did not show significant differences between the shade levels, though the respective maximum (1.44×10^5 MPa m^2 s kg^{-1}) and minimum (1.32×10^4 MPa m^2 s kg^{-1}) results were found for sun-exposed and shade seedlings. In addition, the leaf-specific hydraulic resistance was significantly (P<0.01) higher in shade (1.61 MPa m^2 s kg^{-1}) than in sun (1.09 MPa m^2 s kg^{-1}) seedlings (Table 7.12). Similarly, shade treatments did not affect whole-plant resistance, though the maximum value (2.29×10^5 MPa m^2 s kg^{-1}) was recorded for shade seedlings.

The results of resistance contributions show different patterns for shade and different plant components. The contribution of root and shoot resistances also varied significantly ($P<0.01$) between shade levels, and an inverse trend in root and whole-plant was observed. The percent root resistance of the whole plant was significantly ($P<0.01$) higher in sun (63.3%) than in shade seedlings (57.3%). Similarly, significantly maximum leaf resistance (58.5%) of the shoot was recorded in full sun as compared with shade leaves (55.1%). However, petioles and branches did not differ due to shade levels, though relatively higher resistance contributions of petioles (2.2%) and branches (10.8%) were recorded from open sun-exposed seedlings than from those in the shade. In contrast, higher shoot (42.8%) and main stem cut resistances were obtained from seedlings maintained in moderate shade than from sun-exposed seedlings (Table 7.12). This could be attributed to the reduced vapor pressure gradients and thus water demands between the plant and the atmosphere.

Table 7.12   Hydraulic resistance (R_h, mean$\pm$SDx10^4MPa m^2 s kg^{-1}) in root and shoot components of coffee seedlings and their contributions (%) to whole-plant hydraulic resistance in the sun and shade conditions

Plant part	Shade regime		Pr>F
Resistance (R)	Sun	Shade	
Whole-plant, R_{wp}	22.5$\pm$3.40	22.9$\pm$5.46	Ns
Root, R_r	14.4$\pm$3.05	13.2$\pm$4.06	Ns
Whole-shoot, R_{WS}	8.12$\pm$0.99 b	9.61$\pm$1.82 a	**
Leaf, R_l	3.38$\pm$0.54 b	4.28$\pm$0.75 a	**
Petiole, R_p	3.20$\pm$1.82 b	4.10$\pm$0.54 a	**
Branch, R_{br}	2.32$\pm$0.42 b	3.09$\pm$0.64 a	**
Stem cut, R_{msc}	1.64$\pm$0.33 b	2.24$\pm$0.63 a	**
Contribution (%)			
Root, R_r	63.26$\pm$5.93 a	57.26$\pm$5.94 b	*
Whole-shoot, R_{WS}	36.74$\pm$5.93 b	42.75$\pm$5.94 a	*
Leaf, R_l	58.53$\pm$2.56a	55.14$\pm$3.70b	*
Petiole, R_p	2.22$\pm$0.37	1.93$\pm$0.38	Ns
Branch, R_{br}	10.78$\pm$1.20	10.71$\pm$1.63	Ns
Stem cut, R_{msc}	8.38$\pm$1.69	9.10$\pm$3.10	Ns

Ns = Not significant, *, **, *** = significant at P<0.05, P<0.01 and P<0.001, respectively. Means with different letter within a row are significantly different from each other (Tukey test at P = 0.05).

There was no difference among coffee accessions in patterns of whole-plant hydraulic resistance. However, low and high values were found for the Harenna

$(1.76 \times 10^5$ MPa m^2 s kg^{-1}) and Bonga accessions (II-2 = 2.79×10^5 MPa m^2 s kg^{-1}, II-3 = 2.94×10^5 MPa m^2 s kg^{-1}), followed by Yayu and Berhane-Kontir. On the other hand, seedlings of different accessions did not significantly vary in root and shoot hydraulic resistance. However, the lowest and the highest mean root resistances were measured for the Harenna (I-1 = 8.85×10^4 MPa m^2 s kg^{-1}, I-2 = 1.05×10^5 MPa m^2 s kg^{-1}) and Bonga (II-2 = 1.78×10^5 MPa m^2 s kg^{-1}, II-3 = 1.85×10^5 MPa m^2 s kg^{-1}) accessions, respectively (Table 7.13a). Similarly, the resistances in the whole-shoot, leaves, petioles, primary branches and stem cut were higher for the Bonga accessions (II-2 and II-3). On the other hand, minimum shoot resistances were obtained from the Harenna accessions, suggesting that maximum water transport is proportional to allocation to maximum photosynthetic capacity of such accessions. The removal of various shoot components was seen to reduce resistance, though the magnitude insignificantly differed among accessions. Seedlings from Bonga (II-1 = 2.43×10^4 MPa m^2 s kg^{-1}, II-2 = 2.77×10^4 MPa m^2 s kg^{-1}), Berhane-Kontir (2.13×10^4 MPa m^2 s kg^{-1}) and Yayu (IV-2 = 2.10×10^4 MPa m^2 s kg^{-1}, IV-3 = 2.09×10^4 MPa m^2 s kg^{-1}) populations had maximum main stem cut (20 cm) hydraulic resistances in that order (Table 7.13a). In contrast, resistances were relatively low for the Harenna accessions with mean values ranging between 1.33×10^4 MPa m^2 s kg^{-1} (I-2) and 1.56×10^4 MPa m^2 s kg^{-1} (I-3), whereas the Bonga and Berhane-Kontir accessions had relatively higher resistances in the whole-shoot, but exhibited low resistances in the other shoot parts. This might largely be due to the variation in stem basal diameter and other shoot morphological characteristics.

Seedlings were not significantly different regarding the contributions of hydraulic resistances in roots, whole shoot and shoot segments. However, a maximum root contribution was associated with a minimum shoot resistance in all seedlings, though the differences varied among accessions. The highest root (69.4%), lowest shoot (30.6%) and leaf (52.8%) resistance contributions were determined from accession I-3 of the Harenna population (Table 7.13b). This is in contrast to the highest leaf resistance contribution (62.2%) and lowest petiole resistance (1.5%) obtained from Bonga accession II-1. On the other hand, a relatively maximum resistance contribution in petiole (2.5%) and lateral branch (12.3%) was recorded for the Berhane-Kontir accession, followed by Yayu. Root hydraulic resistance showed a negative correlation with all the root traits considered, though it was significant between root fresh weight,

root volume and length of lateral roots. The resistance contribution of the main stem-cut to whole-shoot resistance was significantly (P<0.05) different among coffee accessions. Hence, significantly the lowest (5.3%) and the highest (13.2%) stem-cut contributions were measured from Bonga and Harenna accessions, respectively. There were no significant differences among the other accessions. In general, the resistance in roots, shoot, leaf, petiole and lateral branch followed similar patterns in most accessions with average contributions of 60.3, 56.8, 39.7, 10.8 and 2.1%, respectively (Table 7.13b).

Table 7.13.   Hydraulic resistance (R_h, means$\pm$SDx10^4 MPa m^2 s kg^{-1}) in root and shoot segments (a) and their percent contributions to whole-plant and whole-shoot resistances (b) in seedlings of the coffee accessions

a)   Resistance component

Acc	R_{WP}	R_r	R_{WS}	R_l	R_p	R_{br}	R_{msc}
I-1	17.6±2.90	8.85±1.36	8.71±1.50	3.72±0.94	3.53±0.88	2.74±0.68	1.57±0.21
I-2	17.5±4.60	10.5±4.57	7.01±0.01	2.97±0.35	2.84±0.39	2.05±0.32	1.33±0.26
I-3	21.0±4.24	14.7±3.61	6.38±0.64	3.00±0.01	2.86±0.01	2.14±0.01	1.56±0.01
II-1	21.0±3.96	11.8±2.55	9.18±1.45	3.47±0.60	3.33±0.59	2.43±0.61	1.95±0.57
II-2	27.9±8.70	17.8±5.09	10.0±3.63	4.26±1.70	4.09±1.73	3.03±1.51	2.43±1.45
II-3	29.4±1.77	18.5±0.85	10.9±0.92	4.79±0.49	4.55±0.50	3.53±0.61	2.77±0.58
III-1	23.6±1.77	14.4±3.32	9.21±1.55	3.98±0.64	3.76±0.60	2.63±0.48	1.74±0.29
III-2	23.8±1.77	14.0±0.78	9.81±0.98	4.03±0.19	3.83±0.21	2.82±0.13	2.13±0.33
III-3	21.3±4.46	13.0±5.42	8.30±0.95	3.51±0.77	3.35±0.76	2.43±0.64	1.78±0.32
IV-1	24.4±1.06	15.4±0.42	8.97±0.59	3.96±0.26	3.75±0.21	2.77±0.27	1.88±0.27
IV-2	20.7±0.14	11.7±1.34	9.07±1.46	4.28±0.96	4.10±0.88	3.02±0.71	2.10±0.44
IV-3	24.2±0.01	15.2±1.41	8.90±1.48	4.02±1.28	3.82±1.29	2.91±1.24	2.09±0.88
Pr>F	Ns	Ns	Ns	Ns	Ns	Ns	Ns
Mean	22.7	13.8	8.87	3.83	3.65	2.71	1.94
CV (%)	17.26	22.54	12.89	14.16	14.56	18.54	22.52

The symbols of resistances include: whole-plant (R_{WP}), root (R_r), whole-shoot (R_{WS}), leaf (R_l), petiole (R_p), branch (R_{br}) and main stem cut (R_{msc}).

b)   Percent resistance contribution

Accession	Root	Shoot	Leaf	Petiole	Branch	Stem-cut
I-1	50.44±0.47	49.56±0.47	57.65±3.46	2.07±0.33	9.08±0.71	13.23±3.16a
I-2	58.43±10.78	41.57±10.78	57.60±5.13	1.96±0.55	11.28±1.03	10.28±0.83ab
I-3	69.38±3.12	30.63±3.12	52.75±5.02	2.27±0.10	11.35±3.32	9.17±0.29ab
II-1	56.20±1.47	43.80±1.47	62.24±0.74	1.51±0.04	9.95±1.82	5.30±0.40b
II-2	64.27±1.83	35.74±1.83	57.82±1.65	1.94±1.05	10.88±1.68	6.33±1.75ab
II-3	63.02±0.87	36.99±0.87	55.99±0.78	2.25±0.29	9.40±1.74	7.02±0.40ab
III-1	60.51±9.62	39.49±9.62	56.73±0.37	2.45±0.03	12.31±0.72	9.72±0.40ab
III-2	58.76±0.95	41.25±0.95	58.79±2.07	2.01±0.41	10.38±0.15	7.16±2.76ab
III-3	59.57±12.91	40.43±12.91	58.02±4.52	1.94±0.05	11.08±0.19	7.73±2.96ab
IV-1	63.19±0.82	36.81±0.82	55.85±0.01	2.34±0.32	11.01±1.31	9.95±0.65ab
IV-2	56.23±6.72	43.77±6.72	53.12±2.91	2.00±0.45	11.82±0.06	10.04±1.25ab
IV-3	63.12±6.00	36.88±6.00	55.49±7.01	2.17±0.44	10.44±1.17	8.99±2.45ab
Pr>F	Ns	Ns	Ns	Ns	Ns	*
Mean	60.26	39.74	56.83	2.07	10.75	8.74
CV (%)	8.03	12.18	4.77	19.37	14.13	20.56

*Ns = Not significant, * = significant at P<0.05. Means with the same letter within each column are not significantly different according to Tukey test at P = 0.05.*

Hydraulic resisntaces in roots and shoot segments showed inverse relations with most extension and destructive growth parameters (Tables 7.14a, 7.14b), though the degree of correlation differed. Among the extension growths, only the number of main tem nodes and main stem internode length were weakly postively correlated with the hydraulic resistances in the whole shoot and its segements. Moisture contensts in leaf, stem and roots were positively correlated with the hydraulic resistances in the whole plant, root and shoot components (Table 7.14b), while all other parameters were negatively correlated. The results reveal that main stem hydraulic resistance was negatively and significantly correlated (Table 7.14b) with stem fresh weight (r = -0.75**) and stem volume (r = -0.81**). The indirect influence of root dry weight, fresh weight and volume was highly significant in that order on hydraulic resistances in root and shoot systems. Lateral root length showed strong (P<0.05) correlations with hydaulic resistances in roots, whole shoot and whole plant. The linear relationships between hydraulic resistances in whole plant, leaf and stem-cut and root to shoot ratio as well as total dry matter yield are presented in Figure 7.16. In addition, main stem diameter had inverse and significant (P<0.01) linear relationships with hydraulic resistance components in main stem cut, whole-shoot, leaf and root parts descending in that order of coffecient of determination (Table 7.14b; Figure 7.17), demonstrating trade-offs between hydraulic capacity and photosynthetic rate. The results show the influence of plant vigor and quality on water movement in coffee seedlings.

Table 7.14   Pearson correlation coefficient between hydraulic resistance in the root and shoot components and (a) extension and b) destructive growth parameters of well-watered coffee seedlings

a) Extension shoot growth

Character	Root	Shoot	Leaf	Petiole	Branch	Stem cut	Whole plant
Ht	-0.62**	-0.47*	-0.30	-0.29	-0.22	-0.42*	-0.67***
BA	-0.53**	-0.72***	-0.67***	-0.67***	-0.64**	-0.77***	-0.69***
NMSN	-0.42*	0.11	0.11	0.12	0.08	0.03	-0.29
NPrBr	-0.12	-0.35	-0.35	-0.34	-0.29	-0.22	-0.22
NBrN	-0.27	-0.35	-0.30	-0.30	-0.33	-0.29	-0.34
PrBrIL	-0.44*	-0.37	-0.24	-0.24	-0.19	-0.40	-0.49*
MSIL	-0.09	0.05	0.08	0.10	0.14	0.14	-0.06
LN	0.01	-0.47*	-0.50*	-0.51*	-0.51*	-0.41*	-0.16
TLA/LAI	-0.19	-0.41*	-0.39	-0.39	-0.35	-0.245	-0.30

*P<0.05; **P<0.01; ***P<0.001 significance levels (n = 12, d.f. = 10). Abbreviations: Ht = height, BA = basal area, NMSN = number of main stem nodes, NPrBr = number of primary branches, NBrN = number of branch nodes, PrBrIL = primary branch internode length, MSIL = main stem internode length, LN = leaf number, TLA = total leaf area, LAI = leaf area index.

b) Root and shoot growth (destructive parameters)

Character	Root	Whole shoot	Leaf	Petiole	Branch	Stem cut	Whole plant
LFW	-0.14	-0.79***	-0.84***	-0.83***	-0.78***	-0.66***	-0.40
LDW	-0.17	-0.68***	-0.74***	-0.74***	-0.71***	-0.61**	-0.39
SFW	-0.54**	-0.83***	-0.81***	-0.80***	-0.75***	-0.81***	-0.74***
SDW	-0.50*	-0.80***	-0.79***	-0.79***	-0.76***	-0.82***	-0.69***
RFW	-0.45*	-0.72***	-0.71***	-0.71***	-0.68***	-0.72***	-0.62**
RDW	-0.37	-0.82***	-0.85***	-0.85***	-0.83***	-0.85***	-0.60**
RV	-0.48*	-0.67***	-0.66***	-0.65**	-0.63**	-0.68***	-0.63**
TRL	-0.17	-0.15	-0.22	-0.23	-0.22	-0.29	-0.19
LRN	-0.12	-0.11	-0.05	-0.04	-0.02	-0.08	-0.13
LRL	-0.46*	-0.43*	-0.36	-0.34	-0.30	-0.37	-0.53**
TDM	-0.40	-0.83***	-0.86***	-0.86***	-0.83***	-0.83***	-0.63**
R:S	-0.25	-0.54**	-0.55**	-0.57**	-0.59**	-0.70**	-0.40
LMC	0.25	0.28	0.32	0.32	0.34	0.32	0.30
SMC	0.05	0.14	0.15	0.16	0.22	0.25	0.10
RMC	0.01	0.40	0.44*	0.46*	0.49*	0.50*	0.15
SCFW	-0.54**	-0.75***	-0.65**	-0.66**	-0.64**	-0.75***	-0.70***
SCV	-0.41*	-0.82***	-0.80***	-0.79***	-0.76***	-0.81***	-0.63**

*P<0.05; **P<0.01; ***P<0.001. Abbreviations: LFW = leaf fresh weight, LDW = leaf dry weight, SFW = stem fresh weight, SDW = stem dry weight, RFW = root fresh weight, RDW = root dry weight, RV = root volume, TRL = taproot length, LRN = lateral root number, LRL = lateral root length, TDM = total dry matter, R:S = root to shoot, LMC = leaf moisture content, SMC = stem moisture content, RMC = root moisture content, SCFW = stem cut fresh weight, SCV = stem cut volume.
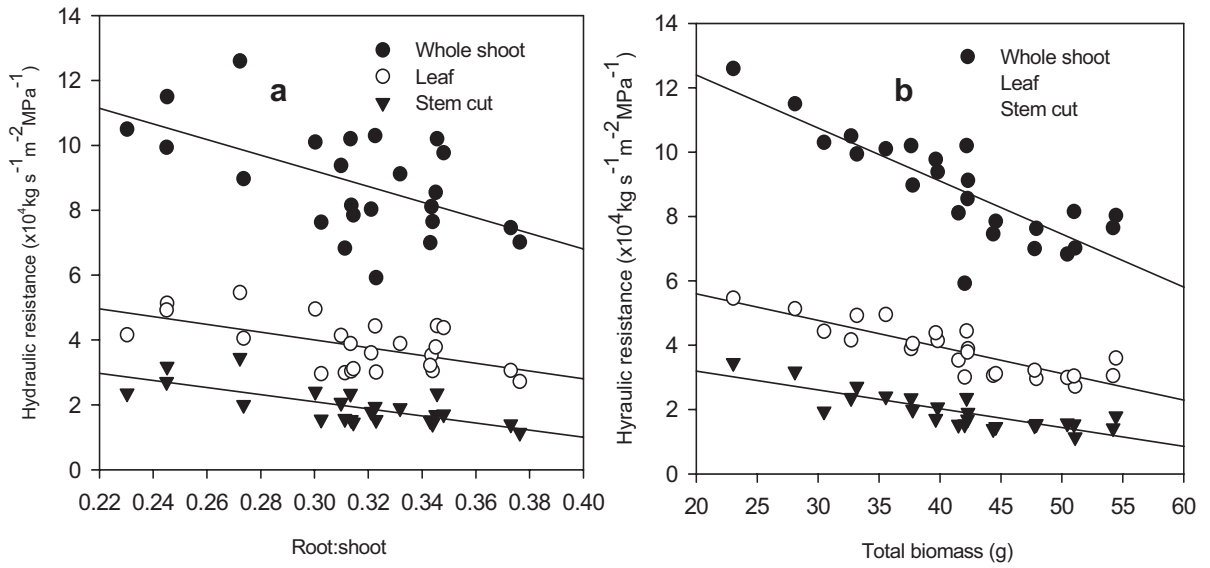
Figure 7.16   Whole-shoot, leaf and stem-cut hydraulic resistances as function of a) root to shoot ratio and b) total dry matter yield of coffee seedlings
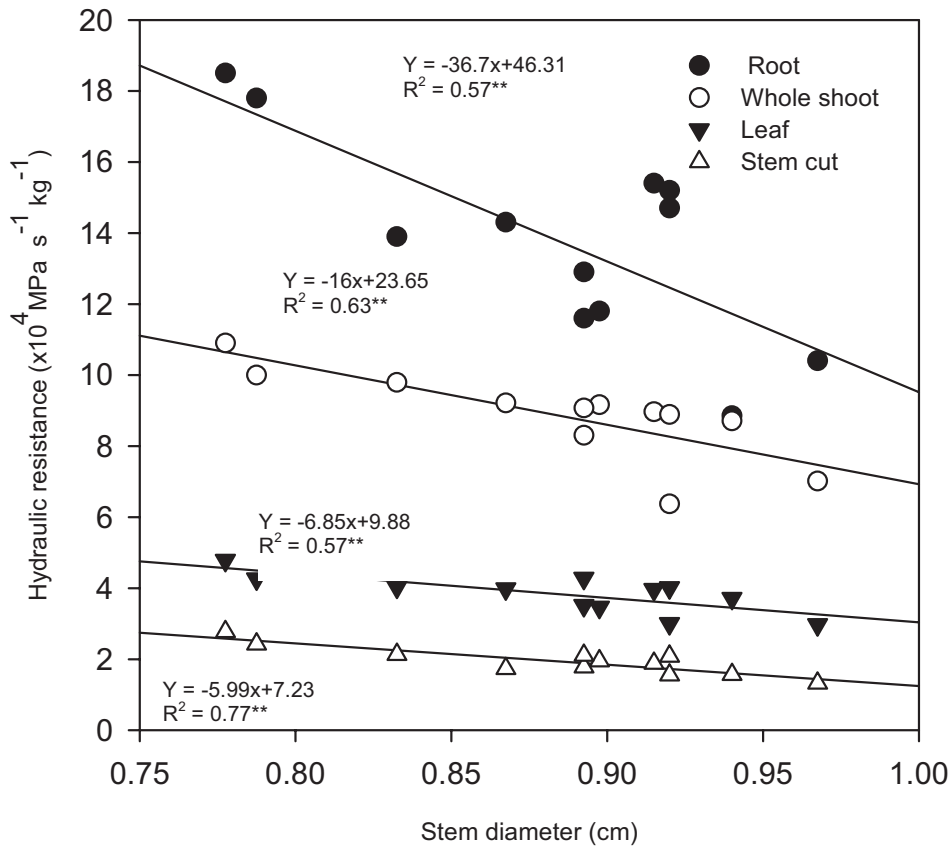
Figure 7.17   Relationships between stem diameter and hydraulic resistance in root and shoot segments of coffee seedlings

The results of the cluster analysis of the accessions using hydraulic resistance characteristics indicate the close similarity between the Yayu and Berhane-Kontir coffee populations. This was because about 67% of the accessions from these forests were clustered in group 1 (III-1, III-2, IV-1 and IV-3). In addition, the remaining accessions were categorized in group 2 (I-3, II-1, III-3 and IV-2). On the other hand, groups 3 and 4 were comprised of Bonga (II-2 and II-3) and Harenna (I-1 and I-2) accessions, respectively (Figure 7.18). This is in line with the principal component analysis (Figure 6.16) and cluster analysis (Figure 6.17) of the same coffee accessions based on the results of morphological growth parameters (Chapter 6).
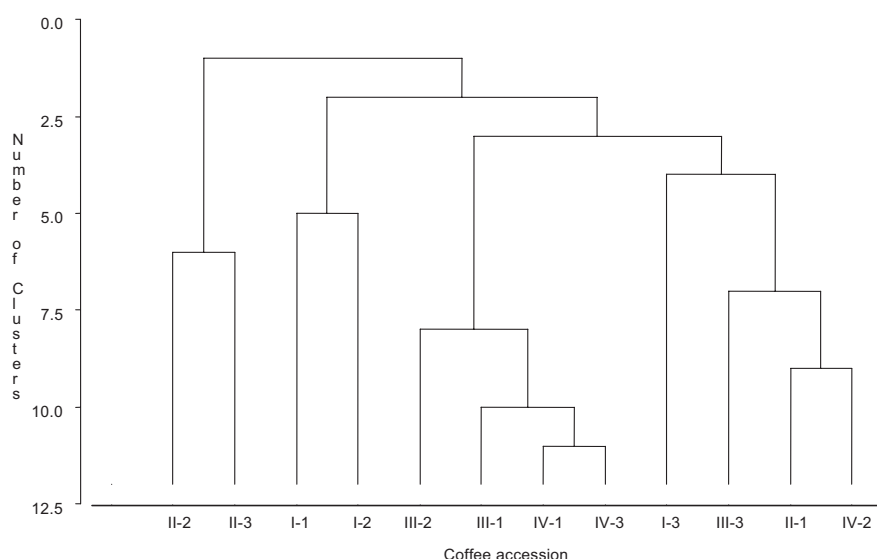
Figure 7.18   Dendrogram for average linkage cluster analysis of coffee accession based on hydraulic resistance characteristics

Hydraulic conductance

The results of the ANOVA show significant differences ($P<0.01$) between shade levels 4 and 8 DAI (Table 7.15). Similarly, on 4 DAI, significant differences ($P<0.05$) were obsereved among accessions and between accession and irrigation (Figure 7.19). Except I-1, II-2 and III-1 for which conductance was significantly reduced, all accessions had higher whole-plant hydraulic conductances in drought-stressed than in the well-watered conditions. This was particularly true for drought-stressed accessions such as IV-1, III-2, I-3 and I-2 in that order, whereas, significantly reduced whole-plant hydraulic

conductances were recored for IV-2, II-1 and III-2. Therafter, no statistically significant variations were observed , neither due to main nor treatment interaction, except the significant (P<0.05) results between shade and irrigation occurring on 8 DAI when drought-stressed seedlings in the sun plot showed values that were significantly different to those of the other treatments (Figure 7.20).

The analysis of variance for hydraulic conductance in root and shoot parts of the coffee seedlings revealed variations due to effect of shading, irrigation and accessions with varying levels of significance. However, interactions were not significant, expect between shade and irrigation effect upon the removal of all lateral branches. Accordingly, except in the main stem cut, significant variations were observed in root (P≤0.05), whole shoot (P≤0.001), leaf (P≤0.001), petiole (P≤0.05) and primary branch (P≤0.001) due to shade regimes. Sun-exposed seedlings exhibited higher water flow both in root and shoot parts. Similarly, the influence of irrigation was significant (P≤0.001), whereby root and shoot hydraulic flows were higher in drought stressed than in well-watered seedlings, which means that application of water raised leaf water potentials and the seedlings were less sensitive to changes in light conditions. This was evident from the weak and indirect correlation between soil moisture and whole-plant hydraulic conductance in moderately drought stressed seedlings (8 DAI).

On the other hand, coffee accessions were comparable in the amount of water flow to root and shoot systems. Nontheless, a significant difference (P≤0.05) was found due to removal of all primary branches and reduction of the main stem length. Consequently, the highest (4.39×10^{-5}kg s^{-1}m^{-2}MPa^{-1}) and lowest (2.91×10^{-5}kg s^{-1} m^{-2} MPa^{-1}) hydraulic conductances for the stem-cut were measured for the Harenna (I-2) and Yayu (IV-3) accessions, respectively. Root and shoot hydraulic patterns were inconsistent among accessions, though the overall average value was slightly higher in the whole-shoot (3.90×10^{-5}kg s^{-1}m^{-2}MPa^{-1}) than in the root (3.60×10^{-5}kg s^{-1}m^{-2} MPa^{-1}) part (Table 7.16). Likewise, treatment interactions were not significant for root and shoot hydraulic conductances. However, the removal of primary branches from seedlings exposed to soil moisture deficits significantly enhanced water flow with values ranging from 3.68×10^{-5}kg s^{-1}m^{-2}MPa^{-1} to 2.99×10^{-5}kg s^{-1}m^{-2}MPa^{-1} in sun and shade seedlings, respectively. In contrast, conductance tended to decline in well-watered

seedlings both in sun and shade conditions with the respective average results of 2.13×10^{-5} kg s^{-1}m^{-2}MPa^{-1} and 2.28×10^{-5} kg s^{-1}m^{-2}MPa^{-1}.

Significant differences in hydraulic conductance in the different parts of the coffee seedlings were obtained on the 4 DAI (P<0.05) and 16 DAI (P<0.01), where significantly maximum average values were recorded in the roots (4.20×10^{-5} kg s^{-1} m^{-2} MPa^{-1}) and whole-shoots (3.85×10^{-5} kg s^{-1}m^{-2}MPa^{-1}), respectively. Similarly, at the inception of drought stress, the lowest hydraulic conductance (2.22×10^{-5} kg s^{-1}m^{-2}MPa^{-1}) was measured in the roots as compared to various shoot parts, though the values did not significantly differ. This was when maximum main stem hydraulic conductivity (4.24×10^{-5} kg s^{-1}m^{-2}MPa^{-1}) was also obtained from the 20-cm long stem cut, followed by the whole shoot (4.17×10^{-5} kg s^{-1}m^{-2}MPa^{-1}). In contrast, the lowest hydraulic conductance was measured in the petiole of coffee leaves throughout the experimental period, except at the beginning of the drying experiment when there was enough moisture in the potting medium. This low conductance was particularly noticeable with prolonged drying, when petioles showed the earliest drying symptoms. This could be due to the blocked water flow via the stalk of the leaf blade to the distal leaf surface leading to water storage in the stem of the seedlings.

In addition, relatively maximum root conductance was recorded between the 4 and 8 DAI where the respective lowest (2.90×10^{-5} kg s^{-1}m^{-2}MPa^{-1}) and highest (3.90×10^{-5} kg s^{-1}m^{-2}MPa^{-1}) overall average conductance results were determined (Table 7.15; Figure 7.20), which is in line with the significantly higher results in drought-stressed coffee seedlings. The transition in root-shoot hydraulic conductance patterns was determined 8 DAI when increased root hydraulic resistant was observed. As a whole, the findings show a negative relationship between root and shoot hydraulic conditions, where maximum conductance was recorded in drought stressed and well-watered seedlings, respectively. Furthermore, the contribution of shading in enhancing hydraulic conductance was greater during the early stages of drought, i.e., up to 8 DAI. This was when the conductance in shade seedlings began to surpass those in the sun. With a longer period of drought, however, the two irrigation regimes showed a more pronounced influence, thought root and shoot showed insignificant variations in hydraulic conductance.

In moderate shade conditions, hydraulic conductance in the roots and shoot of the coffee seedling did not show significant variations over the extended period of drought, except on 4 DAI (P<0.05). Contrarily, significant hydraulic conductance variations in root and shoot segments were displayed on 8 and 16 DAI. Consistently lower root and shoot hydraulic conductance was measured in well-watered than in drought-stressed seedlings. The variations in shoot components particularly between leaves and petioles, were also minimal and lowest even at the 16 DAI. The interaction between shade and irrigation was not significant at the beginning and 12 DAI, possibly reflecting the different responses of the root and shoot systems in relation to the magnitude of water tensions in the soil-plant system. However, significant differences were measured during the other experimental period when drought stressed seedlings showed maximum conductance as opposed to the well-watered ones both in full sun and shade conditions. This was the case in a point for the highly significant gap observed 8 DAI in the open sun plots, which suggests maximum threshold level of drought under such conditions. At 16 DAI, however, well-watered seedlings had significantly higher conductance than the drought-stressed and sun-exposed seedlings (Figure 7.20).

Table 7.15 Whole-plant hydraulic conductance (K_h, means±SDx10^{-5}kg s^{-1}m^{-2}MPa^{-1}) in seedlings of coffee accessions as affected by shade and irrigation levels during different days after irrigation (0-16 DAI)

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

*Ns = Not significant; *P<0.05; **P<0.01; ***P<0.001. Means with the same letter within a column are not significantly different according to Tukey test at P = 0.05.*
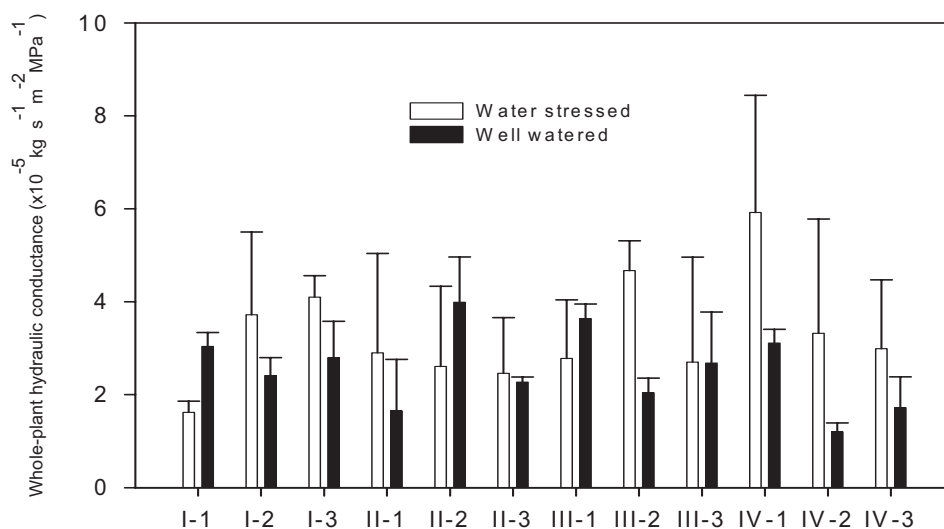
Figure 7.19   Whole-plant hydraulic conductance of coffee accessions in drought stressed (4 DAI) and well-watered seedlings
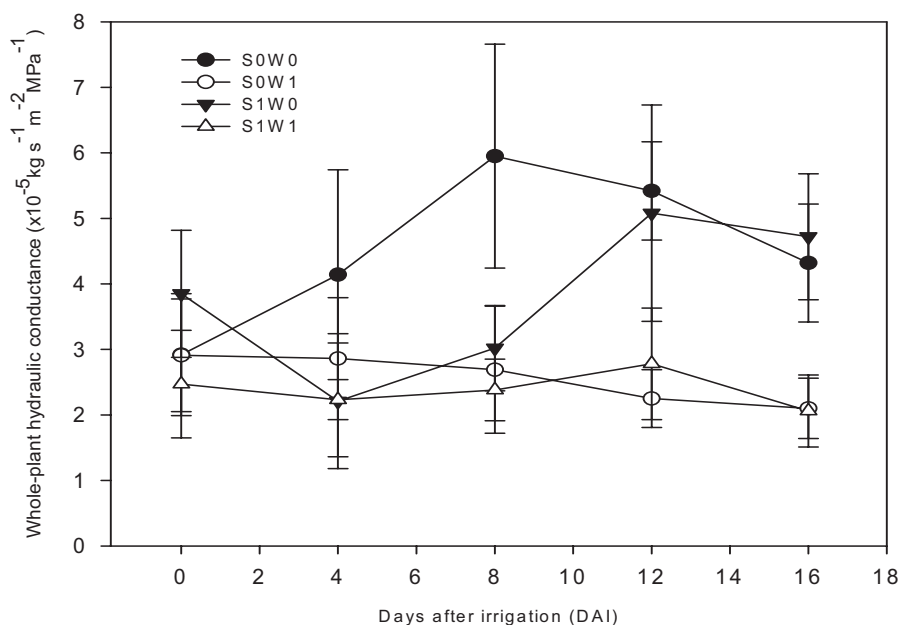
Figure 7.20   Interaction effect of shade and irrigation on whole-plant hydraulic conductance of coffee seedlings during the different days after irrigation. S0W0 = no shade not watered, S1W0 = with shade not watered, S0W1 = not shaded watered, S1W1 = with shade watered

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Table 7.16   Hydraulic conductance (K_h, means±SDx10^{-5}kg s^{-1}m^{-2}MPa^{-1}) in root and various shoot parts of coffee seedlings as influenced by shade, irrigation treatment and coffee accessions

Treatment	Root	Whole shoot	Leaf	Petiole	Branch	Stem cut
Irradiance	*	**	**	*	**	Ns
Sun	4.01±2.57a	4.15±1.11a	3.22±1.08a	2.98±8.65a	3.4±9.83a	3.66±7.95
Shade	3.11±1.91b	3.61±1.15b	2.67±8.69b	2.56±7.40b	2.94±7.39b	3.50±8.09
Irrigation	***	***	***	***	***	***
Stressed	5.40±1.73a	4.75±7.68a	3.74±7.75a	3.34±7.47a	3.81±7.58a	4.04±7.26a
Watered	1.72±7.95b	3.01±7.30b	2.15±3.84b	2.21±4.07b	2.54±4.53b	3.12±5.73b
Accession	Ns	Ns	Ns	Ns	*	*
I-1	4.53±2.21	4.38±1.03	3.14±7.77	3.19±7.36	3.90±1.14a	4.20±5.08ab
I-2	3.62±2.22	4.00±1.63	3.38±1.39	3.39±1.26	3.67±1.08a	4.39±1.03a
I-3	3.45±2.93	4.54±8.99	3.14±7.77	3.01±6.99	3.43±7.52ab	3.70±4.75ab
II-1	3.28±1.98	3.29±9.11	2.64±9.39	2.35±6.75	2.93±1.14ab	3.32±1.24ab
II-2	3.47±1.83	4.11±8.54	2.95±6.92	2.81±6.87	3.32±8.30ab	3.78±3.30ab
II-3	2.74±1.80	4.10±1.73	2.68±8.72	2.50±6.72	3.10±1.05ab	3.13±1.52ab
III-1	4.31±2.57	3.62±7.12	2.94±9.75	2.80±7.37	3.16±5.87ab	3.85±4.16ab
III-2	4.02±2.98	4.11±1.03	3.05±9.27	2.89±6.28	3.00±8.20ab	3.38±9.06ab
III-3	3.79±4.23	3.85±1.24	2.90±1.38	2.70±9.72	3.03±9.07ab	3.49±9.70ab
IV-1	3.66±2.63	3.78±1.20	3.35±1.60	2.86±1.04	3.23±1.07ab	3.62±7.77ab
IV-2	3.12±1.82	3.53±1.70	2.52±1.20	2.40±1.07	2.80±1.04ab	3.21±7.36ab
IV-3	2.75±2.20	3.27±1.37	2.65±1.34	2.37±9.77	2.52±9.28b	2.91±9.35b
Mean	3.60	3.90	2.90	2.80	3.20	3.60
CV (%)	37.80	14.08	18.65	18.18	12.66	14.18
Shade*irr	Ns	Ns	Ns	Ns	*	Ns
Shade*acc	Ns	Ns	Ns	Ns	Ns	Ns
Irr*acc	Ns	Ns	Ns	Ns	Ns	Ns

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

Leaf-specific conductivity

The results of ANOVA for leaf-specific conductivity (LSC) due to main and interaction effects show that the two shade treatments had significant influence on LSC of the coffee seedlings on 4 DAI (P<0.05) and 8 DAI (P<0.001), and higher values were recorded for the drought-stressed and for the sun seedlings (Table 7.17) No significant difference was, however, detected on the first or after extended periods of soil drying, though slightly higher values were measured for the shaded leaves. This was in consistence with the dynamics in the soil moisture content of the pots, as was confirmed from the positive but weak correlation between soil moisture status and LSC in drough-stressed seedlings for 8 DAI. Besides, there were insignificant differences between sun and shade in the overall LSC, though a higher value (2.17x10^{-8} kg m^{-2} s^{-1} MPa^{-1}) was recorded in the sun than in the shade (2.04 x10^{-8} kg m^{-2}s^{-1}MPa^{-1}) (Table 7.17).

In contrast, no significant differences were detected between irrigation levels 8 DAI. However, a significantly higher LSC was observed on 12 DAI P<0.001) and 16 DAI (P<0.05). In addition, the overall result shows significantly (P<0.001) higher LSC in drought stressed (2.32×10^{-8} kg m^{-2}s^{-1}MPa^{-1}) than in well-watered seedlings (1.89×10^{-8} kg m^{-2}s^{-1}MPa^{-1}). Consequently, consistent and maximum values were measured for stressed compared to the well-watered seedlings through out the drying period (Table 7.17). In drought stressed seedlings in the sun plots, the results ranged between 1.88×10^{-8} kg m^{-2}s^{-1}MPa^{-1} and 2.91×10^{-8} kg m^{-2}s^{-1}MPa^{-1} at the beginning and 8 DAI, respectively. This is in contrast to the low values for the irrigated seedlings under shade environments, which indicates the variations in moisture gradients and thus, the demand for water by coffee seedlings.

The results also reveal that the coffee accessions did not vary in LSC during the inception and persistent drought stress periods. The accessions, however, significantly differed on the 8 DAI (P<0.001), when the respective highest (3.25×10^{-8} kg m^{-2}s^{-1}MPa^{-1}) and lowest (1.36×10^{-8} kg m^{-2}s^{-1}MPa^{-1}) results were from the Harenna and Yayu accessions. Similarly, the accessions displayed significant variations (P<0.05) in the overall mean results, which varied from 1.75×10^{-8} kg m^{-2}s^{-1}MPa^{-1} to 2.88×10^{-8} kg m^{-2} s^{-1} MPa^{-1} for the Harenna and Yayu accessions, respectively (Table 7.17). This is in line with the corresponding maximum and low leaf surface area of the same accessions.

Although, insignificant, the results show inconsistent intra- and inter-population variations in LSC under contrasting shade conditions. Hence, on the initial day of drying, the Harenna and Berhane-Kontir seedlings had the highest values in the sun plots. This was unlike Bonga and Yayu accessions, which showed that had higher results under shade conditions. Similarly, most accessions had maximum results in the sun plots on 8 DAI. This was particularly the case for trhe Harenna and Yayu seedlings. In contrast, values were higher for the shaded seedlings of I-3, II-1 and IV-4. accessions. On 12 DAI, most seedlings showed higher values in shade than in sun plots. This was particularly observed for the Harenna (I-1 and I-3) and Bonga (II-2) seedlings, but the Berhane-Kontir and Yayu seedlings that were kept in the sun plots revealed slightly higher values. At 16 DAI, the shaded I-2 and IV-3 accessions showed maximum values as opposed to the maximum values for the sun plot of accession III-1. This was when most accessions had minimum ranges between shade and sun

conditions, illustrating that the roots were not able to withdraw water from the potting soil. All accessions showed relatively maximum values under stressed conditions of 12 and 16 DAI with the highest changes at 12 DAI. At this time, well-watered Yayu (IV-2) seedlings had higher values than the Bonga (II-2) seedlings. Furthermore, the lowest and highest overall average values were measured from IV-2 (1.76×10^{-8} kg m^{-2}s^{-1}MPa^{-1}) and I-2 (2.88×10^{-8} kg m^{-2}s^{-1}MPa^{-1}) accessions. In general, significantly higher values were found in the Harenna accessions as opposed to the Yayu and Berhane-Kontir accessions (Table 7.17). In general, the mean leaf specific resistance followed the order of Yayu>Berhane-Kontir>Bonga>Harenna accessions.

Table 7.17   Leaf specific conductivity (k_l, means±SDx10^{-8} kg m^{-2}s^{-1}MPa^{-1}) in coffee seedlings due to drought stress (0-16 DAI) in sun and shade conditions

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

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

The results of the analysis of variance only show no significant treatment interactions during the drought period due to the shade and irrigation on the first DAI ($P<0.05$) and 8 DAI ($P<0.001$). When soil moisture was higher, drought stressed and well watered leaves showed increased (1.88×10^{-8} kg m^{-2}s^{-1}MPa^{-1} to 2.77×10^{-8} kg m^{-2} s^{-1} MPa^{-1}) and decreased (2.27×10^{-8} kg m^{-2}s^{-1}MPa^{-1} to 1.82×10^{-8} kgm^{-2}s^{-1}MPa^{-1}) trends from sun to shade conditions. However, with progressive drought on 8 DAI, a reverse pattern was observed and drought stressed and well-watered seedlings revealed a declined (2.91×10^{-8} kg m^{-2}s^{-1}MPa^{-1} to 1.70×10^{-8} kg m^{-2}s^{-1}MPa^{-1}) and increased (1.89×10^{-8} kg m^{-2}s^{-1}MPa^{-1} to 2.16×10^{-8} kg m^{-2} s^{-1} MPa^{-1}) LSC in sun and shade environments, respectively (Figure 7.21).
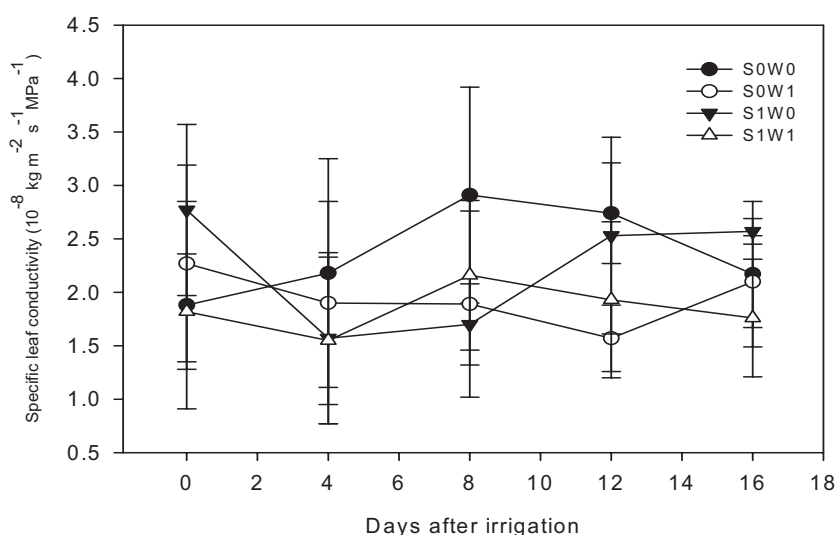
Figure 7.21   Leaf-specific conductivity in coffee seedlings as function of shade and watering treatments (W0S0 = not shaded not watered, S0W1= not shaded watered, S1W0 = shaded not watered S1W1 = shaded watered) for the different days of withholding watering

Main stem conductivity

Reduced irradiance led to significantly enhanced main stem conductivity on the first DAI ($P<0.01$) and when there was severe soil drying on the 12 DAI ($P<0.05$). In contrast, seedlings in moderate shade showed higher average values than those in the sun. Drought stressed seedlings showed significantly higher main stem hydraulic conductivity values at the end of the drought period at 12 DAI ($P<0.001$) and 16 DAI ($P<0.05$) (Table 7.18). The soil moisture contents was in consistence with the patterns

of stem hydraulic conductivity, which had direct correlated positively, but weakly in seedlings 8 DAI.

Similar to leaf specific conductivity, main stem conductivity was significantly different among coffee accessions 8 DAI, though the values did not differ before and after this date. Average values ranged from 4.32×10^{-5} kg m^{-1}s^{-1}MPa^{-1} to 7.20×10^{-5} kg m^{-1}s^{-1}MPa^{-1} in seedlings from the Yayu and Harenna accessions, respectively, with minimum coefficient of variation (CV = 16.3%) among the accessions. The highest main stem conductivity values were measured for II-2 (8.59×10^{-5} kg m^{-1}s^{-1}MPa^{-1}) and III-1 (7.78×10^{-5} kg m^{-1}s^{-1}MPa^{-1}) seedlings, which resulted in the highest average value of 6.50×10^{-5} kg m^{-1}s^{-1}MPa^{-1}. However, there was a decline after this date. In general, main stem conductivity was found to be low in the Yayu seedlings.

Table 7.18   Main stem hydraulic conductivity (k_s, means±SDx10^{-5}kg m^{-1}s^{-1}MPa^{-1}) in seedlings of wild coffee accessions exposed to drought stress (between 0 and 16 DAI) in sun and shade conditions

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

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

The combined effect of shade and irrigation was significant at the beginning (P<0.01) and 8 DAI (P<0.001). Consequently, during the initial application of the treatments, shaded seedlings on the drought stressed plots showed higher main stem conductivity (7.69×10^{-5} kg m^{-1}s^{-1}MPa^{-1}) as compared to the other treatments. This could largely be attributed to shade level, as this had a significant influence on main stem cross-sectional area (P<0.01) as well as on stem conductivity (P<0.01). In contrast, with extended time, drought-stressed and well-watered seedlings showed significantly higher stem conductivity in sun and shade conditions, respectively. In other words, irrigated seedlings in the sun and drought-stressed seedlings in the shade exhibited almost similar responses with the respective average stem conductivity of 4.74×10^{-5} kg m^{-1}s^{-1}MPa^{-1} and 4.81×10^{-5} kg m^{-1}s^{-1}MPa^{-1} (Figure 7.22).

Moreover, coffee seedlings of different coffee accessions showed significant differences (P<0.05) in stem conductivity due to irrigation regimes. Accordingly, drought stressed accessions from the Harenna and Yayu populations revealed higher values than irrigated seedlings. On the other hand, seedlings from II-2, II-3 and III-1 accessions had a higher stem conductivity when well-watered as opposed to soil moisture deficit conditions and thus, a positive range of 1.43×10^{-5} kg m^{-1}s^{-1}MPa^{-1}, 1.21×10^{-5} kg m^{-1}s^{-1}MPa^{-1} and 3.11×10^{-5} kg m^{-1}s^{-1}MPa^{-1} between the two irrigations levels, respectively. On the first day of irrigation, the seedlings of I-1, I-2 and IV-3 had maximum conductivity as compared to other the accessions. Consequently, accessions from Harenna exhibited lower stem conductivity in 16 DAI when most accessions from Bonga (II-1 and II-3), Berhane-Kontir (III-1, III-2 and III-3) and Yayu (IV-1 and IV-2) revealed slightly higher conductivity values, the highest being from the Berhane-Kontir accessions. However, 8 DAI the pattern changed and the drought stressed seedlings of the Harenna accessions showed significantly higher values as compared to others (Figure 7.23). This was followed by the Yayu accessions. All accessions, except II-2, II-3 and III-1, demonstrated higher stem hydraulic conductivity in the plots with irrigation than in those without. The Berhane-Kontir accessions showed only minimum differences between irrigation regimes. The lowest stem conductivity was measured from Bonga accessions (II1 and II-3) in both non-irrigated and irrigated plots. Thus, lowest and highest average stem conductivities were obtained for the Bonga and Harenna accessions, suggesting that the low main stem basal area of such accessions

reduced the water flow. This could also demonstrate the variability in water-use aspects among coffee accessions of geographically varying montane rainforests of Ethiopia.
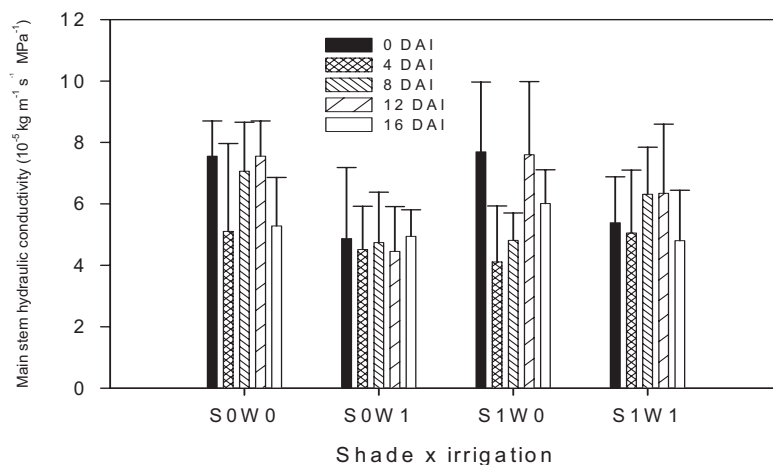

Figure 7.22   Main stem hydraulic conductivity in coffee seedlings with and without irrigation in sun and moderate shade conditions
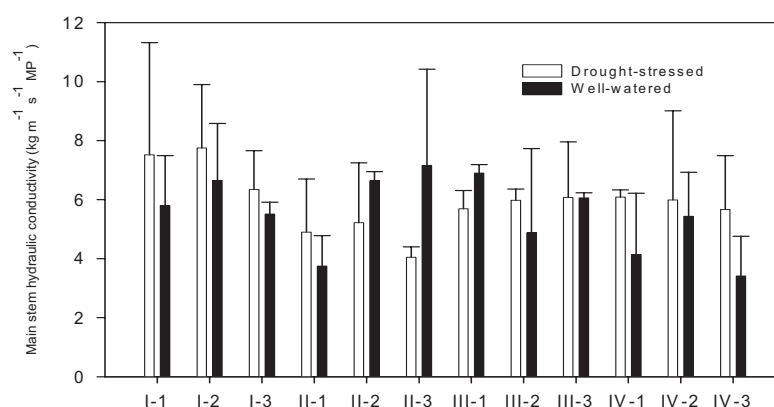

Figure 7.23   Main stem hydraulic conductivity in seedlings of coffee accessions under well-watered and drought-stressed conditions for the period 8 DAI

7.4.8   Stomatal characteristics

Leaf stomata were sparsely distributed and had elliptical guard cells with pores randomly oriented. No stomata were found on the upper leaf surface of the coffee leaves. The contrasting shade levels had significant influence on the density of leaf stomata in coffee in both wet ($P<0.05$) and dry ($P<0.001$) seasons. Maximum and minimum average stomatal densities were determined in sun and shade seedlings, respectively. In addition, the stomatal area index was significantly higher in sun-exposed than in shaded leaves. However, stomatal densities did not differ among coffee

accessions, and the lowest and highest values were determined for the Harenna and Yayu accessions, respectively. This is in line with the maximum and small leaf sizes recorded for the two populations, which indicates the positive relationships between mean leaf area and stomatal density in coffee leaves.

In addition, stomatal frequency was insignificant due to the interactions between coffee accessions and shade levels. However, in all accessions, relatively higher value was recorded in the sun-exposed leaves as compared with shade leaves (Table 7.19). Consequently, the highest values were found for the sun-exposed I-1 and II-3 accessions, while the lowest were for the shade leaves of Berhane-Kontir (III-1 = 224 mm^{-2}) and Bonga (II-1 = 226 mm^{-2} and II-2 = 226 mm^{-2}) accessions (Table 7.19; Figure 7.24). This is similar to the results of the maximum concentration of leaf chlorophyll and high dry matter production of sun-exposed coffee seedlings as discussed earlier.

In contrast, the coffee accessions did not vary in stomatal frequencies in the wet and dry seasons. However, most values showed the same trend due to shade and accessions. Average values for all the stomatal traits were decreased with reduced light intensity, though the change was relatively small, i.e., there was an only 4% reduction in stomatal area due to variation in shade level. This was despite the significant change in leaf growth variables (Chapter 6), mainly due to factors associated with shade and seedling age. This is in contrast to the significantly (P<0.001) higher average number of stomata in the leaves of the sun (271 mm^{-2}) plots, compared to those in the shade (231 mm^{-2}) in the dry months. The higher leaf temperatures in sun and photosynthetic efficiency could be the reasons for the higher values. On the other hand, despite the change in leaf area with irradiance, there was no significant difference among coffee accessions in the overall stomatal number per unit leaf area. This suggests that the photon flux density could be below the maximum level during the study period.

In crop plants, stomatal frequency can vary greatly among different genotypes of the same species growing under identical conditions. This was also observed in the present study, though the accessions were not significantly different for all the stomatal parameters studied. Average stomatal area ranged between 3668±253 and 5033±592 µm^2 for Berhane-Kontir (III-3) and Harenna (I-2) accessions, respectively. In general, stomatal size of the seedlings followed the descending order of

Harenna>Bonga>Berhane-Kontir>Yayu accessions, indicating the rainfall gradients along the respective area of collection. The average leaf stomata dimensions were 76.79 µm long and 70.58 µm wide with the density of 251 mm^{-2} and stomatal area index of 19394.63 µm mm^{-2} (Table 7.19). The findings suggest that coffee accessions in drier areas may be more productive in full sun when soil moisture is sufficient, while accessions from the more humid forests have favourable growth attributes, which make them more drought-tolerant. In general, leaf stomata were noticed to vary in size, shape and distribution pattern, and thus the association between stomata characteristics and other plant physiological traits in coffee remains to be further studies.

Table 7.19   Stomatal density and guard cell dimensions (means±SDx2.5µm) in seedlings of coffee accessions in sun and shade conditions

Treatment	Density (mm^{-2})	Area index (µm mm^{-2})	Area (µm^2)	Density (mm^{-2} leaf area^{-1})	Length (µm)	Width (µm)
Shading	***	**	Ns	Ns	Ns	Ns
Sun	271±48a	22000±4169a	4373±660	69424±12819	78±6	71±6
Shade	231±39b	16789±2672b	4210±629	68716±8304	73±5	71±7
Accession	Ns	Ns	Ns	Ns	Ns	Ns
I-1	290±71	24334±7260	4418±277	71985±7219	84±5	77±5
I-2	223±42	17867±3394	5033±592	63383±5348	80±0	73±0
I-3	267±90	21378±3268	4614±0	71967±14215	80±10	74±19
II-1	214±37	16445±3897	4693±1702	55717±8752	77±5	67±0
II-2	280±47	22623±6411	4035±265	76728±13165	80±10	77±5
II-3	227±28	16623±2074	4837±869	62760±1756	73±0	67±0
III-1	240±47	19423±6034	3847±0	68757±6906	80±10	70±4
III-2	270±89	19800±6568	4436±832	73375±21941	73±0	64±5
III-3	200±10	14667±692	3668±253	60028±14042	73±0	73±0
IV-1	267±47	19556±3457	4222±0	76706±3994	73±0	67±0
IV-2	274±47	20045±3457	3847±0	71271±6923	73±0	67±0
IV-3	264±90	19978±5626	3847±0	76167±12784	77±5	73±0
Mean	251.13	19394.63	4291.21	69070.04	76.79	70.58
CV (%)	12.54	16.17	15.31	16.83	7.33	9.12

*Ns = Not significant; *P<0.05; **P<0.01; ***P<0.001. Means with the same letters within a column are not significantly different by Tukey test (P = 0.05).*

Relationship between stomatal characteristics and leaf water content

Length and width of the guard cells were significantly (P<0.01) correlated in both sun and shade conditions. This indicates the reduced influence of micro-climatic variables, but pronounced species-specific stomatal behavior in wild Arabica coffee seedlings. In addition, there was a significant correlation between the length of guard cell and stomatal area index (r = 0.57*) for sun-exposed seedlings, but not for shade seedlings.

On the other hand, in the shade, the stomatal area index was significantly correlated with the width of stomatal guard cells (r = 0.69**). Moreover, stomatal area index was highly significantly correlated with stomatal density in both light regimes. In the shade, there were slight reductions in all stomatal parameters with increased stomatal density per unit leaf area. In the sun, the size of the guard cells, however, was weakly correlated with the density of stomata per leaf area. Stomatal area was significantly correlated with the length and width of guard cells in the sun and shade conditions. However, the result shows an inverse trend with stomamtal area index in the sun (r =-0.27, P>0.05) and shade (r = -0.43, P>0.05) (Table 7.20a).

The leaf water potential (predawn, midday and diurnal change) was weakly and inconsistently correlated with stomatal characteristics. There was a slight increase in predawn leaf water potential with increasing stomatal density and size, but the reverse was true for the midday and diurnal changes. This could be due to the increased difference in water vapor pressure between the interior air spaces of the leaf and the surrounding air. This was again evidenced from the significant (r = 0.73**) linear regression between percent loss of whole-plant hydraulic conductivity and mean leaf area of the seedlings. Similarly, there was a positive link between percent loss of conductance and leaf area index, though insignificant. Stomatal dimensions were negatively correlated with total leaf area and thus leaf area index, while average leaf area showed weak positive relations.

Predawn relative leaf water content was indirectly and significantly (P<0.05) correlated with stomatal length and width, with a stronger influence on the former dimension. This was not observed with respect to stomatal density. The magnitude of the relationship between stomatal dimensions and relative leaf water content differed among coffee accessions. However, the decline in the predawn relative leaf water content in most Harenna accessions was related to increased stomatal sizes. Conversely, maximum relative leaf water content was linked to reduced stomatal size in the southwest wild coffee accessions. This could also be due to stomatal closure even at predawn if LWP should drop to about 50%. As a whole, there was a decline in relative leaf water content (increased leaf moisture deficit) with increasing size of stomatal guard cells (Figure 7.26). Predawn relative leaf water content in turn had significantly

linear correlation (r = 0.65*) with midday relative leaf water content, indicating the coordination between liquid and vapor phases within a leaf.

Table 7.20   Simple linear Pearson correlation values between (a) stomatal characteristics and (b) stomata and leaf water contents in coffee leaves

a) Correlation between stomatal characteristics in sun and shade conditions

Character	SL	SW	SF	SAI	MLA	SDPLA
			Sun			
SW	0.78**					
SF	0.22	0.16				
SAI	0.57*	0.45	0.93**			
MLA	-0.05	0.29	0.19	0.14		
SDPLA	0.05	0.14	-0.34	-0.27	0.50	
SAPLA	0.95**	0.94**	0.20	0.54	0.12	0.09
			Shade			
SW	0.80**					
SF	0.20	0.48				
SAI	0.51	0.69*	0.94**			
MLA	0.29	0.01	-0.27	-0.13		
SDPLA	-0.03	-0.16	-0.46	-0.43	0.37	
SAPLA	0.93**	0.97**	0.39	0.66*	0.14	-0.12

b) Correlation between stomatal characteristics and leaf water content

Character	PDLWP	MDLWP	DFLWP	PLC	PDRLWC	MDRLWC
SF	0.29	-0.02	-0.20	0.07	0.23	-0.20
SL	0.18	0.09	-0.07	0.05	-0.59*	-0.44
SW	0.04	0.06	0.02	-0.37	-0.66*	-0.44
MLA	0.17	-0.22	-0.39	0.71**	-0.23	-0.22
LAI	-0.36	-0.29	-0.02	0.52	-0.12	0.03
PDLWP	1.00	0.46	-0.27	0.16	0.46	0.41
MDLWP		1.00	0.73**	-0.14	0.41	0.49
DFLWP			1.00	-0.30	0.13	0.23
PLC				1.00	-0.02	0.11
PRRLWC					1.00	0.65*
MDRLWC						1.00

*, ** = Significant correlation at P = 0.05 and P = 0.01 probability levels, respectively. Abbreviations: SL = stomatal length, SW = stomatal width, SF = stomatal frequency, SAI = stomatal area index, MLA = mean leaf area, LAI = leaf area index, SDPLA = stomatal density per leaf area, SAPLA = stomatal area per leaf area, PDLWP = predawn leaf water potential, MDLWP = midday leaf water potential, DFLWP = diurnal difference leaf water potential, PLC = percent loss of hydraulic conductance, PRRLWC = predawn relative leaf water content, MDRLWC = midday relative leaf water content.

As far as the interactions are concerned, the results show that stomatal density was not statistically different due to shade and accessions when compared in the wet

season alone. However, the average density of stomata varied from 236 to 266 mm^{-2} for Yayu (IV-3) and Harenna (I-1) accessions, respectively (Figure 7.24). In the dry season, the value for the Harenna accession I-1 was also the highest (290 mm^{-2}), while the lowest was obtained for the Berhane-Kontir accession III-3 (200 mm^{-2}). The stomatal density of leaves in the wet season was in line with the average leaf size of the accessions, indicating the positive relationships between leaf surface area and number of stomata within a small field of view.

However, the interaction between seasons (wet and dry) and shade levels (sun and shade) was significant (P<0.05) for the frequency of leaf stomata. Consequently, the highest (282 mm^{-2}) and lowest (220 mm^{-2}) average values were recorded in the dry season under sun and shade conditions, respectively (Figure 7.25). The reduction in stomatal density in the shade plots was higher (22%) during the dry season as compared to the decline in the wet season (11%). In the sun, the number of stomata increased from the wet to dry seasons, with an increment of 6% over the wet month. Conversely, there was a 6.9% reduction in the shade environment for the dry month.

On the other hand, neither season nor shade showed significant interaction with coffee accessions. Nevertheless, the seasonal change in leaf stomatal frequency was in consistence for each coffee accession. However, 67% of the accessions, mainly from Harenna and Yayu, showed an increasing number of stomata in the dry months, indicating that stomatal movements are actively controlled in coffee seedlings. In contrast, most accessions from the Bonga population revealed a reduction in stomatal density. All accessions had a higher stomatal frequency in the dry than in the wet season, though the range differed among accessions. Based on the results of stomatal density and size, the accessions were similar and could be grouped into 3 cluters. The first cluster consisted of 58% of the accessions and most of them were from the Yayu and Harenna populations. The second cluster (33% of the accessions) consisted of the Bonga and two others from Harenna and Berhane-Kontir one from each. The farthest cluster distance was between accessions of the same wild coffee population (III-2 vs. III-3), indicating again the existence of immense intra-variability within a population. There were also great differences in the patterning and shape of stomata in the coffee leaves. In most cases, stomata were found in patches or clustered only in the abaxial part of the leaf.
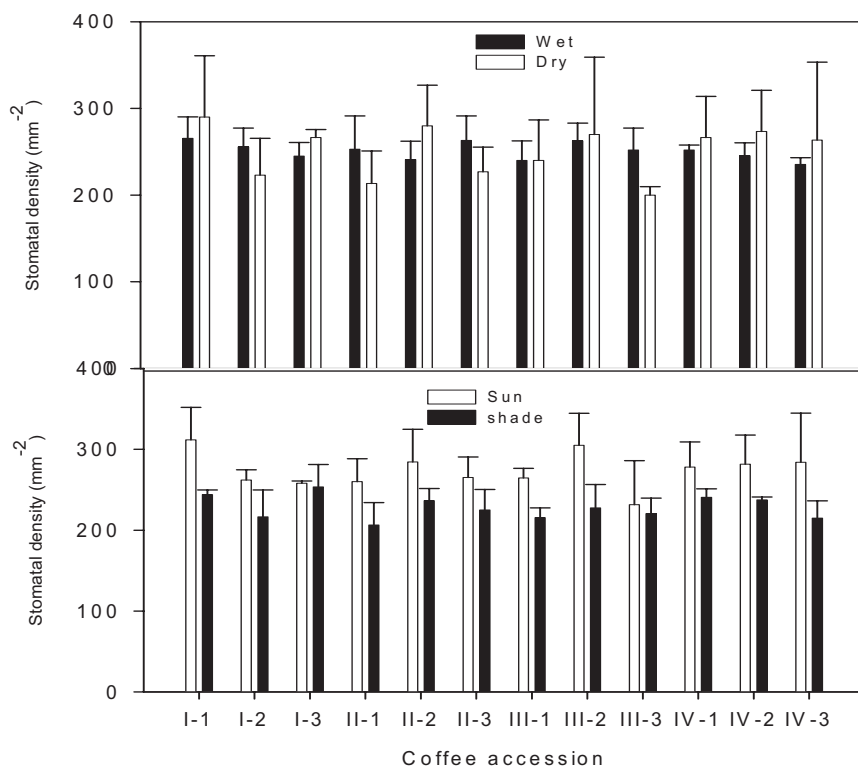
Figure 7.24   Influence of season and shade level on leaf stomata density of coffee
              seedlings under nursery conditions
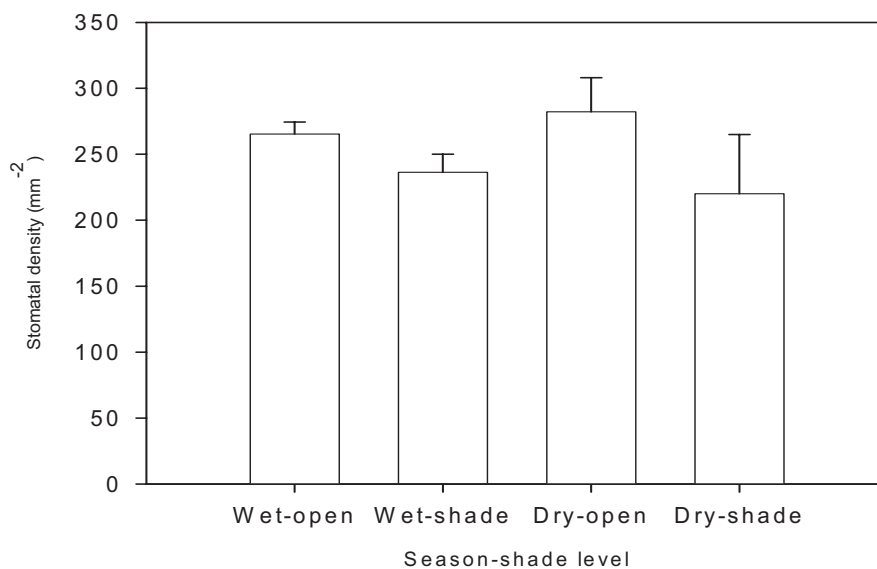

Figure 7.25   Stomatal density in coffee seedlings as influence by the interaction
              between season and shade level under nursery conditions
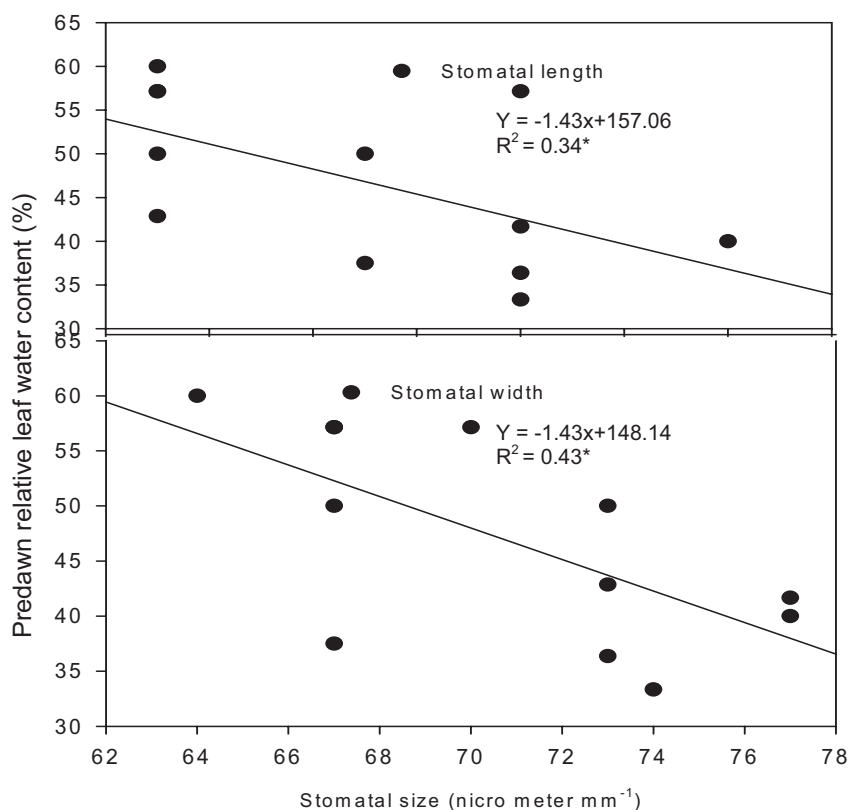
Figure 7.26   Effect of stomatal length and width on predawn relative leaf water
            contents of coffee seedlings

7.5   Discussion

7.5.1   Soil-plant water relations

The significantly higher soil and leaf water contents in shade than in sun seedlings
could in part reflect reduced moisture gradients along soil to leaf pathways due to low
vapor pressure deficits, photosynthetic flux density and leaf temperature. The variation
in soil-leaf water contents between shade and among accessions could be related to the
extent of water loss largely through evapo-transpiration. Hopkins (1995) showed the
influence of temperature on stomatal opening, metabolism, respiration and
photosynthesis and consequently the intercellular CO_2 content within a plant leaf. High
temperature and excessive transpiration in full sun could bring about such severe
drought-stress as compared to the shaded plots. The variation in growth stage of the
seedlings could primarily attributed to such differences with varying ranges of
sensitivity to the induced drought stress conditions. Hence, the benefits of shade
increases with increased age and transpiring leaf surface. This could largely be

explained in terms of the water-use efficiency of the seedlings with distinct morphological and physiologogical behaviors. In the shade, seedlings may allocate photosynthates more to the stem if mortality or probability of gap formation is large. However, it could allocate photosynthates more to the leaves if large stems are strongly advantageous in competition after gap formation.

The predawn leaf wilting values show that cavitated tracheids may refill overnight and that this is more likely in less drought-stressed seedlings. In those seedlings, cavitation on successive days occurred in populations with progressively less vulnerable tracheids in response to day-to-day decline in shoot water potential. The generally high rates of seedling drying in Herenna compared to other accessions suggests their greater vulnerability to cavitations. The higher PLC in the root than in the shoot parts could be related to xylem traits (length, thickness, density). Higher rates of cavitation have been ascribed to large vessel or tracheid size (Zimmermann, 1983), with larger tracheid or vessels reported to cavitate at lower tensions than smaller conduits. This has been shown in certain species (Tyree and Sperry, 1989), but not for interspecies comparisons (Cochard and Tyree, 1990). The moisture gradients and thus deficit symptoms at leaf level may be associated with biochemical constituents and thus, activities of the cells. According to Hashimoto et al. (1984), stomata tend to have smaller apertures and to close more readily at the leaf margins compared to those in the leaf center, although stomata near main veins tend not to open wide. The causes for this are probably related to the different rates of water availability and loss in these different tissue areas (Hashimoto et al., 1984). Also, stomata near veins often appear restricted in movement due to the rigidity the veins confer on the epidermis. Many such responses can plausibly be thought of as examples of feed forward, of conservative responses to a diminishing supply of water or to a diminishing ability of the roots to access soil water, which affects root water potential. This could be attributed to the production of hormones (xylem ABA that can trigger stomatal closure) and energy allocation of the plant not to invest on new growth.

The negative leaf growth in Harenna accessions could be due to the significantly high leaf mortality rate in the drought stressed seedlings. Leaf abscission may be considered as a whole-plant mechanism to limit transpiration, but leaf senescence might be merely a consequence of stress, since the drought-sensitive

Harenna accessions lost considerable foliage under the influence of drought stress. This might also show the highly restricted water availability in the remaining leaves that triggered drying of the seedlings. This is in agreement with the water storage capacity of the stem of the same coffee seedlings. According to Turner (1979), tolerance to drought may result from either a reduction of water loss or maintenance of water uptake. He pointed out that reduction in water loss follows an increase in stomatal and cuticular resistance, a reduction in absorbed radiation or a reduction in leaf area. Reduced radiation absorption arises through leaf movement like leaf folding so that the angle of incidence to incoming radiation provides less area for absorption, the development of pubescence, which insolates the leaf surface, or the development of increased waviness and reflecting qualities of the leaf surface (Hale and Orcutt, 1987).

Moreover, the results also show that leaf rolling was highly significantly higher in the sun than in the shade plots, indicating the morphological adaptation in coffee seedlings to drought stress. Leaf rolling may reduce transpiration by as much as 70% and the leaf area exposed to incident radiation by as much as 68% (Begg, 1980). The response of Scots pine and Sitka spruce saplings (Jackson et al., 1995) to drought treatment supports the present findings on the variability among coffee seedlings to induced soil water deficits. The findings support the presence of a trade-off between xylem embolism and hydraulic conductance. Variation in vulnerability to cavitation could be related to the morphology of the inter conduit pit membrane in root and shoot parts, though not quantified in this study. Hence, consideration of safety margins of each coffee population is of paramount importance in the use and conservation of wild coffee populations in the remaining rainforests of Ethiopia.

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. Tausend et al. (2000b), 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 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

Harenna accessions, which have open crowns. At least partially, the findings could explain why the use of compact cultivars resistant to coffee berry disease often results in the low productivity in lowland humid climates of the Berhane-Kontir region with high evaporative demand. Therefore, selection of cultivars for drought-prone environments should consider aspects concerning crown architecture.

The high soil and leaf moisture contents in the Berhane-Kontir accessions as compared to Yayu and Harenna may be related to the variability in root water uptake capacity of the accessions in response to soil and atmospheric drought stress. In other words, the growth response and hydraulic features of coffee seedlings indicate the conservative behavior of the Berhane-Kontir accessions as opposed to the relatively high-xylem vulnerable and opportunistic Harenna accession with respect to utilization of soil-available water. This supports findings on 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 several authors (Clearwater and Meinzer, 2001; Hubbard et al., 2001), photosynthesis and stomatal conductance is partly constrained by the hydraulic architecture in a number of plant species. In line with the present findings, other studies on different species and ecological conditions suggest the maintenance of a homeostatic balance between water transport capacity and supporting leaf area (Becker et al., 2001; Cernusak and Marshall, 2001; Maherali and DeLucia, 2001; McDowell et al., 2002). Stout and Sala (2003) also pointed out that several functional and structural regulations, including greater stomatal sensitivity to drought stress, shifts in biomass allocation and enhanced capacity to store water in offsetting high xylem vulnerability of Ponderosa pine. 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 patterns of the hydraulic conductances measured in the same accessions in the present study (Table 7.15). Moreover, the results are in agreement with the work done by Sobrado (2003), who showed trade-offs between water transport and leaf water-use efficiency in pioneer and forest tree species.

Most coffee accessions showed relatively severe drought stress symptoms 8 and 12 DAI in the 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 sun and shade plots, respectively. The average conductance loss was higher in the sun than in shade plots, indicating loss in turgor and water potential of the leaves following the occurrence of cavitation. There was also a significant reduction in percent loss of root hydraulic conductance to 84 and 74% with a loss of leaf hydraulic conductance to about 52 and 40% in the open sun and shade plots, respectively. The findings demonstrate that the sensitivity of the coffee seedlings to water deficits varied depending on site conditions and plant parts. This supports the findings of Maherali and DeLucia (2000a), and corroborates with seedling growth in the shade and sun plots, particularly with leaf and root parameters. 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 between species. 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 optimised for drawing water from a particular temporal and spatial niche in the soil environment. The response of the coffee seedlings, as evident from the soil-plant water contents, may be related to the difference in growth characteristics and drought-stress coping mechanisms. Much research on drought tolerance in coffee has been conducted using pot-grown seedlings. According to DaMatta (2004b), this approach has only a limited agronomic relevance since: (i) it is difficult to simulate in small volumes of soil the natural development of drought down a root profile; (ii) some responses to drought stress are hardly manifested in nursery sites where there is limited exposure period to irradiance; and (iii) adaptations to drought stress may not be resolved at a young developmental stage as in a mature tree. In addition, traits such as leaf composition of cuticle and surface reflectance, which may contribute both to decrease in transpiration and avoidance of photo-inhibitory damage and excessive leaf temperature, have not

been fully explored. Comprehensive studies are required to identify the specific underlying biochemical responses and molecular bases for further breeding programs.

Soil moisture content showed highly significant difference due to shade, irrigation and interaction between shade and irrigation treatments, but not due to coffee accessions and accession by shade treatment. The higher soil moisture in the shade plots indicates the roles of shading in ameliorating the microclimate and reducing water loss mainly through evaporation. The accessions were comparable in terms of exhausting soil moisture, which was in line with the growth uniformity among the accessions during the later stages. The temporal decline in soil moisture was significantly high with terminated irrigation both in sun and conditions. This was much more marked until 8 DAI, indicating the highest water tension between the soil and the leaf during the first days. Both in sun and shade plots, the drop in soil moisture was minimal thereafter, indicating that the availability of soil moisture was below the demand of the seedlings. The variation in well-watered seedlings under shade conditions could most likely be attributed to either diurnal climatic changes or to intra-population differences among coffee seedlings. In general, the present results show that drought stress for a maximum of 4 days in the sun and 8 days in the shade environments seem to be critical drought stress periods for coffee seedlings.

With regard to plant water status, there were significant variations between shade regimes and coffee accessions across the drought stress periods. The decrease in leaf water content could have triggered stomatal closure to reduce transpirational water loss. Such stomatal movement is regulated by a variety of environmental and internal factors such as light, CO_2 levels, water status of the plant and temperature. It can be expected that stomata will open in the light in order to admit CO_2 for photosynthesis or partially close when CO_2 levels are high in order to conserve water while allowing photosynthesis to continue. 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. At any given time, 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. The difference in water relation among the coffee accessions due to different levels of drought stress can be explained by the diurnal fluctuation in leaf water status.

Accordingly, the reduced midday leaf water with a wide range in the LWP and RLWC for the Bonga accessions indicates their tolerance to a low water potential. On the other hand, accessions from Berhane-Kontir (III-2), Yayu (IV-3) and Harenna (I-1) exhibited significantly reduced midday LWP and diurnal fluctuations, most likely indicating their distinct drought stress avoidance startegies, which triggered additional stomatal closure. Fikru (2005) and Doberstein (2005) found similar trends in the leaf water potential of coffee populations. According to the results on the photosynthetic efficiency on the accessions in this study (Beining, 2006), the accessions 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 accessions to cope with drought stress and as a conservative water saving strategy. Moreover, the reduced predawn LWP and midday leaf water contents in the Bonga as opposed to the Berhane-Kontir accessions could reflect their ability to re-equilibrate at the maximum LWP at night. On the other hand, the significant drop in LWP for the Yayu and Harenna accessions could be attributed to their maximum root contact with the soil and high shoot surface with a high loss of water vapor due to the increased magnitude of the vapor pressure gradient between the leaf and the surrounding air.

When coffee seedlings displayed symptoms of severe drought stress 8 and 12 DAI in sun and shade environments, respectively, the midday LWP of -1.42 and -1.60 MPa were measured in 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 level 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 CO_2 assimilation (Salisbury and Ross, 1992). In the present study, there were differences according to accessions showing an early drop in leaf water potential of –2.1MPa, specifically in the most drought-stressed

treatment (no irrigation and without shade). The high and low water flow measured in the seedlings of the Harenna and Yayu coffee seedlings were in line with the morphological variability of the accessions (Chaper 6).

Coffee plants retain a high relative leaf water content under dehydrating conditions, and are considered water saving rather than drought-tolerant species (DaMatta et al., 1993; Nunes, 1976). This may be attributed to (i) an efficient stomatal control on transpiration (Nunes, 1976) and/or (ii) low cell-wall elasticity (DaMatta et al., 1993, 2003; Meinzer et al., 1990b). A small water loss, therefore, causes a shift in turgor so that leaves tend to maintain a high relative water content to retain a high symplast volume. Thus it appears that under water deficit conditions, the maintenance of a high relative leaf water content is more important than osomotic adjustment per se in conferring drought tolerance to the coffee plant (DaMatta et al., 1993). The present results on the water relations of coffee seedlings are in agreement with the work done by Tausend et al. (2000b) on the water utilization of three Arabica coffee cultivars. According to the results, coffee accessions from the same forest populations responded differently to the induced low soil moisture. Pinheiro et al. (2005) quoted the work of Kramer and Boyer (1995), who showed 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 (Turner, 1997; Kramer and Boyer, 1995 as cited by Pinheiro et al., 2005). This is in agreement with the recent findings on cultivar-specific responses of improved coffee cultivars to soil moisture deficits (Tesfaye, 2006).

The results 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). He reported that the osmotic potential of guard cells and, consequently, the size of the stomatal opening is determined by the extent of K^+ accumulation in the guard cells. The accumulation of ions (K^+, Cl^- and malate $^{2-}$) in the vacuole of the guard cells would lower both the osmotic and the water potential of the guard cell, thereby stimulating the osmotic uptake of water and increased turgor and causing the stomata to open (Hopkins,

1995). This was observed in this study in that both predawn and midday relative leaf water contents of the drought-stressed seedlings decreased with accumulation of K in the coffee leaves. This was significant for midday and was more pronounced in Harenna as opposed to the southwestern accessions, particularly those from the Yayu forest. The findings clearly demonstrate the degree of stomatal opening in relation to soil moisture status. The low leaf water status in the Harenna accessions could be attributed to accumulation of K ions, which reveal the initiated stomatal opening and loss of water from the leaves in moderately drought-stressed seedlings. The osmotic effect of K in the coffee seedlings is in line with Doberstein (2005). There was no marked accumulation of other inorganic solutes in any of the coffee accessions. The decline in leaf water potential in the Harenna seedlings was in agreement with the increased carbon assimilation capacity of the accessions, again indicating a trade-off between productiviy and vulnerabiltiy to xylem embolism in Arabica coffee seedlings.

From the present finding, it can be concluded that seedlings of wild coffee accessions considerably differ in water relations, which might primarily suggest their inherent growth characteristics and adjustments to environmental stresses. The morphological and physiological responses to water availability demonstrate that accessions of different wild coffee populations might use different survival strategies under drought stress at the seedling stage. The southwest populations exhibited retarded growth rates and conservative water-use strategies, while the accessions from the the drier Harenna climate exhibited fast growth and high biomass yields, i.e., they were opportunistic in water-use strategies. The response of the seedlings to the simulated short-term drought stress could primarily indicate the major role of stomata in photosynthesis and in preventing excess water from loss, i.e., a homeostatic function. The strong correlation between leaf water status and leaf accumulation of K in relation to stomatal movements and resource-use efficiencies of diverse coffee types calls for further investigation. The information would also help in providing insights into the physiological basis of survival and is essential in the utilization and conservation of the accessions. However, detailed biochemical investigations on the underlying drought resistance strategies (leaf to atmospheric signals) and repeated field evaluations are of great importance to identify drought stress-tolerant coffee types and promote the *in-situ* conservation of the accessions in their respective geogrphical areas.

7.5.2   Soil-plant chemical compositions

The variations in the relationships between soil and leaf compositions due to shade levels could be attributed to the substantially higher temperatures in the air, leaves and soil in un-shaded conditions (Table 6.2; Figure 6.2). In non-transpiring plants, the concentrations of minerals in the xylem stream will be higher and the velocity of transport will be lower than in transpiring ones. However, mineral transport will occur at the same rate as long as there is photosynthesis and transport of carbohydrates to roots for storage, growth and respiration (Zotz et al., 1998). According to Kumar and Tieszen (1980), leaf photosynthetic rates were strongly reduced when air temperature was above 25°C, which can be experienced in unshaded conditions. Moderate shading optimizes the microclimate and thus seedling physiology. The reduced variation between shade levels in this study could be attributed to the limited experimental period (3-4 months). This calls for further investigations on the response of different coffee accessions, among others, seasonal micro-climatic dynamics, plant nutrients and moisture gradients.

The significant differences between irrigation regimes in leaf organic matter and major plant nutrients suggest that gradual soil drying for a 16-day period seems to be critical, causing reduced nutrient uptakes and changes in the patterns of carbon accumulation in the sun-exposed seedlings. This is in agreement with the report of Wintgens (2004). According to other reports (Coste, 1992; Wrigley, 1988), high leaf nitrogen can be associated with leaf age and thus, tolerance to soil moisture deficits. Moreover, the accessions from Harenna forest showed significantly (P<0.05) high leaf phosphorus as compared to others, particularly to those from the Berhane-Kontir and Yayu accessions. The lowest and highest leaf phosphorus was determined from Berhane-Kontir (III-3) and Harenna (I-2), respectively. This suggests variations in the soil phosphorus status and extent of phosphorus damage in photosystem II in full sun as reported by Nunes et al. (1993).

In addition, the interactive effect between shade and irrigation was significant on leaf organic matter contents, but not on other parameters. This could be explained in terms of the stress-alleviating contribution of shade to limited availability of soil moisture. This supports the work done by Tesfaye (1995) on the production of high quality coffee seedlings under optimum shading. Similarly, leaf nitrogen in most coffee

accessions increased in the drought-stressed seedlings. This illustrates the reduced availability and uptake of nitrogen ions in dried soils. In contrast, in the irrigated plots, the accessions from Harenna and Bonga had maximum concentrations of leaf nitrogen. This suggests an increased use of the available soil nitrogen in the irrigated pots, though the extent of the response was accession specific. The least leaf nitrogen was determined for the Berhane-Kontir accessions in both watered and drought-stressed plots. Such accumulation of inorganic ions in response to water deficit stress could reveal the contribution of these ions in regulating water movements in guard cells. Osmotic adjustment generates a more negative leaf water potential, thereby helping to maintain water movement into the leaf and consequently leaf turgor. Osmotic adjustment has been associated with maintenance of gas exchange under drought conditions (Turner, 1997).

In this study, however, the amplitude of osmotic adjustment was small and more pronounced in some accessions from Harenna and hardly explain the low stomatal sensitivity to drought. It should be noted that leaf water deficits might develop faster upon discontinuing irrigation in coffee genotypes having a greater amplitude of osmotic adjustment (DaMatta, 2004b). Therefore, osmotic adjustment seems of limited importance (Munns, 1988) in determining drought tolerance in Arabica coffee seedlings. Similar findings have been reported for several other woody species (Fan et al., 1994). According to Blake et al. (1991), where it occurs, osmotic adjustment either may not persist for long under drought, or functions over a limited range of water potential values. In general, the present findings demonstrate the inter- and intra-population variability in response to the induced heat and soil moisture gradients. Hence, more investigations are necessary to characterize the specific shade requirements and degree of drought stress for different coffee populations by taking into account gradients of altitude, moisture and soil fertility gradients.

7.5.3   Hydraulic resistance

Shoot hydraulic resistances were significantly higher in the shade and the contributions of leaf resistance to the total shoot resistance were 58.5% and 55.1% for the sun and shade coffee seedlings, respectively. This could be related to the variations in photosynthetic photon flux density, leaf-to-air vapor pressure difference and thus bulk

leaf water potential. Sun seedlings demonstrated lower whole-shoot resistances compared with the seedlings growing in the shade. Seedlings in shade conditions might be primarily constrained by low light availability in the morning and by limited water supply to the leaf at the midday. This is evident from the greater negative leaf water potentials in the sun than in the shade plots. The results indicate that stomatal openness can be controlled by leaf water status and temperature. The average whole-plant hydraulic resistance was higher for the shade seedlings than for the sun-exposed seedlings, mainly due to the resistance pattern in the roots. This supports the most widely accepted theory for movement of water through plants, i.e., cohesion-tension theory, which states that the driving force is provided by evaporation from the leaf and the resulting tension or negative pressure. According to Sack et al. (2005), sun-establishing species had a higher proportion of leaf resistance in the xylem. Across species, component resistances correlated linearly with total leaf resistance. Leaf specific conductivity strongly correlated with indices of stomatal pore area, indicating a coordination of liquid- and vapor-phase conductance shifted relative to that of temperate woody species. According to Sack et al. (2005), leaf hydraulic properties are integrally linked in the complex of traits that define differences in water use and carbon economy across habitats and vegetation zones.

The hydraulic resistances in the branches of the coffee seedlings were in consistence with the morphological growth differences (Table 5.2a). Consequently, seedling height was indirectly related to whole-shoot and whole-plant hydraulic resistances. Similarly, the resistances in the various shoot parts were inversely correlated with stem diameter and number of leaves, and the values were highly significant and significant, respectively. This was evident from the highly significant and positive correlations between leaf area-specific hydraulic resistance and hydraulic resistances in the root (r = 0.51*) and above-ground seedling parts. Thus, the results demonstrate the importance of crown architecture, particularly stem size and leaf growth, in the hydraulic pathways of coffee seedlings grown under controlled nursery conditions. The compact coffee types from Yayu and Bonga with short height, narrow basal area and reduced leaf surfaces may have morphological plasticity to tolerate drought and thrive better under limited soil moisture conditions. In contrast, the differences in growth habit of the Harenna and Berhane-Kontir accessions with the

highest values for most parameters could have resulted in decreased hydraulic resistance and thus required the availability of sufficient soil moisture. The variations in hydraulic resistance patterns in the coffee accessions indicates the adaptive mechanisms for withstanding drought-stress conditions. This supports the work done by Tausend et al. (2000b) on the water balance of *Coffea arabica*.

The low root resistances in the Harenna accessions may be associated with the growth habits, as root resistance was significantly and negatively correlated with plant height, main stem diameter at the base, number of nodes on the main stem and length of internode on primary branches. The low whole-plant resistance for the Harenna accessions have caused high rates of transpiration in the presence of sufficient water and increased water-use efficiency. In addition, root and shoot growth were negatively correlated with hydraulic resistances. As a result, significant values were recorded for leaf, branch, stem, root and total dry mass. Moreover, values were also significant between hydraulic resistances in shoot components and root to shoot ratio. On the other hand, the correlation between hydraulic resistances and moisture content of leaves, stems and roots was positive, though in most cases insignificant. The correlation between root moisture content and hydraulic resistances in leaves, petioles, lateral branches, stem cut and stem hydraulic conductivity was negative and strong. The findings suggest the presence of a higher hydraulic resistance in the root part than in the shoot parts of all coffee accessions both in the sun and shade plots. Unlike in the root system, hydraulic resistance tended to decline in the whole shoot and its various components in the shade seedlings. In addition, positive and significant correlations between relative leaf water content and hydraulic resistance were observed in the whole shoot and its components. This is in contrast to the positive, although not significant, correlations found between leaf water content and hydraulic resistance in the root part and thus, whole-plant system.

The differences in hydraulic resistance and contribution in the root and shoot segments due to shade regime could be explained in terms of the rate of water uptake and water use, which was much higher in the sun conditions. In well-watered coffee seedlings, the resistance contributions across root and shoot components followed the order of root>leaf>whole-shoot>branch>petioles, suggesting the increased susceptibility to loss of hydraulic conductivity and xylem vulnerability to drought-stress

conditions. This was confirmed through the strong negative links between root to shoot ratio and hydraulic resistances in the shoot parts, i.e., the higher the root growth, the better the hydraulic conductance. Nevertheless, in segment cuts there is no root resistance, thus leaf water will be reduced as compared to the intact plants in the field. This agrees with several authors (Tausend et al., 2000b; Tsuda and Tyree, 1997). As the water potential is higher in the root than in the shoot during steady state evaporation this pattern of hydraulic resistance and vulnerability segmentation guarantees high water flow and/or water-use efficiency when soil water is sufficient. However, this does not provide an adaptive advantage in dry environments, as roots may become dried due to cavitation before leaf death. Roots usually have wider conduits and higher hydraulic conductivity and are more vulnerable to xylem embolism (Ewers et al., 1997). The present results on the hydraulic architecture of coffee seedlings support these findings, and agree with the existence of a trade-off between xylem conductivity and resistance to caviation (Zimmermann, 1983). Tsuda and Tyree (1997) also reported a trade-off between vulnerability patterns and whole-plant resistance, as plants with low whole-plant resistance tend to be more vulnerable to cavitation and exhibit vulnerability segmentation when compared with plants with high whole-plant resistant. In this case, the distal portion is more vulnerable than the basal portion, which provides the ability to conserve soil water by shedding leaves and allows the roots to survive in a dry soil. In plants with low resistance, a steep pressure gradient across the whole plant may not develop, and thus vulnerability segmentation will confine cavitation to the distal region. However, in plants with high resistance, high evaporation may induce a great pressure drop, thus cavitation might develop at the distal portion without vulnerability segmentation. On the other hand, at the same evaporation, leaf water potential is lower in plants with higher resistance and more favoured to prevent cavitation over normal ranges of the environment. However, more information is needed to clarify the trade-off between whole-plant hydraulic resistance and xylem vulnerability to cavitation in Arabica coffee gene pools.

Moisture contents (in leaf, stem and root) and hydraulic resistances in root and shoot parts were negatively correlated. This reflects the constrained balance between water transport in root-to-leaf conductance and carbon gain. Katul et al. (2003) have elaborated this as assimilation and leaf-specific conductivity is mediated by stomata to

meet the demand for photosynthetic CO_2 assimilation while controlling water loss from leaves in a manner that minimizes caviation in the plant hydraulic system. The difference between root and shoot parts can be accounted for the resistance of the xylem and by the physical location of the two organs in the soil-plant-atmosphere continuum. Whitehead (1998) presented evidence that short-term changes in stomatal conductance are linked closely to the hydraulic properties of the conducting system to minimize loss of hydraulic conductivity through xylem by cavitation. He described homeostatic mechanisms that operate to ensure the long-term balance between evaporative demand and the potential hydraulic conductivity of trees growing in different environments. He also examined two hypotheses: 1) height growth in trees is limited by the capacity of the conducting of the system; and 2) the decline in productivity with stand age is attributed to a decrease in conductivity.

Hydraulic resistance components were negatively correlated with fresh main stem density especially in the Berhane-Kontir accessions, indicating high hydraulic resistances with increased stem water storage and decreased stem size. The accumulation of more biomass with age and development of more xylem elements can contribute to low stem resistance. Santiago et al. (2004) found a proportional decrease in leaf specific conductivity and leaf area with increasing wood density. They suggested that the biophysical structure of wood might contain a physical function to specific operating ranges and reflect life-history trade-offs at whole-organism level. In addition, main stem diameter was strongly negatively correlated with hydraulic resistances in main stem-cut, whole shoot, leaf and root parts in a descending order, demonstrating trade-offs between hydraulic capacity and photosynthetic rate. Meinzer et al. (1990) pointed out that coffee genotypes with greater soil-to-leaf hydraulic conductance can deplete soil moisture more rapidly and experience symptoms of physiological stress earlier when water is withhold.

7.5.4   Hydraulic conductivity

Sun-exposed and drought-stressed seedlings showed higher leaf specific conductivity (LSC) than those in the shade and irrigated treatments. The seddlings significantly differed due to moderate drought not exceeding 8 DAI; before and after this date no differences were detected. This corresponded with the soil moisture status in the potting

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media, indicating the moisture gradients in the soil-plant-air continuum. The observed differences in LSC demonstrate anatomical plasticity that enables the xylem to compensate for changes in hydraulic requirements. This also be the reason for the variations in growth habits and hydraulic architecture in the seedlings of coffee accessions. Further, significantly higher overall average LSC values were found in the Harenna accessions as opposed to the Yayu and Berhane-Kontir accessions. This could be related to the wider stem diameter and increased total leaf surface area supported by the main stem segment, which indicates the differences in functional xylem area and shoot morphological attributes. The findings indicate the movements of stomata in regulating transpirational water loss and photosynthetic process. Therefore, comprehensive investigations are imperative to determine relations between rates of water use and hydraulic architecture in coffee plants. This supports the work done by Joyce and Steiner (1995) in white ash, who suggested that: 1) a systematic variation in LSC distributions exists within the crown of white ash; 2) within-crown variability in LSC is primarily the result of variations in mean vessel diameter; and 3) there is a physiological linkage between LSC and crown morphology that is maintained through a positive feedback mechanism during branch ontogeny. In the present study, the effect of irrigation levels was minimal under moderate shade, where little or no differences were observed particularly with prolonged drought stress. This shows the advantage of shade in reducing evapo-transpiration, thus helping to conserve the available soil moisture. According to Sperry et al. (2002), many aspects of plant water use, particularly in response to soil drought, may have as their basis the alteration of hydraulic conductance from soil to canopy. The regulation of plant water potential by stomatal control and leaf area adjustment may be necessary to maximize water uptake on the one hand, while avoiding loss of hydraulic contact with the soil water on the other. Hence, modelling the changes in hydraulic conductance with pressure gradients in the continuum allows the prediction of water use as a function of soil environment and plant architectural and xylem traits. Large differences in water use between species can be attributed in part to differences in their hydraulic equipment, which is presumably optimised for drawing water from a particular temporal and spatial niche in the soil environment. According to Meinzer (2002) components of dynamic variation in apparent hydraulic conductance in intact plants include exchange of water between the transpiration stream and internal

storage compartments via capacitive discharge and recharge, cavitation and its reversal, temperature-induced changes in the viscosity of water, direct effects of xylem sap composition on xylem hydraulic properties, and endogenous and environmentally induced variation in the activity of membrane water channels in the hydraulic pathway.

With the exception of significant interaction effects occurring between shade and irrigation levels on the first and eight day after terminating irrigation, the other interactions were not statistically significant throughout the drought period. This could be due to the supply and demand between soil and seedlings during the induced drought stress periods. In this regard, the above discussed variability in root and shoot growth parameters of the coffee seedlings can play a great role in the absorption of water from the soil, transpirational loss and storage of water in various seedling parts. Tyree and Ewers (1991) reported that trees growing in climates with high evaporative demand will have a low leaf to sapwood area ratio and thus, the expansion of the conducting area relative to transpiring area increases LSC. To support higher transpiration rates, a low leaf to sapwood area ratio in desert versus montane trees could increase leaf-specific hydraulic conductance. Alternatively, a high sapwood volume to leaf area ratio in the desert environment may increase the contribution of stored water to transpiration (Maherali and DeLucia, 2001). In the latter study, it was reported that by preventing xylem tensions from reaching levels that cause xylem cavitation, high leaf-specific hydraulic conductance in desert ponderosa pine may facilitate its avoidance. Thus, the primary benefit of low leaf to sapwood allocation in progressively arid environments is to increase leaf specific hydraulic conductance and not to increase the contribution of stored water to transpiration.

In addition, a number of studies have identified hydraulic limits as the cause of partial or complete foliar dieback in response to drought. The interactions between root to shoot ratio, rooting depth, xylem properties and soil properties in influencing the limits to canopy water supply can be used to predict which combinations optimise water use in a given circumstance. Xylem caviation results in the net withdrawal from the affected tissues (Tyree and Yang, 1990). This water becomes then available for transpiration and has been proposed as one of the main components of plant water storage (Zimmermann, 1983). The hydraulic approach can improve the understanding of

the coupling of canopy processes to the soil environment and the adaptive significance of stomatal behavior.

There is substantial experimental evidence that stomatal conductance is positively correlated with the hydraulic conductance of the soil- root- leaf pathway in a wide range of plant species (Bond and Kavanagh, 1999; Meinzer and Grantz, 1990; Meinzer et al., 1999; Sperry and Pockman, 1993). Therefore, in addition to the effect of path length, changes in crown architecture may determine whole-plant conductance (Becker et al., 2000). The strong positive correlation between root moisture content and leaf hydraulic resistance in the present study implies that leaf water conductance was restricted and ultimately the photosynthesis rate was declined. This finding therefore suggests moderate soil and atmospheric drought stress to optimize the available resources and improve seedling vigor. It seems likely that stomatal conductance is adjusted to maintain xylem water potential above the critical point where runaway embolism would occur (Tyree and Sperry, 1988). Such effects of hydraulic conductance on gas exchange were reported for intact plants by Meinzer et al. (1995) and Andrade et al. (1998) and for experimentally manipulated seedlings of ponderosa pine by Hubbard et al. (1999). Tausend et al. (2000b) also shown that differences in crown architecture can significantly influence plant gas exchange. In Arabica coffee, hydraulic conductance is positively correlated with total daily transpiration (Tausend et al., 2000a). A major component of differential adaptation to drought among Arabica coffee appears to be behavioral, and may be governed by rates of water use or efficiency of extraction of soil water (DaMatta et al., 2003; Meinzer et al., 1990b; Pinheiro et al., 2005). Thus, genotypes with higher hydraulic conductance should have higher rates of water use. This means that they may deplete accessible soil water more rapidly and/or have a deeper root system than genotypes with lower hydraulic conductance. The strong association of total transpiration with hydraulic conductance might dampen variation in water potential with variation in water availability, which may help to avoid non-stomatal limitation to photosynthesis and xylem cavitation (Tausend et al., 2000b). This would be advantageous with non-limiting soil water or with brief periods of water deficit, but disadvantageous with longer drought periods, since a high hydraulic conductivity would hasten the development of severe drought stress.

Hence, knowledge of the nature of the target environment to which cultivars should be bred is crucial for the success of coffee breeding programs. The proportional decrease in leaf hydraulic conductivity and leaf photosynthetic rate with increasing wood density suggests that the biophysical structure of wood may constrain physiological functions to specific operating ranges and reflect life-history trade-offs at the whole organism scale. In high-density wood, there is simply less volume available for water transport or storage. Therefore, wood density should capture some of the trade-offs between mechanical and hydraulic functions (Roderick, 2000). Relatively low leaf hydraulic conductivity and saturated water content in species with dense wood may therefore constrain gas exchange to conservative rates, such that bulk leaf water potential is maintained within a safe operating range. Wood density has been linked to support against xylem implosion by negative pressure (Hacke et al., 2001), indicating that species with high density wood may better resist cell wall collapse, and are likely to withstand lower leaf potential (Santiago et al., 2004). High-density wood is also an excellent predictor of mechanical properties, and stem elasticity is positively correlated with wood density. Thus wood density offers resistance to various environmental forces. The main benefit of low wood density, on the other hand, is high growth rate, and it appears central to a suite of plant traits related to patterns of carbon gain, ranging from leaf biochemistry to whole organism and community level processes. Further studies on seasonal variation in hydraulic properties (e.g., Brodribb et al., 2002) are likely to increase the understanding of co-ordination with leaf functional traits and how temporal patters, shape trade-offs in plant physiological functions.

7.5.5   Stomatal characteristics

The results indicate the substantial variations in stomatal length and width due to shade regimes. The potential total area of the guard cells and stomatal index were higher in the sun-exposed than in the shade seedlings. Stomatal pores were generally symmetrical, suggesting that there is a high degree of coordination between the daughter guard cells in coffee leaves. However, there was considerable variation between pore aperture and other stomatal characteristics over a single leaf and even between adjacent stomata. The findings of this study on the density and sizes of stomata are consistent with the other leaf characteristics examined in reduced and maximum light intensities. Besides other

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exogenous factors (light, water, major nutrients), the low leaf dry mass and total biomass production in the shade seedlings could be related to the modifications in stomatal characters. Therefore, the causes of variability in stomatal characteristics could be more related to microenvironments than to coffee accessions. In this case, the considerable heterogeneity in the stomatal length and mean stomatal area (4% wider) in the sun-exposed leaves needs in-depth investigations on the patterns of variations within a leaf and their functional significances in the immense Arabica coffee genetic deversity and wide agroecologies of Ethiopia.

The significant variations in stomatal characteristics of the same coffee accession under the different shade treatments provide insights into the fact that environmental factors are involved in the morphogenesis of stomata. Accordingly, the higher stomatal frequency in the sun leaves could be related to the increased intensity of light throughout the study period. The decrease in stomatal frequency in the shade may be due to the expansion or greater number of epidermal cells. 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 CO_2 concentration. Many authors (Woodward, 1987; Woodward and Bazzaz, 1988) showed that stomatal frequencies decrease with increased CO_2 concentrations. According to Woodward (1987) both stomatal index and frequency decrease with increased CO_2 concentration. Willmer and Fricker (1996) reported that water availability, light intensity, temperature and CO_2 concentrations were among the external factors affecting stomatal variables. Stomatal frequencies are usually higher in plants grown in full sunlight with high photon flux density than in plants grown in the shade with low photon flux density. Ross-Karstens et al. (1998) reported similar trends of increased stomatal density in greenhouse grown coffee due to increased light intensity. They also found a significantly reduced stomatal density with the enhancement of CO_2 concentration for coffee leaves in closed vessels.

The maximum stomatal densities of the coffee accessions from Harenna and Berhane-Kontir demonstrate their adaptive capacity in hotter and drier areas as compared to those accessions from the more humid southwestern rainforests (Bonga and Yayu). Hence, such accessions would be productive in full sun conditions as long

as soil moisture is sufficient. The accessions from Bonga and Yayu had a suitable leaf anatomy for controlling the limited available water. This is similar to the results for leaf chlorophyll and dry matter production of the same coffee accessions under the two light regimes (Chapter 6; Table 6.6; Figure 6.14), indicating the influence of CO_2 concentration and light intensity on photosynthetic rate. According to Willmer and Fricker (1996) plants growing in dry soils and low humidity generally have higher stomatal frequencies than plants growing in wet soil and in high humidity.

The decrease in most stomatal characteristics in the Berhane-Kontir accession III-3 might be related to the response of the leaves to high leaf temperature, particularly in the sun plot, because these seedlings were relatively younger compared to the Harenna and Yayu seedlings, which showed the highest average values for most of the stomatal characteristics. In general, the results reveal that, because of changing leaf area due to the difference in light intensity and leaf temperature the stomatal characteristics did not significantly differ among coffee accessions. This may be because the photon flux density was below the maximum level to bring about considerable changes as it did on other leaf growth characteristics such as leaf number and surface area. Exceptional was the accession II-2 from Bonga, which had maximum values for some stomatal parameters including the highest stomatal density per average leaf area (76728 mm^{-2}). This corresponds with the findings of Ciha and Brun (1975) on soybean. They reported that drought stress resulted in a greater stomatal frequency, smaller leaf area and significantly lower stomatal numbers per leaflet than in non-stressed leaves. The present study, therefore, testifies the stomatal adaptive mechanisms of coffee trees. The adaptive significance of stomata occurring on one-leaf surfaces is unclear, although hypostomaty is considered to be an evolutionary primitive character, and as plants adapted to growth in more open sunlit habitats, amphistomaty may have evolved almost simultaneously (Mott et al., 1982). An unsubstantiated belief is that hypostomatous leaves are better adapted to dry conditions that amphistomatous leaves. Certainly, the side of a leaf facing the sun may be slightly warmer than the opposite side in the shade and this would lead to a higher evaporative water loss from this side. However, amphistomaty may increase CO_2 uptake by reducing the length of the CO_2 diffusion pathway to the mesophyll (Parkhurst, 1978) and via its influence on stomatal resistances and boundary layer resistances (Mott et al., 1982).

Stomatal size usually decreased with increasing frequency, but this feature was not observed in coffee during the dry season. The overall seasonal average, however, show negative correlation between stomatal density and size due to shade and coffee accessions. This is in agreement with previous reports (Coste, 1992; Wrigley, 1988). Seasonal variations in the light regulation of stomatal initiation and deployment could be mediated by phytochromes (light quality) and growth hormones. Patchy stomatal opening is often more pronounced as a result of sudden changes in environmental conditions, and stomata within an area respond in concert apparently independent from the neighbouring areas (Mott et al., 1993). It has also been suggested that a specific leaf anatomy predisposes this pattern of behavior. Terashima et al. (1988) observed patchy opening in heterobaric leaves. These are leaves, which have bundle sheath extensions that extend to the epidermis so that the mesophyll is separated laterally into patches as opposed to homobaric leaves, which lack a bundle sheath extension (Larcher, 2003). A general view is that heterobaric leaves have stomata approximately opposite each other on both leaf surfaces between which run air-space channels. Another suggestion is that the patches of stomata are in a transitory stage in response to sudden environmental changes, and eventually an optimized aperture will be reached by all stomata (Cardon et al., 1994). Not all species exhibit patchy responses, however, and the extent to which they occur may depend critically on the severity of the imposed stress and the speed of application (Gunasekera and Berkowitz, 1992).

The significantly wider gap between shade treatments in the dry season could be explained in terms of increased air and leaf temperatures against which leaves may form more stomata with reduced sizes to reduce water loss. In other words, the minimum change during the wet season in the sun plots could be related to the reduced vapor pressure gradient due to cloud cover and high relative humidity. The increased age of the seedlings between the initial (wet) and final (dry) data measurements could also be among the possible reasons for the stomatal dynamics. The relationships between stomatal attributes were in consistence with this response. Overall, seasonal climatic variables, coffee accessions, seedling age and growth characteristics in all treatments were found to affect leaf stomatal behavior. The results agree with the reports of several authors (Coste, 1992; Wrigley, 1988), who reported a negative correlations between number and size of leaf stomata in coffee plants. According to

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literature (Coste, 1992; Hopkins, 1995; Wrigley, 1988), transpiration and CO_2 assimilations are regulated via the stomatal opening, which is dependent on the plant water demand and environmental conditions. Ross-Karstens et al. (1998) pointed out the significant influence of CO_2 and light intensity on stomatal aperture and density of different plant species. In the present study the influence of stomatal size on predawn RLWC was different among accessions, the Harenna accessions displaying a higher drop in leaf water content. This may be related to the high photosynthetic capacity of these accessions compared to the others. The leaf stomata were elliptical in shape, and varied in size and distribution patterns. In Ethiopia, there is no information on the molecular control of stomatal initiation and spacing patterns in cultivated and wild coffee. The mechanisms determining the formation and arrangement of stomata and their ecological implications for adaptation require further investigations as is the case with respect to the association between stomata characteristics and other physiological traits.

8   OVERALL SUMMARY

Though Arabica coffee has evolved in the montane rainforests in southwestern Ethiopia and is a shade-adapted plant, its morphological and physiological characteristics were seen to be significantly different along the prevailing climatic gradients and site characteristics. Highly significant differences were observed among the four selected montane rainforests (Harenna, Berhane-Kontir, Bonga, and Yayu) in the distribution of silt and soil bulk density. In contrast, the proportion of clay particles did not show significant differences; the average clay values followed the order of the populations Harenna>Berhane-Kontir>Bonga>Yayu. There were highly significant variations in available water holding capacity of the soils. With regard to soil chemical properties, the soils at the four rainforest sites did not reveal significant variations for most parameters, except Mg, CEC and C:N ratio. Variations were noted between the surface and subsurface soils of the four sites, indicating the inherent vegetation characteristics of the studied forests. At Harenna, surface soil had significantly higher total nitrogen and organic matter contents than sub-surface soil. The decline in available phosphorus with depth was also significant at the Harenna and Yayu sites.

The results show variations in moisture contents in the soil-plant systems at all study sites, mainly due to variations in seasonal rainfall patterns and site physical characteristics. Soil moisture results follow the order of summer>spring>autumn>winter seasons in the southwestern areas. In contrast, at Harenna in the southeast, soil moisture was slightly lower in the summer than in the winter. There were also significant diurnal differences between predawn and midday leaf water potential during the relatively wet seasons, i.e., the values were highly significant in winter and summer at the Harenna and Yayu sites, respectively, indicating the variability in site features, tree morphology and stand structures. This is evident from the seasonal changes in leaf adjustments and root growth systems, most likely as mechanisms for coping with low availability of soil moisture. Highly significant variations in the size and length of coarse lateral roots were found among the coffee populations: a high proportion of coarse lateral roots was determined in Bonga and Berhane-Kontir, while the fine and medium lateral roots were high for the coffee trees in Yayu and Harenna. Coffee trees did not reveal significant differences in whole plant

root and shoot hydraulic conductance. Highly significant variations were, however, detected in main-stem hydraulic conductance and in stem-specific hydraulic conductivity. Coffee trees in the Berhane-Kontir and Harenna forests revealed high hydraulic conductance values both in root and whole shoot as compared to Bonga and Yayu. The average branch hydraulic resistance values declined in the order of Bonga>Yayu>Berhane-Kontir>Harenna, indicating the resistance proportion to the growth characteristics of primary branches.

The coffee accessions from Harenna and Yayu were fast in seedling emergence and subsequent early growth stages, but the underlying mechanisms in seed and microclimatic conditions were not in the scope of this study. Morphologically, the Harenna and Berhane-Kontir populations had open canopies, while the Yayu and Bonga populations had intermediate to compact canopies. The open and intermediate types showed better seedling growth vigor with high root and shoot dry matter production under optimum environments compared to the compact canopies. At the same time, the Harenna seedlings were the first to be affected by induced drought stress, and their recovery after re-watering was poor. This means that the Harenna accessions were more vulnerable to xylem embolism and operated closer to their hydraulic limit than the Berhane-Kontir and Bonga accessions. The opportunistic Harenna accessions were more efficient in conducting water to their leaves but had less control over water use compared to the accessions in the southwest, particularly the Berhane-Kontir seedlings. However, in all cases, there was a decline in leaf water potentials and relative leaf water contents from shade to sun plots. In the sun, overall adjustment of the leaf area occurred in order to maintain homeostasis of other physiological growth parameters. Stem diameter, leaf number and seedling height were amongst the morphological parameters strongly linked to hydraulic properties in that order. Among the root parameters, the most important variables were root dry weight, root fresh weight and lateral root length.

The coffee seedlings from Harenna and Yayu were tall and more efficient in water conductance than those from Bonga and Berhane-Kontir. This indicates that the Harenna seedlings had a high hydraulic efficiency in terms of root and shoot biomass production capacity. They could extract water rapidly when it was plentiful, but needed mechanisms to limit water use when it became scarce. The results in general show that the accessions from the southwest were more resistant to drought than those in Harenna

in the southeast, the latter showing the highest mortality rate due to extensive drought over a 16-day period. On the other hand, the Bonga and Berhane-Kontir seedlings showed strong resistance to embolism due to a conservative strategy that relied on the low vulnerability of the conducting system. The results in part demonstrate the variability in morphological attributes and growth stages of seedlings. The reduced soil moisture in the sun compared to the moderate shade plots reflects the gradients between soil-plant-air in vapor pressure and water demand. The ability of the accessions to postpone dehydration was more important than dehydration tolerance, and plant water relations were unable to adjust to drought stress in the high productive coffee types. The high productivity of the Harenna accessions could be due to high average values of leaf size, leaf chlorophyll, leaf nitrogen and stomatal density. These accessions were damaged through drought stress at an early stage, although they possessed greater plasticity to avoid damage via such features as high root to shoot ratio, deep roots, thick leaves, high recovery rate, wider changes in diurnal leaf water potentials and high accumulation of potassium ion. This could be due to relatively poor stomatal control of transpirational water loss. The high water conductance and related features could explain why the Harenna accessions experienced symptoms of drought stress earlier than the other accessions after irrigation was suspended. The Berhane-Kontir accessions, on the other hand, were shallow rooted, but they might have closed stomata more efficiently than the others and hence dried more slowly. Similar to Berhane-Kontir, growth and stomatal closure seemed to maintain higher leaf water potential in the Bonga accessions. These accessions showed substantially lesser root growth than the drought-sensitive Harenna accessions.

Therefore, physiological and morphological characteristics, such as stomatal conductance, crown architecture, root depth and water-use efficiency, are recommended as potential traits for selecting coffee cultivars with superior performance under drought conditions. The focus on the most important root and shoot growth parameters can curtail the problems of drought stress in drought-prone areas and where there are occurrences of dry spells at critical growth stages of mature coffee trees in field conditions. However, there is much yet to be done about the behavior of the stomata and vascular tissues and the response of coffee populations to water and atmospheric droughts. Generally, there were trade-offs between growth performances of the coffee

trees and resource-use efficiency along climatic gradients both in nursery and field conditions. The effect of major plant nutrients on soil microbial activity, drought, disease, insect, plant vigor and coffee quality are also an area of future research. Further investigations are required to understand the ecological adaptation of wild coffee populations and their accessions in environments similar to the respective montane rainforests in southeast and southwest Ethiopia.

9   GENERAL CONCLUSIONS AND RECOMMENDATIONS

9.1   Conclusions

The findings of this study show that wild Arabica coffee populations in the four montane rainforests had different phenotypic and agronomic traits, ecophysiological behavior and reacted differently to induced drought stress and different shade treatments. The shoot and root morphological characteristics followed the prevailing climatic gradients, whereby the Harenna and Berhane-Kontir forests hosted coffee trees with broad leaves and crowns in contrast to the narrow canopies of the Yayu and Bonga rainforests. Phenotypically, the coffee populations at Harenna and Berhane-Kontir were close; this also applied to the Yayu and Bonga populations. The proportion of lateral roots of varying size followed annual precipitation gradients and soil textural distribution. Consequently, the Harenna and Yayu populations had a higher proportion of fine lateral roots than those at Bonga and Berhane-Kontir. This could serve as a drought-stress avoidance mechanism in the drier Harenna and sand-dominated Yayu soils. Thus, drought tolerance of the wild coffee populations could not be correctly predicted from the rainfall gradients alone. This could be attributed to the vegetation cover conserving the available soil moisture for an extended period of time. There was high litter fall mainly from indigenous shade trees and hence, the soils were characterized by high soil organic matter, which also improved water and nutrient retention capacities of the soils. Nonetheless, the micro-climatic variables such as high relative humidity, low light, low temperature and hence reduced vapor pressure deficits can impair the normal physiological activities of coffee trees and hence, poor growth and developments are inevitable phenomena in the forest ecosystem, leading to a trade-off between plant species diversity and coffee productivity. To exhaust the present findings, more transects within the forest areas remain to be investigated during the different seasons. As to what extent ecophysiological variables can dictate the existing multiple cropping remains uninvestigated.

The results also show that moderate shade created more favorable microclimatic conditions for the coffee seedlings by decreasing leaf and soil temperatures. The water content of the seedlings was higher in moderate shade than in the sun, mainly due to reduced transpiration loss. However, seedling growth

performance and dry matter assimilation were poorer in the shade than in the sun plots, which could be related to reduced root growth, high specific leaf area, low chlorophyll content, low stomatal density, and reduced leaf nitrogen in the shade seedlings. This was a trade-off between growth performance and resource use capacity of coffee trees and hence, production of high quality seedlings requires judicious manipulation of environmental conditions vis-à-vis growth stage of coffee seedlings. In general, provision of moderate shade is of paramount importance for the germination and early development of coffee seedlings. Nonetheless, with increasing age, the seedlings need to be hardened off through gradual reduction of overhead shade and through increased irrigation intervals. The Harenna accessions showed the highest values for seedling emergence, root to shoot ratio, leaf chlorophyll, leaf nitrogen, leaf potassium contents, stomatal density and thus, total biomass production, while these values were lowest for Berhane-Kontir. The results of the *ex-situ* hydraulic conductance measurements in the coffee seedlings were in consistence with the *in-situ* measurements, and the results follow the order of Harenna>Berhane-Kontir>Yayu>Bonga. The reverse was true for branch hydraulic resistance patterns, though these varied with branch aging and growth characteristics. The removal of plant parts was also found to enhance water movement in the coffee trees and seedlings, which testifies the practical implications of leaf defoliation and pruning practices. Moreover, the Berhane-Kontir seedlings showed highest leaf water potentials, largely due to low transpiration even when soil water was abundant, whereas seedlings from the Harenna accessions showed high stem- and leaf-hydraulic conductivity, which eventually fell below the critical threshold of the leaf and soil water potentials. Accordingly, with limited soil moisture, high irradiance and low humidity, the Harenna accessions were the first to exhibit leaf wilting and early damage and failed to recover from the prolonged severe drought stress, while accessions from Berhane-Kontir were less affected. The values for Bonga and Yayu were intermediate.

In contrast to the research hypothesis, which states that accessions from the driest Harenna areas are less drought tolerant than those from the wet southwestern regions, both root and shoot hydraulic conductance of the coffee trees and seedlings were highest for the Harenna coffee trees and accessions, followed by the wettest Berhane-Kontir. This primarily reflects the influence of growth vigor (above all stem diameter and leaf growth) in water transport efficiency and thus high carbon

assimilation rate. This could be related to large stem diameter and greater average leaf size, but such coffee accessions become vulnerable to cavitation under persistent severe drought stress. In essence, the different wild coffee populations showed different morpho-physiological strategies for coping with environmental stress. Considerable accession variability in root, total biomass and related traits was observed, which provides an option to select coffee accessions with better root types for achieving good growth and development under water-limiting conditions. In this regard, the accessions from Harenna showed better root characteristics and may be suitable for water-limited areas within certain limits of drought-stress ranges. Unlike the southwestern accessions, the Harenna seedlings were noted to accumulate higher leaf potassium with terminating irrigation, indicating osmotic water regulation effects. Similarly, the Harenna coffee trees and seedlings effectively exploited soil moisture by their extensive rooting system. At the same time, they showed a liberal use of available soil water, though they ran the risk of being damaged under low soil moisture conditions. Conversely, the accessions from Berhane-Kontir followed a conservative water use strategy even under optimal environmental conditions where reduced biomass production was recorded, though the seedlings regulated high water status during the 16-day period of soil drying. This study shows that drought-stressed coffee seedlings exhibited critical drought-stress effects 8 and 12 DAI under sun and shade conditions, respectively. This could, however, vary depending on the climatic conditions and growth stage of the seedlings, suggesting further investigations. Based on the present findings, sustainable use of wild coffee populations, therefore, requires above all protection of the fragmented natural forests for multi-site *in-situ* conservation of wild coffee germplasm in environmental conditions similar to their respective original habitats. For this, additional research is necessary to explore the effects of agroforestry practices on microclimate, resource partitioning, coffee physiology, productivity and quality in order to provide adequate recommendations on the selection and management of associated shade trees according to ecological conditions of each region.

9.2   Recommendations

The results show inter- and intra-population variability among the four wild coffee populations in phenotypic traits and hydraulic characteristics. Multi-location *in-situ*

conservation strategies are necessary for the wild coffee populations with different morpho-physiological characteristics and mechanisms for coping with drought-stress conditions. In this regard, establishment of on-farm community-based conservation approaches, improving the major constraints associated with traditional coffee production systems and landraces should be the priority step. Nevertheless, activities on collection, characterization and *ex-situ* conservation at ideal field gene banks are also equally important to complement the *in-situ* conservation of the gene resources. In this regard, 60 coffee accessions, which were collected from the studied four wild coffee populations, were transplanted at the field gene bank of the Jimma Research Center and are ready for further research. Moreover, simulation of the original forest habitats through, among others, use of ideal shade trees, multiple cropping, soil conservation techniques and pruning practices are important. For this, indigenous farming systems and cropping patterns for each forest area should be considered to mimic the original ecology and target corrective forest management options. This should include the adoption of appropriate coffee-based agroforesty systems, and expansion of fruit and multipurpose trees like bamboo and leguminous trees. The findings will help to design future research and development options, particularly on the level of human interventions towards the sustainable management, conservation and utilization of coffee genetic resources in the montane rainforests of Ethiopia. In this regard, the following future research areas can be drawn:

1. Determination of the level of management inputs to manipulate the dense shade and high coffee tree population densities, which are irregular and non-productive in terms of reproductive efforts. Most coffee trees are old and constrained by biotic and abiotic stresses. Therefore, population adjustment, slight pruning and restoration of the dried mother trees are important to improve tree vigor and maximize water-use characteristics and ultimately maintain the local gene pool.

2. Adoption of improved management practices to improve the productivity of landraces and improved coffee cultivars per unit land area. To this end, diversification of other income sources using locally adapted crops, spices and other non-timber forest products is also crucial to maintain the coffee landraces. These areas can serve as a buffer zone to undisturbed forests.

3. Analysis of water dynamics in the soil-plant-atmosphere within the multi-stories of the forest canopy cover as well as in the bare lands adjacent to the forest areas.

4. Determination of resource-use efficiency of coffee trees and associated plants during different seasons and growth stages.

5. Investigations of the dynamics of carbon sequestration, nitrogen sources and mineralization rates in the southwestern forests to determine the reasons for the low C:N ratio.

6. Development of appropriate perennial and multipurpose tree-based agro-forestry systems for each forest coffee unit as buffer zones to the relatively undisturbed montane rainforests.

7. Assessment of the relationships between ecological factors (climate and soil) and coffee yield and quality attributes in the forest coffee production systems.

8. Identification of drought-stress-tolerant coffee cultivars requires further evaluation of wild coffee accessions under their respective ecological conditions. For this, nursery sites could be established to raise seedlings from the corresponding wild coffee populations and use these to fill the gaps within the forest ecosystem.

9. Identification of the main biotic and abiotic stresses in each forest ecosystem. This would enable design of corrective forest management options; germination and regeneration of coffee seedlings should deserve high research priority.

10. Evaluation of promising coffee accessions using different pot sizes and soil types would help to examine the potential root proliferation and shoot growth systems and thus osmotic regulation effects in dry soil conditions. The comparison should be based on natural rainfall patterns that include different levels (mild, moderate and severe) and rates (fast and slow) of soil drying conditions. The use of drought-tolerant coffee cultivars (improved and landraces) would also be important for comparison purposes.

11. The present findings on morphological growth and hydraulic characteristics need further research on genetic diversity and disease reactions of the respective wild coffee accessions. Evaluation and identification of promising accessions for

yield and quality parameters would provide information on suitable coffee cultivars for each region.

12. Further investigations on the anatomy of vascular tissues, particularly on xylem elements (trachied and vessels), contributions of phytohormones and biochemical constituents in relation to size and architecture of coffee trees are required to fine-tune the underlying mechanisms and traits involved (in order of importance) in tolerance to drought stress of wild coffee trees and accessions established at the field gene bank.

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11 APPENDICES

Appendix 1 Correlation matrix values between soil chemical properties at each montane rainforest of Ethiopia

Location	Variable	TN	OM	pH	EC	K	Ca	Mg	CEC	AvP
Harenna	OM	0.93**								
	pH	-0.22	0.002							
	EC	-0.07	0.22	0.84*						
	K	0.78	0.93**	0.16	0.42					
	Ca	0.77	0.94**	0.31	0.52	0.95**				
	Mg	0.46	0.60	0.46	0.47	0.79	0.70			
	CEC	0.84*	0.97**	0.01	0.28	0.96**	0.95**	0.61		
	AvP	0.86*	0.93**	-0.09	0.20	0.96**	0.86*	0.71	0.93**	
	C:N	-0.55	-0.22	0.54	0.60	0.00	0.08	0.05	-0.03	-0.24
Bonga	OM	0.97**								
	PH	0.71	0.84*							
	EC	0.11	0.15	0.04						
	K	0.22	0.18	-0.10	0.38					
	Ca	0.36	0.22	-0.20	-0.09	0.80				
	Mg	0.12	0.03	-0.25	-0.10	0.86*	0.90*			
	CEC	-0.70	-0.66	-0.59	0.61	0.28	-0.15	0.03		
	AvP	0.81	0.76	0.45	-0.06	0.62	0.75	0.66	-0.56	
	C:N	0.51	0.69	0.90*	0.23	-0.04	-0.34	-0.23	-0.32	0.32
Berhane-Kontir	OM	0.99**								
	pH	-0.31	-0.37							
	EC	0.22	0.14	0.78						
	K	0.80	0.72	0.20	0.66					
	Ca	0.86*	0.87*	-0.67	-0.18	0.50				
	Mg	0.80	0.78	-0.62	-0.12	0.53	0.97**			
	CEC	0.02	-0.05	-0.51	-0.42	0.04	0.32	0.48		
	AvP	-0.44	-0.36	-0.24	-0.77	-0.71	-0.21	-0.28	0.04	
	C:N	0.36	0.48	-0.21	-0.18	-0.103	0.35	0.15	-0.64	0.29
Yayu	OM	0.99**								
	pH	-0.04	0.02							
	EC	0.07	0.03	-0.93**						
	K	0.55	0.60	0.28	-0.43					
	Ca	0.57	0.60	0.53	-0.66	0.90*				
	Mg	0.71	0.68	-0.18	0.37	-0.02	0.11			
	CEC	0.80	0.76	0.12	-0.14	0.33	0.57	0.71		
	AvP	0.40	0.47	0.20	-0.31	0.94**	0.80	0.01	0.16	
	C:N	0.97**	0.99**	0.07	-0.04	0.71	0.69	0.61	0.71	0.60

*; ** = correlations are significant at 0.05 and 0.01 levels, respectively (2-tailed).

Appendices

Appendix 2   Growth characteristics of primary branches used for measurement of hydraulic resistances at the study sub-sites within each montane rainforest of Ethiopia

Site	LDW	SDW	FDW	FrNr	SV	NN	LMC	SLA	SLM
Harenna	NS	NS	NS	NS	NS	NS	NS	NS	NS
PIS1	3.07±1.27	3.51±2.52	2.83±4.10	15.33±22.31	4.22±1.35	2.67±0.52	73.91±10.07	152.48±35.83	0.007±0.002
PIS2	3.02±1.59	3.02±1.70	1.70±2.20	10.17±13.00	3.87±1.08	2.67±0.52	78.09±7.65	156.33±61.08	0.008±0.004
PIS3	4.63±3.09	5.57±4.41	1.00±1.15	5.83±6.77	4.55±1.31	2.67±0.52	73.53±1.96	143.56±16.43	0.007±0.001
Bonga	*	NS	NS	NS	NS	NS	*	NS	NS
PIIS1	3.63±1.64a	3.45±2.40	2.07±3.22	17.17±23.05	3.17±0.41	2.83±0.41	72.07±3.31 ab	134.93±14.61	0.008±0.001
PIIS2	2.40±1.01b	2.89±1.79	1.65±2.53	5.33±7.05	4.00±0.89	3.00±0.63	71.50±4.25 b	116.19±9.62	0.009±0.001
PIIS3	2.36±1.04b	3.19±2.08	2.82±4.57	9.00±14.30	3.83±0.75	3.33±0.82	74.07±1.36 a	123.83±16.42	0.008±0.001
B-Kontir	NS	NS	NS	NS	NS	NS	NS	NS	NS
PIIIS1	3.32±1.48	3.15±1.64	2.83±4.27	14.67±22.34	3.67±0.52	3.33±0.82	74.67±2.86	143.71±18.64	0.007±0.001
PIIIS2	1.99±1.80	2.77±2.24	0.40±0.69	4.17±5.15	4.17±0.75	2.83±0.98	74.72±1.08	152.90±26.86	0.007±0.001
PIIIS3	3.14±1.09	3.22±2.02	2.26±4.16	12.00±20.33	3.83±0.75	2.50±1.05	73.32±3.16	158.72±43.74	0.007±0.002
Yayu	NS	NS	NS	NS	NS	**	NS	NS	NS
PIVS1	3.61±1.27	4.34±2.49	1.47±2.17	9.00±13.25	4.33±0.82	2.17±0.41b	75.03±1.35	147.00±13.07	0.007±0.001
PIVS2	3.39±1.64	4.15±3.32	0.07±0.11	0.33±0.52	4.50±1.38	3.50±0.84a	74.47±3.18	124.48±18.46	0.008±0.001
PIVS3	2.06±1.18	2.88±2.10	0.10±0.25	0.50±1.22	3.67±1.21	4.17±1.17 a	75.17±2.17	151.00±13.77	0.007±0.001

*Ns = Not significant; *P<0.05; **P<0.01 significance levels (Tukey test at P = 0.05). Abbreviations: LDW = leaf dry weight, SDW = stem dry weight, FDW = fruit dry weight, FrNr = fruit number, SV = stem volume, NN = number of nodes, LMC = leaf moisture content, SLA = specific leaf area, SLM = specific leaf mass.*

Appendix 3   Average number, diameter and length of lateral roots (means±sd) in wild coffee trees at the study sub-sites of each montane rainforest of Ethiopia

Location	№ of lateral roots				Diameter of lateral root (cm)			Length of lateral root (cm)			
	Large	Medium	Small	Total	Large	Medium	Small	Large	Medium	Small	Taproot
Harenna	NS	NS	*	NS	NS	NS	NS	NS	*	NS	NS
PIS1	9.50±0.71	14.00±4.24	33.00±2.83a	56.50±6.36	0.79±0.01	0.23±0.01	0.09±0.01	113.39±33.43	33.24± 3.53b	23.53±13.05	83.25±25.81
PIS2	8.50±3.54	11.00±4.24	20.50±0.71b	40.00±7.07	0.90±0.25	0.31±0.06	0.11±0.01	109.15±15.55	46.69± 6.30b	12.70± 1.46	85.25±16.62
PIS3	5.50±3.54	19.50±4.95	25.50±0.71b	50.50±2.12	0.72±0.06	0.32±0.03	0.11±0.01	125.57±53.12	86.98±14.44a	24.30± 0.03	114.50±10.61
Bonga	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
PIIS1	13.00±0.00	9.50±7.78	23.50±21.92	46.00±29.70	0.35±0.13	0.22±0.04	0.11±0.00	67.52±30.21	47.31±8.92	29.04±2.50	69.33±16.02
PIIS2	12.00±5.66	9.00±2.83	3.50±4.95	24.50±13.44	0.63±0.22	0.23±0.01	0.06±0.08	85.44±12.46	76.19±32.07	14.52±20.53	64.20±15.98
PIIS3	19.00±2.83	5.00±2.83	6.50±2.12	30.50±3.54	0.48±0.01	0.22±0.00	0.12±0.01	71.59±5.20	52.19±2.15	28.56±4.41	71.25±1.77
B-Kontir	*	NS	NS	NS	NS	NS	NS	NS	**	NS	NS
PIIIS1	16.00±0.00a	10.00±7.71	9.50±2.12	35.50±4.95	0.51±0.11	0.21±0.01	0.11±0.00	100.59±18.98	51.52±5.72b	31.78±4.58	70.73±3.63
PIIIS2	11.00±1.41b	6.50±2.12	22.50±10.61	40.00±14.14	0.52±0.08	0.23±0.04	0.13±0.02	69.17±11.43	69.68±6.39a	29.52±0.01	95.05±24.11
PIIIS3	13.50±0.71ab	8.00±7.07	10.50±10.61	32.00±16.97	0.59±0.04	0.26±0.01	0.12±0.03	91.68±9.69	70.42±8.62a	34.81±1.60	92.95±2.76
Yayu	*	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
PIVS1	11.50±2.12ab	15.50±4.95	48.50±12.02	75.50±14.85	0.46±0.01	0.25±0.04	0.11±0.01	80.72±13.71	54.43±6.64	27.71±0.32	129.32±100.67
PIVS2	15.00±0.00a	11.00±0.00	22.50±0.71	48.50±0.71	0.45±0.11	0.23±0.04	0.12±0.02	76.98±13.34	49.69±7.81	21.37±8.17	91.00±28.28
PIVS3	8.50±0.71b	11.00±1.41	20.00±2.83	39.50±2.12	0.42±0.06	0.20±0.03	0.11±0.02	74.35±11.73	52.34±7.87	23.79±2.13	93.60±22.49

NS =Not significant, *, ** = significant at P<0.05 and P< 0.01, respectively. Means with the same letter(s) within a column are not significantly different according to Tukey mean grouping at P = 0.05.

Appendix 4   Physical and chemical properties of the potting medium used for *ex-situ* study

Variable	Value
Physical property	
Sand (%)	30.56
Silt (%)	35.28
Clay (%)	34.16
Texture class	Clay loam
FC (at 0.33 bar)	49.45
PWP (at 15 bar)	26.87
Available water (bar)	22.58
Chemical property	
Total nitrogen (%)	0.50
Organic matter (%)	9.19
Organic carbon (%)	15.81
pH-H_2O (1:2.5)	4.83
C:N	31.61
EC (1:2.5)	0.13
Available P (ppm)	20.95
K (meq/100g)	8.15
Ca (meq/100g)	13.38
Mg (meq/100g)	5.11
CEC (meq/100g)	36.70
Base saturation (%)	72.59

Appendix 5   ANOVA (mean squares and pr>F) for the hydraulic resistance in primary branch of wild coffee trees at each montane rainforest of Ethiopia (Nested design)

Source	DF	Harenna	Pr>F	Bonga	Pr>F	B-Kontir	Pr>F	Yayu	Pr>F
Total	71	2.69E+10		1.34E+12		7.61E+10		2.38E+11	
Tree	5	8.08E+10	0.10	4.25E+12	0.54	1.48E+11	0.73	9.39E+11	0.43
Branch	12	3.37E+10	0.103	4.95E+12	<0.0001	2.62E+11	<0.0001	8.83E+11	<0.0001
Error	54	2.03E+10		2.65E+11		2.82E+10		2.94E+10	
Mean		1.50E+05		7.66E+05		3.74E+05		4.26E+05	
SEM		3.35E+04		2.43E+05		4.53E+04		1.14E+05	

Appendix 6   Mean squares and Pr>F for hydraulic conductance in root and shoot component parts of wild coffee trees (Nested design)

Source	Df	Root	Pr>F	Whole shoot	Pr>F	Leaf	Pr>F	Fuit/petiole	Pr>F	Branch	Pr>F	Stem cut	Pr>F
Total	3	7.34E-09		2.25E-08		1.27E-08		4.72E-09		7.54E-09		3.78E-08	
Pop	3	1.94E-08	0.06	5.60E-08		1.51E-08	0.11	9.02E-09	0.44	2.13E-08	0.16	2.15E-07	0.004
Site	8	5.15E-09	0.55	2.00E-08		1.50E-08	0.34	5.70E-09	0.28	9.53E-09	0.03	2.08E-08	0.011
Error	12	5.78E-09		1.57E-08		1.06E-08		2.99E-09		2.77E-09		4.75E-09	

Appendix 7   Two-way ANOVA for leaf water potentials in coffee seedlings during different days after irrigation (DAI) in sun and shade

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. Abbreviations: DAI =Days after irrigation, Df = Degree of freedom; PD = Predawn, MD = Midday, DD = Diurnal difference.

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