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

[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

[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).

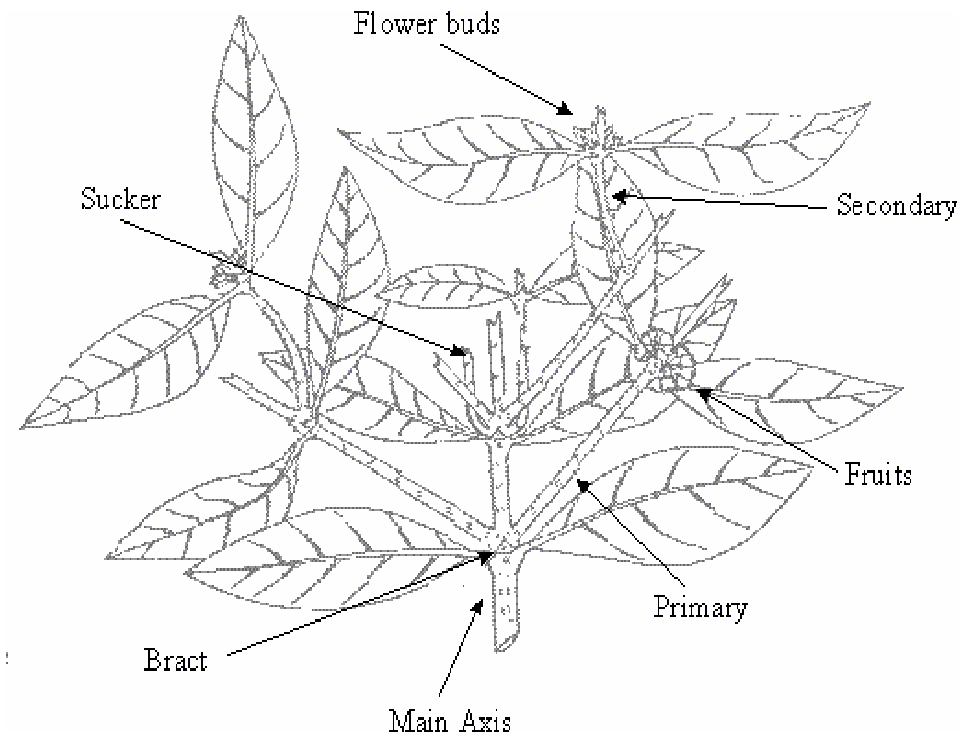

Figure 2.1 Shoot morphology of mature Arabica coffee tree

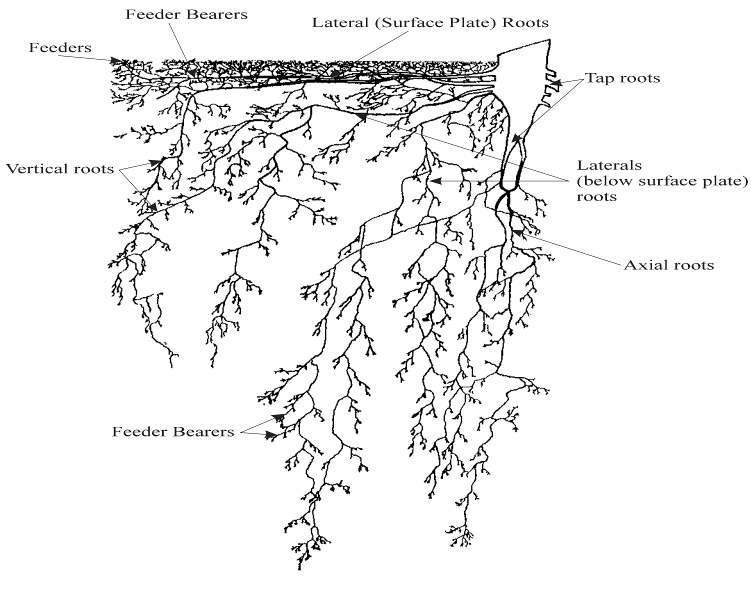

Figure 2.2 Root system of mature Arabica coffee tree

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).

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 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