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SCHOOL OF GRADUATE STUDIES
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Growth and Physiological Response of Two *Coffea arabica* L. Populations under High and Low Irradiance



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ABBREVIATIONS

SH	Stem height
NB	Number of branches
SG	Stem girth
IL	Internode length
SLA	Specific leaf area
A	Assimilation rate
A_{net}	Net assimilation rate
A_{max}	Maximum assimilation rate
gs	Stomatal conductance
E	Transpiration Rate
Ci	Internal carbon dioxide concentration
WUEi	Instantaneous water use Efficiency
WUE	Water use efficiency
PAR	Photosynthetic active radiation
μm	Micro mole
HI	High irradiance

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ABSTRACT

The objective of this study was to evaluate the effects of varying irradiance on the growth and physiology of Coffea arabica. Growth measurements such as stem height (SH), number of branches (NB), stem girth (SG), internode length (IL) and specific leaf area (SLA) were measured, whereas, net assimilation rate, transpiration rate and water use efficiency were measured for gas exchange measurements. Two Coffea arabica populations (Bale and Sheko) were grown in pots placed in the greenhouse of Addis Ababa University under two irradiance regimes, high irradiance (HI)/direct sunlight and 20% of shade (20% HI) for six months. The result of this study shows that stem height, number of branches and stem girth was found higher for exposed coffee plants than the shaded in both populations. However, the Bale coffee population achieved higher growth rate than Sheko coffee population under their respective irradiance level with respect to the three parameters. Specific leaf area in shaded coffee plants was found to be higher than exposed in both populations. But under shade environment, Sheko coffee plants attained lower value than Bale, where, under high irradiance the reverse is achieved. Internode length was also higher in shaded coffee plants of Bale populations, whereas, it showed the same growth with exposed ones in Sheko populations. For internode length, Shaded Bale coffee plants showed higher growth rate than shaded Sheko coffee plants. But under high irradiance Sheko coffees achieved higher value than Bale. As stated for gas exchange measurements, net assimilation rate (A_{net}) and stomatal conductance (gs) for exposed coffee plants was higher in both populations than shaded. But transpiration rate (E) for both coffee populations under direct sunlight was found lower than under shade. Compared to Sheko coffee plants, Bale coffees showed higher value for daily integrated net assimilation rate and transpiration rate under their respective irradiance level. Moreover, as a result of higher net assimilation rate and lower transpiration rate in exposed coffee plants, it was expressed that integrated daily water use efficiency (WUE) was found higher in exposed coffee trees in both populations. And comparing the two populations, under high irradiance Bale coffees exhibited higher daily integrated water use efficiency than Sheko, while both populations showed similar value under shade. Exposed Bale coffee plants had higher light saturated rates of photosynthesis than the shaded one, which shifted from $200 \mu \text{mol Photons m}^{-2} \text{s}^{-1}$ to $600 \mu \text{mol Photons m}^{-2} \text{s}^{-1}$.

But leaves of Sheko coffee trees under high and low irradiance levels were saturated between 800 $\mu\text{mol Photons m}^{-2} \text{s}^{-1}$ and 900 $\mu\text{mol Photons m}^{-2} \text{s}^{-1}$ respectively.

Furthermore, it is observed from the result that the coffee plants exhibited substantial phenotypic plasticity for most of growth and physiological traits in response to varying irradiance level; thereby the magnitude of plasticity differed markedly among the populations. In particular, plants originating from drier climate (Bale region) showed the highest amount of plasticity suggesting fast adaptation to changing irradiance.

These results suggest that this species performs well under high irradiance light though it has been grouped under shade adapted plants .It provides the growth and physiological response and reveal the difference among the two coffee populations in morpho-physiological characteristics. This differential response to light conditions may contribute to its ability to succeed in natural and agricultural environments or to endure control strategies. Moreover, this study contributes as baseline information for further research on the management and use of coffee production.

Key words: *Coffee, Growth, Net CO₂ assimilation, Stomatal conductance, Internal CO₂ concentration, Irradiance Photosynthetic active radiation*

1. INTRODUCTION

1.1. Background and Problem Statement

Coffee, an evergreen tropical crop, is one of the most valuable commodities in the international agricultural trade (Chaves *et al.*, 2008). For many years, it has been the second highest commodity following oil as a source of foreign exchange and a major employer globally (Muffett, 2002; Wexler, 2003; DaMatta, 2004a). Globally, it is reported that over US\$ 90,000 million could be generated from coffee international trade each year (Chaves *et al.*, 2008). It also provides job opportunities for about 500 million people employed in all activities from cultivation to the final product for consumption (DaMatta and Ramalho, 2006; Chaves *et al.*, 2008).

Among some 100 species of the *Coffea* genus; Arabica coffee (*Coffea arabica* L.) and robusta coffee (*Coffea canephora* Pierre ex Froehner) economically dominate the world coffee trade being responsible for about 99% of world bean production (Taye Kufa, 2006; Davies *et al.*, 2006 cited in DaMatta *et al.*, 2007). However, out of the overall world coffee production, 70% of the consumption is from Arabica coffee, while the rest comes from robusta coffee (Vieira *et al.*, 2006). In its center of origin and genetic diversity in Ethiopia, Arabica coffee evolved as an understory shrub in the deeply shaded forest canopy cover of southwestern montane rainforests (Righi *et al.*, 2007; Carr, 2001) close to the equator, at latitudes of 1400 and 1800 meters where a place which has a dry season that lasts for 3 to 4 months, and the annual precipitation ranges from 1,200 to 2,000 mm throughout the year with temperatures varying from 18 to 22°C (Righi *et al.*, 2007). Therefore, the coffee plant is considered to be a shade-obligatory (DaMatta, 2004; Chaves *et al.*, 2008; Franck and Vaast, 2009).

Arabica coffee grows both as a wild as well as a cultivated cash crop in many regions of the world now days (Masresha Fetene and Solomon Habtemariam, 1995). In early plantations, coffee bushes were planted under shade canopy in order to simulate their natural habitat

accounting for the fact that it has evolved as an understorey shrub showing all physiological and structural characteristics of a shade adapted plant (Grades, 2007; Wexler, 2003; Muffett, 2002; Meinzer *et al.*, 1990; Yacob EDJAMO², 1991; DaMatta, 2004; Perfecto *et al.*, 1996; Demel Teketay, 1999; Carelli *et al.*, 1999). In many situations, however, coffee grows well without shade and even outyields shaded coffee (Beer *et al.*, 1998). This is particularly found under optimal or near-optimal edaphoclimatic conditions for coffee cultivation, where shading provides little, if any, benefit to the crop (DaMatta 2004). Shading was therefore abandoned as a regular cultural practice in several regions, and complete transition from traditional “shade” to modern “sun” coffee growing system started following the development of new varieties of coffee that thrives in direct sunlight which traces back in the late 1970s (Vaast *et al.*, 2006; Perfecto *et al.*, 1996; Gorsline, 2006). These modern sun-coffee plants have a more compact canopy and shorter branches allowing higher planting densities under their own dense shade leading to an increased production per hectare than traditional shade-coffee” plants (Perfecto *et al.*, 1996; Meinzer,*et al.*, 1990; Vaast *et al.*, 2006; Wexler, 2003; Muffett, 2002; DaMatta and Ramalho, 2006; Faminow and Rodriguez, 2001). In addition, this production system allows coffee growers to increase their production dramatically within a short period. Moreover, this approach is usually practiced using intensive application of chemical fertilizers, which contributes for a faster growth rate or more beans in short time, and an increased pruning (Steiman, 2003 cited in Adugna Debela, 2007; Perfecto *et al.*, 1996).

DaMatta *et al.*, (2007) noted excessive shading by upper two to three canopy strata of various tree species under forest environment is reported to reduce the growth and productivity of the coffee plant. In such conditions, the plants spent much of their photosynthesis activities for maintenance purposes and also achieve reduced whole-tree carbon assimilation (DaMatta, 2004; DaMatta *et al.*, 2007; Franck and Vaast, 2009). Moreover, coffee productivity considerably decreases as a result of death of heavily shaded productive middle and bottom primary branches which is induced by dark respiration (Tesfaye Woldmariam *et al.*, 2002 cited in Taye Kufa, *et al.*, 2007). Dense shading also results in reduced coffee fruit load through their effects on coffee physiology, such as longer internodes, fewer nodes formed per branch and flower buds at existing nodes (Montoya *et al.*, 1961 and Castillo and Lopez, 1961 cited in DaMatta, *et al.*, 2007; Vaast *et al.*, 2006; Franck and Vaast, 2009). Unlikely, under optimal growing conditions yields

are higher in high irradiance (Beer *et al.*, 1998). Coffee has low rates of net carbon assimilation (A_{net}), typically below $11 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Franck *et al.*, 2006; Araujo *et al.*, 2008) which has been related to diffusive rather than biochemical limitations (Chaves *et al.*, 2008; DaMatta *et al.*, 2007). Actually, the stomatal limitations are associated with a strong stomatal sensitivity to increasing leaf-to-air vapor pressure deficit (VPD) along the day (Ronquim *et al.*, 2006 cited in Franck and Vaast, 2009; Vaast *et al.*, 2007) and result in large reductions of A_{net} , particularly in the afternoon (DaMatta and Ramalho, 2006). Moreover, this species is prone to photoinhibition of photosynthesis when exposed to full solar irradiance (Ramalho *et al.*, 2000 cited in Franck and Vaast, 2009). Nevertheless, photoinhibitory limitations of A_{net} in high irradiance have been shown to be of secondary importance as compared to g_s limitations in commercial Arabica coffee varieties according to Chaves *et al.*, (2008) who attributed this feature to an acclimation to high irradiance in order to prevent photoinhibition. On the other hand, heavy shading due to light penetration by the upper strata can result increased competition for light for photosynthesis which, in turn, leads to undesirable growth of single stemmed coffee trees with thin and reduced reproductive efficiency (Franck and Vaast, 2009). Although coffee leaves exhibit typical shade acclimation features, theoretically allowing them to maintain (A_{net}) in low light (Holmes 1967 cited in Franck and Vaast, 2009). Araujo *et al.*, (2008) recently found a low physiological plasticity to low light in coffee leaves located inside the canopy, resulting in reduced A_{net} as compared to exposed leaves. Limitation of photosynthesis by low light availability has been proposed as one of the main reasons for lower yields of coffee grown in agroforestry systems in optimal coffee production areas such as southeastern Brazil (DaMatta *et al.*, 2007) and the Central American highlands (Beer *et al.*, 1998).

From the above, it may be reasoned that coffee leaves, regardless of exhibiting low A_{net} , should have enough plasticity to acclimate themselves to contrasting light environments. So far, however, there has been no consistent examination about growth and physiological mechanisms associated with such plasticity in coffee.

The major goal of this study was therefore, to investigate the growth, morphological and physiological responses as adaptive mechanisms in two *Coffea arabica* populations grown under high and low solar radiation and to evaluate the differences between the two populations. Growth

and Leaf gas exchange measurements were carried out in the experiment. The two populations were taken from two different ecologies; “Bale” from southeast Ethiopia and “Sheko” from southwest Ethiopia which are pot-planted in the greenhouse of Addis Ababa University.

1.2. Hypothesis of the study

It was hypothesized that:

- I. Irradiance gradient would impact the growth and gas exchange of *Coffea arabica*.
- II. High irradiance negatively influences the growth and photosynthesis of the species.
- III. The growth and gas exchange response of *Coffea arabica* to high and low irradiance would vary among populations.

2. OBJECTIVES OF THE STUDY

2.1. General Objectives

To determine, the impact of varying light irradiances on growth, morphology and physiology of *Coffea arabica* and examine the degree of variations among two populations.

2.1.1. Specific Objectives

1. To investigate growth, Photosynthesis and morphological characteristics of two coffee populations as influenced by two differing light irradiances.
2. To investigate the morphological and physiological mechanisms by which *Coffea arabica* adapt with different irradiance levels.
3. To compare the morphological and physiological traits those are affected by varying irradiances between the two populations.

3. LITRATURE REVIEW

3.1. *History of Arabica coffee*

3.1.1. *Origin*

In spite of the fact that coffee is an old world crop, there are no early historical references to it. Thus, its history had been an agenda of great controversy among many plant scientists. Different legendary stories exist to explain the location where *C.arabica* was originally domesticated and discovered. About the origin of coffee, the most popular and best-known story is that of a goat herd, Kalid who observed his normally docile goats prince excitedly, skipping, rearing and bleating loudly, after chewing berries from some a shiny dark-leaved shrub nearby, around 9th century in Ethiopia (Wiersum *et al.*, 2007). He also tried the berries himself and enjoyed their stimulating effect. Meanwhile, a monk who found Kalid in a novel sense of ecstasy decided to try the berries and took some of it back to monastery. He roasted and brewed them and tried the beverage on his brethren so as the monks in the monastery started using it and were kept alert during their long night prayers. While the legends attempt to condense the discovery of coffee and its development as a beverage into one story, it is believed that the monks of Ethiopia may have chewed on the berries as a stimulant for centuries before it was brewed as a hot drink.

The other historical belief indicates that all base populations of Arabica coffee descended from the few trees that survived various efforts to spread Arabica coffee from southern Arabia, now Yemen, in to the main coffee producing areas (Lashermes *et al.*, 1995). This is due to the fact that the first records of the beverage as a medicine and economically important crop in the 15th century and the tree was obtained from Yemen (Merid Aregay, 1988; Demel Teketay, 1999). Likewise Linnaeus believed Arabica coffee to have originated in Arabia; accordingly he gave it the scientific name *Coffea arabica*.

Despite this quaint story, from botanical data, the origin of Arabica coffee is determined with fair degree of confidence currently as of Ethiopian origin. Most authorities agree that the origin and genetic diversity of Arabica coffee is the cool, shady environment in the understory of forests in the southwest Ethiopian highlands (Carr, 2001; DaMatta and Ramalho, 2006; Merid Aregay,

1988; Wexler, 2003; Muffett, 2002; Taye Kufa, 2006; Adugna Debela, 2007), “Kaffa” region where the plant was first discovered blossoming (Tadesse Mekuria *et al.*, 2004). In view of this, the term “Coffee” is explained to come from “Kaffa” the name of the region which is inherited from the hieroglyphic nouns ‘KA’ which is the name of God and ‘AFA’ which is the name of Earth and all plants that grow on earth (Tadesse Mekuria *et al.*, 2004;). Moreover, all botanists who have traveled around the forests of the southwestern highlands of Ethiopia agree that Ethiopia is the center of diversity of *Coffea arabica* (Charrier and Berthaud, 1985). They have confirmed by the presence of wild coffee plants with a high genetic variability in Ethiopia within small area as compared to the wild coffee populations of Yemen that showed low genetic diversity (Lashermes *et al.*, 1995). Therefore, since the dawn of history, coffee has been in “Kaffa” and it was from this region in the early time the use of the extract of coffee bean spread over the entire Ethiopian highlands.

3.1.2. Spreads of Arabica coffee

Arabica coffee was first introduced to Yemen for cultivation from Ethiopian highlands (Merid Aregay, 1988; Vieira *et al.*, 2006). However, its historical introduction to Yemen as to when, how and by whom still remain unclear. Some legends suggest that Arab traders and their penchant for carrying things around have been responsible for the movement of seeds from Ethiopia to Yemen (Lashermes *et al.*, 1995). Another account put forward that coffee was brought to Arabia from Ethiopia, by Arab slave raiders may have noted the practices of Ethiopian aborigines used to carry ground coffee mixed with oils or fats, made up into balls to comfort and stimulate them during arduous journeys, or that captured slaves were found with dried coffee fruits in their custody (Haarer, 1962 cited in Demel Teketay, 1999). Furthermore, it has been suggested that Arabica coffee could have been introduced to Yemen by Persian invaders who traveled into Ethiopia from the Nile Valley or by Ethiopians who had traveled once to Arabia with the first coffee seed (Wellman, 1961).

After its spread throughout the Arab world and as they knew the value of this little bean, they tried to limit cultivation to only the Arabic regions. Despite their best efforts, the race to make off with some live coffee trees or beans was eventually won by an Indian called Baba Budan, who first introduced fertile coffee beans, the berries with their husks unbroken into South-West

India on his return from a pilgrimage to Mecca in the 17th century (Wrigley, 1988). Coffee then spread to other parts of India, but not till the early 19th century that the British began to develop coffee estates. From the Arabian Peninsula coffee is believed to travel to the East. The Arabs are credited with first bringing coffee to Sri Lanka (Ceylon) as early as 1505 (Wrigley, 1988). The Dutch who invaded Sri Lanka saw the future in coffee for coffee-house trade in Europe, began expanding existing scattered coffee farms there by about 1658 (Demel Teketay, 1999). Coffee started to be grown for profit by Europeans in Sri Lanka and India. After seeing its excellent production and the wealth it brought in Sri Lanka, the Dutch took coffee plants from India to an island in Indonesia called Java in 1696 and introduced in to the Dutch East Indies (now Indonesia) for the first time (Demel Teketay, 1999). However, the coffee plants which was successfully established and become the origin of all early coffee in the Dutch East Indies were the one brought from Malabal after loss of the coffee plants established in Java due to earthquake and flood in 1699 (Demel Teketay, 1999).

A coffee plant was introduced to Amsterdam Botanical Garden in 1706 where it afterwards produced seeds and seedlings which were distributed to the principal Botanical Gardens in Europe (Demel Teketay, 1999). In 1714, Antoine de Jussieu (Professor of Botany) gave a coffee tree the name *Jasminum arabicum laurifolium* after the tree was sent by King Louis XIV of France to the Jardin des Plantes in Paris (Demel Teketay, 1999). The French, meanwhile, attempted to establish coffee to Reunion (earlier Bourbonne) from seeds and small plants purchased from the port of Mocha (in Yemen) two times, but were successful in the third time in 1717 or 1778. They were able to survive a single coffee plant which was originally from Ethiopia in 1720 (Demel Teketay, 1999). This single tree is purported to be the origin of the millions of trees in existence today and become as known “Bourbone Coffee”. Several years later large coffee plantations were developed in the island and then the coffee plant continued its journey to the Caribbean Island of Martinique and all countries of the Americas except Brazil, French Guiana and Surinam (Wrigley, 1988). Meanwhile, in 1718, the Dutch transplanted the coffee to Surinam and soon after the plant became widely established in South and Central America, specifically it was introduced to French Guiana in 1722 and to Brazil in 1727 (Wrigley, 1988).

3.2. Botany and Taxonomy of *Coffea arabica*

3.2.1 Botany of *Coffea arabica*

Coffee is an evergreen woody plant that belongs botanically to the genus *coffea*, which in turn is a member of the family *Rubiaceae*, one of the largest flowering plant families containing 500 genera and 6000 species (Demel Teketay, 1999; Alemayehu Kiros, 2007). A number of ornamentals derive from the family, notably gardenia (*Gardenia*), madder (*Rubia*), partridgeberry (*Mitchella*), and ixora (*Ixora*), however, *Coffea* is by far the most economically important genus of all (Wellman, 1961).

Discussions about the genus *Coffea* show that the number of species encompassed in the genus *Coffea*, as it has been recognized by different authors, are dissimilar. DaMatta and Ramalho (2006) mentioned that 90 species exist in the genus, whereas, Vieira *et al.*, (2006) note about 100 species to survive. On contrary, 103 species of the genus *Coffea* is enumerated by Davis *et al* (2006) cited in Solomon Balami (2007). Meanwhile, Wrigley (1988) generalizes the number of species belonging to *Coffea* as recognized by different authors, ranging from 25-100. However, what is more has been commonly agreed by most botanists over this issue is, the existence of three most economically important species in the genus: *Coffea arabica* L., *Coffea canephora* Pierre ex Froehner and *Coffea librica* Bull ex Hiérn. It is also reported that all members of *Coffea* to be indigenous to Africa, Madagascar and the Mascarenes (Demel Teketay, 1999; Alemayehu Kiros, 2007). In addition, Bridson (1982) cited in Demel Teketay (1999) stated that probably 25 good species to exist with an additional 11 poorly known ones in Africa.

3.2.2 Taxonomy of *Coffea arabica*

Coffee is first classified as a separate genus, *Coffea*, in the *Rubiaceae* family by the Swedish taxonomist Carolus Linnaeus in his *Genera Plantarum* (1737) (Solomon Balami, 2007; Vieira *et al.*, 2006; Demel Teketay, 1999), though its first botanical description giving the name *Jasminum arabicum laurifolia* (Oleaceae) was made by Antoine de Jussieu based on a single plant cultivated in Paris obtained from the botanical garden of Amsterdam in 1714 (Demel Teketay, 1999). In line with this, the name *Coffea arabica* descends till today after Linnaeus coined the name in his *Species Plantarum* (1753). The works of both Linnaeus and Jussieu was based on

specimens of direct or indirect Arabica origin. On the other hand, different authors have described *C.arabica* giving different names based on Ethiopian material.

Historical classifications carried out based on morphological data by Berthaud and Charrier (1988); Bridson and Verdcourt (1988) and Bridson (1987) cited in Solomon Balami (2007) state that coffee trees are classified in to two genera; the genus *Coffea* L. and *Psilanthus*. The *Psilanthus* genus comprises *Paracoffea* and *Psilanthus* (Hook f.), while *Coffea* L. includes two subgenera, *Baracoffea* and *Coffea*. In other classification carried out by Leroy (1980) cited in Demel Teketay (1999) the genus *Coffea* encompasses three subgenera, *Coffea*, *Baracoffea* and *Psilanthopsis*. As the morphological characters traditionally used to separate species are weak and often exist a degree of overlap, the taxonomy of the genus *Coffea* is difficult (Demel Teketay, 1999; Lashremes *et al.*, 1997 cited in Solomon Balami, 2007). The fact that some species are more closely interrelated than others, nevertheless such species clusters have not been clearly defined by sound taxonomic characters, morphological or others (Wrigley, 1988).

However, more recently, *Rubiaceae* is recognized to encompass eleven genera based on morphological and molecular data (Davis *et al.*, 2007; Davis *et al.*, 2006 cited in Solomon Balami, 2007). These are, *Argocoffeopsis*, *Belanophora*, *Calycosiphonia*, *Coffea* L., *Diplospora*, *Discospermum*, *Nostolachma*, *Psilanthus*, *Tricalysia*, *Sericanthe* and *Xanthea*. Among this subgenus, *Coffea* contains by far most of the species and includes all those commercially important including the most cultivated *C.arabica*, *C.canephora* and *C. liberica*.

As Demel Teketay (1999) explains between 40 and 50 infraspecific taxa of *C. arabica* have been mentioned, which are taxonomically better referred to as cultivars. Two varieties of *C.arabica*; var.*arabica* and var. *bourbon* are recognized by many authors (Lashermes *et al.*, 1995). Var. *bourbon* is more slender in habit than Var. *arabica*, has smaller beans but higher yield, resists coffee berry disease better, has green-tipped young leaves and fruit-bearing branches which bend down at the tips only, though, Var. *Arabica* has bronze-tipped young leaves and pendulous fruit-bearing branches (Demel Teketay, 1999). All other intraspecific taxa are assumed to have been descended from these two varieties and currently, a plethora of modern cultivars, derived from

these cultivars, are now grown in greater quantities than the originals (Lasherms *et al.*, 1995). Besides, the botanical variety designation lacks utility outside of breeding.

3.3. Morphological and physiological features of Coffea arabica

3.3.1. Morphology of Coffea arabica

The plant

Arabica coffee is an upright, dicotyledonous shrub or small tree up to 5 m to 6 m in height and 7cm in diameter at breast height (Charrier and Berthaud, 1985; Fitchl and Admasu, 1994). The species is well known by its two types of branches (Demel Teketay, 1999; Taye Kufa, 2006) ; orthogeotropic which grow vertically and is commonly called suckers, and plagiogeotropic branches which have different orientation angles in relation to the main stem and is commonly called primaries (Taye Kufa, 2006). Primary branches give rise to secondary branches, which in turn split to tertiary branches and that also branch to form quaternary branches (Wintgens, 2004 cited in Taye Kufa, 2006). The green epidermis of both orthogeotropic and plagiogeotropic branches is useful in order to distinguish each new growth in addition to the amount of current new growth is proportional to the number of berries (Tewelde-Berhan Geberegzabiher, 1974 cited in Fikru Meko, 2005). Furthermore, the bark of the species is light grey, thin, and becomes fissured and rough when old; and the wood is light-colored, hard, heavy, and tough (Charrier and Berthaud, 1985).

Leaves

The leaves of Arabica coffee are simple with short petioles and interpetiolar stipules; and arranged oppositely on stems and decussate, with successive pairs of leaves arising at 90° angles from each other around the stem. They are evergreen, glabrous, shiny and dark green in color; ovate to elliptical blades of 4-8 inches long; prominently veined with interveinal areas raised; and waxy and smooth with entire margin and acuminate tips at both ends (Gilman, 1999; Duke, 1983). The life span of Arabica coffee leaves is less than a year. Moreover, on the lower surface of the leaves there are small cavities called domatia bulging out on the super surface of the leaves (Fikru Meko, 2005). According to Wrigley (1988), 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 domatia have been used to distinguish *Coffea* species and varieties

Flowers

Flowers grow in the axils of the leaves and the flowers are white in color, pleasant fragrant, profuse, aggregates (inflorescence) (Gilman, 1999). The floral parts are pentamorous (5 parts); united sepals; 5 linear petals fused into a slender corolla tube at their base; 5 stamens inserted in the corolla tube; long anthers on slender upright filaments; pistils with inferior, bicarpellate ovary containing 2 ovules and a short style with 2 short pointed stigma (Pochet and Flémal, 2001 all cited in Fekru Meko, 2005).

Reproduction

Reproduction and distribution of Arabica coffee is by seeds (Taye Kufa, 2006). The plant takes approximately 3 years to develop from germination to first flowering and fruit production (Wrigley, 1988). Coffee usually flowers and fruits once per season, but in some areas it flowers at different times (Charrier and Berthaud, 1985). For example, in Puerto Rico blossoming occurs from January to April (Barrett, 1925 cited in Charrier and Berthaud, 1985), while in Nicaragua from February through May (Stevens *et al.*, 2001 cited in Charrier and Berthaud, 1985). In addition in south-central Brazil flowering occurs from August to November (DaMatta *et al.*, 2007). In Panama Roubik (2002) observed one to five flowerings during his five years study of Arabica coffee, between January and early May. The temporal and physiological hierarchy of flower bud initiation and differentiation within each branch, and also among different nodes of the same plagiotropic branch is supposed to be one of the unrestrained factors responsible for several blossom periods in Arabica coffee, in addition to the occurrence of sporadic and sometimes low-intensity rains during the latter phases of flower bud development (Rena and Barros, 2004 cited in DaMatta *et al.*, 2007).

Four to five months before anthesis, buds that will develop into flowers are usually induced, but the flower buds are soon arrested remain dormant until stimulated by a temperature shock and

supply of one set of rain in the season following a dry period (Carr, 2001). The time between breaking of the dormancy and anthesis may vary four to ten days depending on temperature and atmospheric humidity (Taye Kufa, 2006). After two days, flower buds start to wither and its all parts drop except the ovaries. A flash movie on the steps of coffee bean development clearly can be referred from Michael Griffin Coffee Research Institute using the link <http://www.coffeeresearch.org/agriculture/beandevol.htm>. Accordingly, to summarize it in short, the ovaries will then develop into drupes in a rapid growth period that takes about 15 weeks after flowering. During this time the integument takes on the shape of the final bean. After the rapid growth period the integument and parchment are fully grown and will not increase in size. The endosperm remains small until about 12 weeks after flowering. At this time it will suppress, consume, and replace the integument. The remnants of the integument are what make up the silverskin. The endosperm will have completely filled the cavity made by the integument nineteen weeks after flowering. The endosperm is now white and moist, but will gain dry matter during the next several months (Eirira *et al.*, 2006). During this time the endosperm attracts more than seventy percent of the total photosynthesates produced by the tree. The mesocarps will expand to form the sweet pulp that surrounds the bean. The cherry will change color from green to red about thirty to thirty-five weeks after flowing (Eirira *et al.*, 2006).



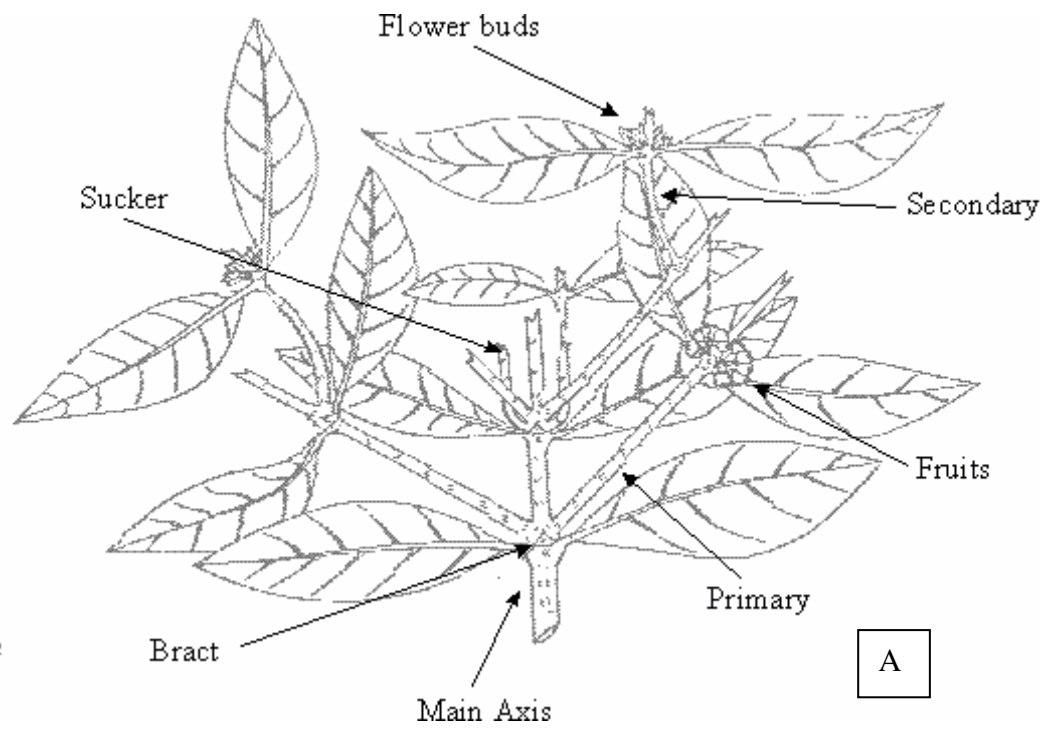
Figure 1(A) Beans on coffee tree, (B) Red berry beans of coffee trees

Chromosome number

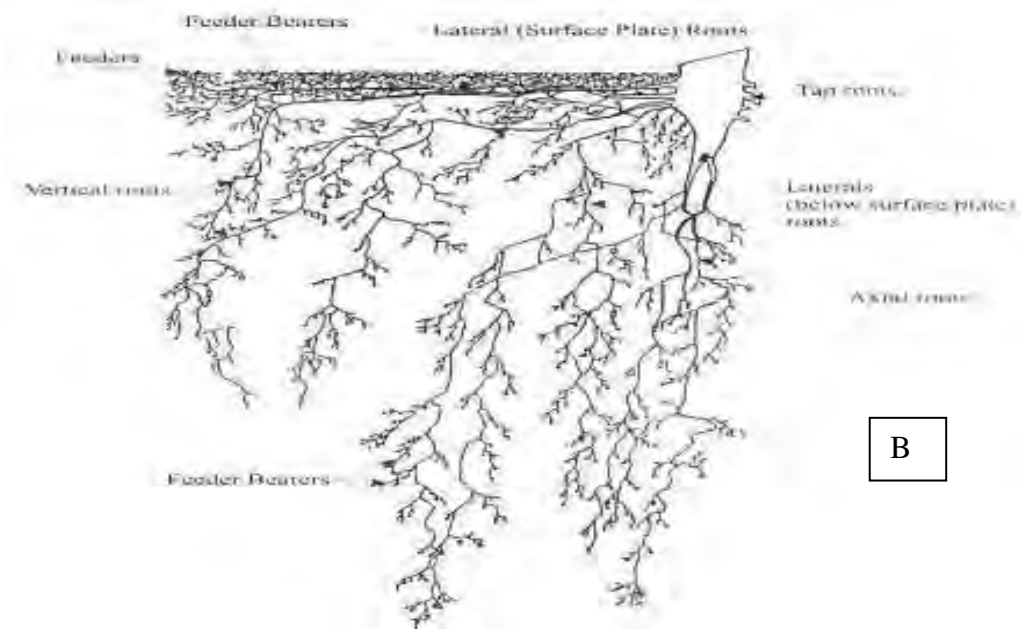
Unlike all coffee species that exhibit the characteristics of C_3 plants and are diploid with 22 chromosomes, Arabica coffee is the only known autogamous (95%) allotetraploid ($2n=4X=44$) species in the genus (Lashermes *et al.*, 1995).

Roots

The typical root system of a mature Arabica coffee tree is concentrated in the first 0.30m layer from the soil surface and distributed in a circle of about 1.50m in a diameter around the trunk (Alfonsi *et al.*, 2005 cited in DaMatta *et al.*, 2007). The system consists of a tap root, axial vertical roots; lateral roots, some of which are more or less parallel to the ground (surface plate roots) and others deeper roots that firmly evenly in the soil and sometimes become vertical, feeder bearers evenly distributed, and feeder-born roots at all depths (Taye Kufa, 2006; Combrony, 1992; Caste', 1992 cited in Fekru Meko, 2005). It is morphologically characterized by a thick, short and often multiple tap roots extending from 30-45 cm below the soil surface. But rarely extends beyond 45 cm (Schaffer and Andersen, 1994). Four to eight axial roots may be encountered which often originate horizontally but point downwards 25 to 30 cm in an assembly originating from the branching of the tap root (Schaffer and Andersen, 1994). The deep lateral roots may branch uniformly and sometimes revert to vertical roots. About 80-90% of the feeder root is in the first 20 cm of soil and is 60-90 cm away from the trunk of the tree (Mavolta, 195-196 cited in Tee, 2010). It is reported that the root system of coffee is highly plastic and the horizontal and vertical growth of coffee roots can be affected by the plant genotype, age as well as environmental conditions such as texture, structure, depth, aeration, moisture and fertility of the soil (Taye Kufa, 2006; Caste' 1992 cited in Fekru Meko, 2005; Schaffer and Andersen, 1994). To be thick and strong the root system requires an extensive supply of nitrogen, calcium and magnesium. During planting the main vertical roots are often clipped to promote growth of the horizontal roots, which then have better access to water and added nutrients in the top soil.



A



B



Figure 2: (A) the Shoot and (B) the root morphology of Arabica coffee tree (Taye Kufa, 2006); and (C) a mature coffee tree

3.3.2. Physiology of Coffea arabica

Coffee as a shade adapted plant, however in many situations can grow well without shade even out-yielding shaded coffee. The species has a very small rate of net CO₂ assimilation (typically in the range of 4-11 $\mu\text{molm}^{-2}\text{s}^{-1}$ with current atmospheric CO₂ concentration and saturating light as compared to many other tropical tree crops (Araujo *et al.*, 2008). Coffee plant exposition to high irradiance can seriously impact on the performance by limiting photosynthesis, resulting in reduced net carbon gain and plant growth (Grades, 2007). When 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). In fact, coffee plants show a certain ability to acclimate to sunlight (DaMatta and Ramalho, 2006), though this depends on competition for water and nutrients, pest and disease incidence (Muschler *et al.*, 1998 cited in Grades, 2007), which implies the need of optimal growing conditions and often high levels of external inputs for sun-grown coffee (Fournier 1988; Muschler 1997). Climate conditions where plants have to cope with an exposure to high irradiances are also often accompanied by high temperatures and each effect may be superimposed by the other. However, with coffee cultivation under open sun becoming a common practice in many parts of the world, coffee is frequently exposed to temperatures of 40°C and more (Araujo *et al.*, 2008), which is more than double the optimal temperature range for Arabica coffee. Thus, overheating of the leaves is a common feature, which may have devastating effects on plant metabolism by disrupting cellular homoeostasis and uncoupling major physiological processes. The results are not only a depressed growth but also an inadequate storage capacity, abortion of flowers, acceleration of development and ripening of fruits, and hence a loss of quality (Grades, 2007). However, 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 (Taye Kufa, 2007).

3.4. Ecological requirements of Coffea Arabica

As to the ecological requirements, climate and soil are major factors that affect the productivity and longevity of a coffee plantation and associated trees other than management. Among the climatic factors temperature, rainfall, altitude, humidity and wind are the most important parameters. Since coffee trees are sensitive to the prevailing limitation of these climatic conditions, knowledge of the response of coffee plants to these ecological requirements is very crucial and to set future counteractive management alternatives.

Temperature

Temperature is the most important climatic factor that highly influences the growth and development of coffee plant (Carr, 2001). Arabica coffee can withstand fluctuations in

temperature, if it is not too extreme (Taye Kufa, 2006). The ideal average temperature ranges between 15°C and 24°C though it can tolerate temperatures much below or above these limits for short periods (Charrier and Berthaud, 1985; Taye Kufa, 2006). In day air, physiological processes can be influenced by increase in temperature above 30°C. Moreover, continues exposure to temperatures as high as 30°C accelerates leaf loss and induces a general decline in tree health (Drinnan and Menzel, 1995 cited in Carr, 2001; Franco, 1958 cited in DaMatta and Ramalho, 2006). Temperatures above optimum facilitates rapid growth, too early bearing, overbearing, early exhaustion, dieback and disease attack (Demel Teketay, 1999; Fekru Meko, 2005). Higher temperatures can also cause flower shedding and reduced fruit formation while slow, stunted and uneconomic growth, high production of secondary and tertiary branches and the so-called “hot-and cold” disease in cold temperatures (Demel Teketay, 1999). Frost also destroys both leaves and fruits (Willson, 1985 cited in Charrier and Berthaud, 1985). Nunes *et al.* (1968) cited in Carr (2001) state that temperatures below 12°C inhibit growth and development and above 24°C, net photosynthesis begins to decrease and is negligible at 34°C. Arabica coffee prefers a climate tempered by altitude. Taye Kufa (2006) explains that with increased altitudes, coffee growth and fruiting can be affected by physiological problems due to temperature drops.

Rainfall

Rainfall is the second most limiting climatic factor, next to the ambient temperature for coffee plant (Carr, 2004; Taye Kufa, 2006). Coffee cannot tolerate water logging as well as extended drought conditions. The rainfall requirement of coffee plants depends on factors such as: the retention property of the soil, atmospheric humidity and cloud cover and cultivation practice (DaMatta and Ramalho, 2006; DaMatta *et al.*, 2007). Arabica coffee needs an optimum total rainfall range 1500-1800mm that is evenly distributed over the growing period of 8 to 9 months (Taye Kufa, 2006). A short dry spell, lasting 2-4 months, corresponding to the quiescent growth phase, is important to stimulate flowering for Arabica coffee (Haarer, 1958 cited in DaMatta and Ramalho, 2006). In this 2-4 drier months when growth slows, young wood hardens and flower buds develop (Van Hilten *et al.*, 1992 cited in Demel Teketay, 1999). Intense rainfall throughout the year (without dry seasons) is implied to be often responsible for scattered harvests and low yields (Cannell, 1985 cited in Carr, 2001).

Altitude

Altitude is important for its direct influence on climate (Demel Teketay, 1999). Temperature is significantly affected by altitude in that for every rise of 1000m there is a fall of about 6°C in temperature (Demel Teketay, 1999). Arabica coffee grows best at higher altitudes and is often grown in hilly mountain areas (Wrigley, 1988). It is an upland species native to southwest Ethiopian tropical forests growing as an understory tree at altitudes of 1600-2800m (DaMatta and Ramalho, 2006). Though the altitude for growth of coffee differ from country to country, the favorable conditions for the growth of Arabica coffee are found on the equator at approximately 1525-1830m above sea level (Demel Teketay, 1999). For example, the optimum altitude is 1370-1680m, 1590-1770m and 920m on Mount Kilimanjaro in Tanzania, in Kenya and Mexico, respectively. In equatorial areas Arabica coffee is a highland crop growing between 1000 and 2000m above sea level (Willson, 1985 cited in Demel Teketay, 1999). Until limited by frequent and lengthy frost, *Coffea arabica* can be grown at lower altitudes further from the equator (Taye Kufa, 2006; Demel Teketay, 1999).

Humidity

Humidity has a significant impact on the vegetative growth of the coffee tree. It plays a role in governing the loss of water or moisture by evapotranspiration. When it is high, loss of water is reduced and vice versa. Especially it is important during the dry season as high humidity decreases the stress on the coffee trees thereby extending the rainless period through which the plants will survive without damage (Demel Teketay, 1999). Arabica coffee requires a less humid atmosphere, comparable to that of the Ethiopian highlands (Haarer, 1958; Coste, 1992 cited in DaMatta and Ramalho, 2006).

Wind

Wind may have different effects on the growth and yield of Arabica coffee. Excessive wind can cause physical damage to the trees. Wind stress may lead to a reduction of leaf area and internode length of the orthotropic and plagiotropic branches (Caramori *et al.*, 1986 cited in DaMatta *et al.*, 2007). In addition, it damages severely leaves and buds, and aggravates shedding of developing flowers and fruits (Camargo, 1985; Matiello *et al.*, 2002 cited in DaMatta and

Ramalho, 2006). Cold wind increases the effect of low temperature leading to an increased effect of the so-called “hot-and-cold” diseases (Demel Teketay, 1999). Hot wind increases evapotranspiration as a result creates water stress in 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 (Taye Kufa, 2006).

Soil

Arabica coffee will succeed on soil derived from various parent materials. In fact it grows well in the clay-siliceous soils of granite as it does on soils of volcanic origin with diverse characteristics or even on alluvial soils (Taye Kufa, 2006). Soil structure which allows good drainage is the most important property for coffee plant growth. This is the fact that the plant cannot tolerate waterlogged soil and Water-logging will reduce yield by a substantial amount and kill the coffee trees if it is prolonged (Taye Kufa, 2006; Demel Teketay, 1999). Water capacity and depth are the other two properties to be considered. Since it provides sufficient available water higher water capacity helps to maintain evapotranspiration during dry season while deep soils allows root proliferation by offering a larger volume of soil which contains more water and nutrients around the coffee trees (Demel Teketay, 1999). Deep soils are especially necessary in areas where there is a long dry season coupled with lower rainfall. Arabica coffee can grow well on deep soil. The other important properties of soil for the growth and productivity of coffee are pH and quantity of nutrients available. It can perform on soils with Ph of a slightly acidic character while the best conditions are pH 5.3-6.5 (Taye Kufa, 2006; Charrier and Berthaud, 1985). Even so, there are also highly productive coffee plantations on soils with pH of 7.0. Highly organic enriched areas and also areas prosperous with Phosphorus which is an important element in shoot growth and leaf initiation are highly suitable (Taye Kufa, 2006).

3.5. Coffee Production in Ethiopia

The production of coffee is of an enormous relevance for Ethiopia, playing a dominant role in economic, social, cultural and environmental terms. It is the central agricultural export product. In the 2008/09 crop year, an average of about 27000 metric tonnes of coffee is produced in the country (EAFCA, 2010). Out of this 60% of the exported coffee is specialty. Nevertheless, a special feature of Ethiopian coffee production is that domestic consumption is considerably high,

as coffee is a traditional beverage throughout the country; FAO estimates that about 50 percent of the total harvest is used within Ethiopia, and that some farmers grow coffee only for home consumption (Dercon 2002 cited in Grades, 2006). For the rapidly growing population, coffee is a means of subsistence or even sole source of income. In line with this, the livelihood of 25 % of the total population is estimated to depend on its production, processing and marketing directly or indirectly (Tadesse Woldemariam Gole and Feyera Senbeta, 2008). In contrast to other coffee producing countries, the Ethiopian coffee production is dominated by smallholder agriculture, contributing with more than 90-95 percent to the total harvest with an average farm size of 0.5ha (Tadesse Woldemariam Gole and Feyera Senbeta, 2008; Tadesse Mekuria *et al.*, 2004).

The major coffee producing administrative zones in Ethiopia are Keffa, Sidamo, Ilubabor, Wellega, Gedeo and Harerghe followed by Shoa, Gamu Gofa, Arsi, Gojjam, Bale and Wello producing substantial amounts mainly for local consumption (Dercon and Lulseged Ayalew, 1995; Mesfin Amaha, 1991 cited in Demel Teketay, 1999; Tesfaye Wakgari, 2006). The estimated coffee production area in Ethiopia is about 400,000 ha (Taye Kufa, 2006); although there are a potential 6 million ha of suitable coffee producing land (Tadesse Mekuria *et al.*, 2004). It is reported that 80% of the average annual national production, which is about 250,000 ton (Taye Kufa, 2006), is dry processed (natural) coffee and about 35% is locally consumed (Alemayehu Kiros, 2007). The country's annual national average per capita coffee consumption is 3kg. Both small-scale coffee farms and large-scale modern plantations contribute 90% and 10%, respectively to the country's coffee production. Ethiopian coffee growers produce nine spectra of the finest single-origin/ specialty coffee which are namely: Jimma, Nekemet, Illubabor, Limu, Tepi, Bebeke, Yirgacheffe, Sidamo and Harar, which are now well diffused into the trade circuits of the coffee industry (Tadesse Mekuria *et al.*, 2004).



Figure 3 the major coffee producing areas of Ethiopia

Source: Volkmann, 2008

The production system of coffee in Ethiopia is generally grouped into four (Tadesse Woldemariam Gole and Feyera Senbeta, 2008). These production systems and the area they cover are represented in Table 1.

Table 1: Coffee production systems in Ethiopia**Source: Esayas Aga *et al.*, 2003**

Coffee production system	Area cover (%)
Forest coffee	10
Semi-forest coffee	35
Cottage (Garden) coffee	50
Plantation coffee	5

Forest coffee

Forest coffee areas are largely located in southwestern parts of the country which is the center of its origin (Tadesse Woldemariam Gole and Feyera Senbeta, 2008); including the administrative zones of west Wellega, Illubabore, and Sheka-Kefa Bench-Maji, viz. Yayu and Anfillo. The forest coffee known as also wild coffee is a self-grown coffee tree under naturally growing heterogeneous species of overhead shade trees. In this system, coffee berries are simply collected from naturally grown coffee. It has a wide diversity for selection and breeding for disease resistance and also offers high yields and top-quality aroma and flavor. The Management to improve coffee growth and production in forest coffee doesn't involve human intervention (Tadesse Chanie, 2006). As Volkmann (2008) notes forest coffee among local people but also among experts is perceived differently, ranging from 'purely organic', 'untouched' or 'unmanaged' forest to planting with spontaneous or introduced seedlings or regularly weeding and cutting of competing undergrowth

Semi forest coffee

This production system is also found in the south and south-western parts of the country; including Ilubabor, Jimma, Keffa-Sheka, Benchi-Maji and west Wellega zones (Arega Zeru, 2006). The semi-forest coffee system also known as semi-wild coffee, coffee berries are collected from forest coffee lands of considerable sizes that are located near the main roads, rural towns or peasant villages covered with coffee trees standing in scattered manner (Volkmann, 2008). These types of plantations are believed to have evolved from forest coffee production

system. In order to improve productivity, coffee plantations are managed with little cultural practices such as weeding and shade regulation as well as clearing competing understory trees and shrubs regularly (Solomon Balami, 2007).

Garden coffee

Sometimes garden coffee production system is referred to as small holder coffee, which is produced in plots of varying sizes around dwellings. In this system, coffee is planted and managed in the farmer's backyard within small area (Volkman, 2008). The coffee is planted at low densities, ranging from 1,000 to 1,800 trees per hectare, is mostly fertilized with organic waste and is intercropped with other crops. It is mainly found in southern and eastern part of the country; Sidamo, Gedeo, west Harerge and west Wellega (Arega Zeru, 2006).

Plantation coffee

Plantation coffee includes that grown on plantations owned by private coffee farmers or the government on a large scale and some well-managed smallholder coffee farms. In this production system, recommended seedlings are used, and proper spacing, mulching, manuring, weeding, shade-regulation and pruning are practiced. Only state-owned plantations use chemical fertilizers and herbicides. They are intensified plantations found in Limu, Tepi and Bebeke (Arega Zeru, 2006).

Taye Kufa (2006) reminds that the Ethiopian coffee is de facto wild and organic and ranks highly in intrinsic quality of the bean due to the diverse agro-ecological zones, immense genetic diversity, predominant subsistence and traditional production systems and other socioeconomic aspects. Besides, the coffee cultivation system is considered as a natural way of coffee growing since it involves “the concept of naturalness” where organic fertilizers are used instead of chemical fertilizers (Tadesse Mekuria *et al.*, 2004). Among 80 coffee producing countries, Ethiopia stands Seventh globally and third in Africa after Uganda and Ivory Cost (Taye Kufa, 2006; Damatta and Ramalho, 2006; Muffett, 2002; Demel Teketay, 1999; Schmitt *et al.*, 2005).

3.5.1. Constraints associated with wild Coffea arabica production in Ethiopia

In Ethiopia, *Coffea arabica* is found under forests. These forests are therefore of particularly high conservation importance and have a significant economic value. This is mainly to the fact that the forests contain the reservoir of genetic diversity of *Coffea arabica*, which can be used as a gene-pool from which breeders can craft more productive varieties to meet the needs of world-wide efforts to improve the productivity, resilience and quality in cultivated Arabica coffee farms (Demel Teketay, 1999; Hindorf and Ritschel, 2006; Grades, 2007). However, the Afromontane forest vegetation representing the natural habitats of Arabica coffee, including the coffee forests is diminishing at unprecedented rate due to human pressure and deforestation (Tadesse Woldemariam *et al.*, 2008). As many scientists reported such traditional production system contributes highly to maintain environmentally friendly environment while producing high sustainability and quality fully organic coffees in the country (Tadesse Mekuria *et al.*, 2004; Grades, 2007; Tadesse Woldemariam Gole and Feyera Senbeta, 2008). Thus, changing the natural habitat of Arabica coffee not only has exaggerated the ecology and the economy of the country, but also has contributed extremely for the permanent loss of genetic diversity of Arabica coffee from its origin including other forest biodiversity (Taye Kufa, 2006; Grades, 2007).

The immense human pressure on the coffee forests, mainly because of unsustainable resource use is one of the constraints for coffee production in the country. Farmers have cleared forests on and around their farms to sell the timber, for firewood and charcoal production (Grades, 2007; Tadesse Woldemariam *et al.*, 2008). Deforestation for agriculture, mainly for cultivation of other cash crops, settlement and establishment of plantations is also causing a reduction of the forest cover leading to destruction, fragmentation and degradation of the coffee habitats (Tadesse Woldemariam Gole (2003); Tadesse Woldemariam *et al.*, 2008; Tadesse Woldemariam Gole and Feyera Senbeta, 2008). Poor management practice is also one of the factors that limit the growth conditions of coffee from optimal and suitable environments which results in either severe competition or inefficient utilization of the available above and below ground resources (Taye Kufa, 2006).

3.5.2. Conservation Mechanism

As Tadesse Woldemariam Gole and Feyera Senbeta (2008) and Grades (2007) noted optimal forest management for coffee production and biodiversity conservation must be carried out through different conservation programmes and operations have to be carried by developing guidelines, standards and indicators for monitoring. These include capacity building practitioners through training, baseline inventory of forest conditions, initial opening or clearing, weeding, enrichment planting, monitoring and rehabilitation of degraded forest areas through planting indigenous shade tree species and coffee.

3.6. Plants response to shade and high irradiance light irradiance

Among the many environmental factors, light is perhaps the most influential factor involved in the survival, growth and reproduction of tropical species. Light responses usually provoke physiological alterations, which are determinant for CO₂ assimilation and optimization of gas exchange (Goncalves *et al.*, 2005). Light can also influence other physiological processes both quantitatively and qualitatively. For this reason, environments that are either shaded or under high irradiance light can inhibit the photosynthesis processes simply because there is too little or too much light (Zhang *et al.*, 2003 cited in Goncalves *et al.*, 2005).

The different light intensities promote changes in both the physiology and morphology of the plants, which are features that result from the interaction between gene expression and the environment (Righi *et al.*, 2007). The ability of an individual species to successfully grow in a low or high light environment (holding quality constant) can be based on how rapidly and how efficiently allocation patterns and physiological behaviour are adjusted in order to maximize resource acquisition in that particular environment. The occurrence of two kinds of leaves, i.e. sun and shade leaves, in the same plant can be considered as a special case of adaptation. Leaves adjust (anatomically, morphologically, and physiologically) to the light environment under which they expand and develop. Knowing how plant species respond morphologically and physiologically to contrasting light conditions can be critical in helping to explain and predict their occurrence and abundance patterns under specific environmental conditions. For successional and weed species, this information can be useful to understand the successional

process and to explain their invasive potential and competitive ability under different management situations in cultivated areas. Ultimately this information can help in the development of more effective control practices. As an example, the level of solar radiation can modify the structure of the leaf during coffee development. Higher solar radiation availability may cause leaf thickness, increases in specific mass by increasing the total cell number (DaMatta, 2004). Many researches verified that sun grown coffee had thicker leaves and an increased cell density in comparisons to shade grown coffee. This adaptation mechanism has been reported to *Solanum crinitum* LAM by the work of Dias-Filho (1997). Likewise, he investigated in his other research the sun-shade acclimation characteristics of *Vismia* by measuring its rate of growth, biomass allocation patterns, and photosynthetic features in response to high and low photon flux densities (Dias-Filho, 1995).

3.6.1. Shade Preference of Coffee

In its center of origin and genetic diversity in Ethiopia, Arabica coffee grows permanently under condition of shade in the tropical forest (Righi *et al.*, 2007; Carr, 2001). Although the crop is said to be shade loving plant, it thrives best in moderate shading (Yakob *et al.*, 1996 cited in Taye Kufa *et al.*, 2007). Excessive shading by upper two to three canopy strata of various tree species under forest environment is reported to reduce the growth and productivity of the coffee plant (DaMatta, 2004; DaMatta *et al.*, 2007). In such conditions, the plant spent much of their photosynthesis activities for maintenance purposes (Tesfaye Woldemariam *et al.*, 2002 cited in Taye Kufa *et al.*, 2007) resulting in lower whole-tree carbon assimilation (DaMatta, 2004; DaMatta *et al.*, 2007). Heavy shading due to light penetration by the upper strata can result increased competition for light for photosynthesis which, in turn, leads to undesirable growth of single stemmed coffee trees with thin and reduced reproductive efficiency (Taye Kufa *et al.*, 2007). Moreover, coffee productivity considerably decreases as a result of death of heavily shaded productive middle and bottom primary branches which is induced by dark respiration (Tesfaye *et al.*, 2002 cited in Taye Kufa *et al.*, 2007). Dense shading also results in reduced coffee fruit load through their effects on coffee physiology, such as longer internodes, fewer nodes formed per branch and flower buds at existing nodes (Montoya *et al.*, 1961 and Castillo and Lopez, 1961 cited in DaMatta, *et al.*, 2007; Vaast *et al.*, 2006). Because the fruit load is the key component of coffee production, its reduction results in decreased productivity (DaMatta *et*

al.,2007).The study of Vaast *et al* (2006) shows that a rather dense shade level of 45% reduced by only 18% the productivity of trees over three consecutive production cycle in optimal ecological conditions for coffee growth. Temporary shading has also been adopted for young coffee plantations for protection against frost, as that obtained with the use of shelter shrubs such as pigeon pea (*Cajanus cajan*) (DaMatta and Ramalho, 2006) and also in intercropping systems with fast growing trees to increase ground cover and maximize the efficiency rate of nutrient and water utilization during the juvenile phase of the coffee crop (DaMatta *et al.*, 2007).

3.6.2. Advantages of Shade for Coffea arabica Production

Now a days, the idea of shade-grown coffee has become a well-recognized trend which is often defined with terms such as “sustainable coffee” and “environmentally friendly coffee”. In line with this, the use of shelter for coffee plantations can be allotted in to sustainable production, ecological sustainability and level and quality of input available to improve the environment for the coffee tree.

3.6.2.1. Sustainable production

Under shade conditions coffee tends to flower and produce a good crop each year, whereas under full-sun conditions, the crop tends to alternate between years with heavy flowering and light flowering leading to a biennial production trends (DaMatta, 2004a;Vaast *et al.*,2006). This owes to the fact that the commitment of sun-grown coffee tree to fill all the beans that are formed after the fruit expansion stage, due to failure to evolve satisfactory mechanisms to maintain its fruiting burden in balance with carbohydrate and mineral resources when grown under high irradiance exposure (Cannell 1985 cited in DaMatta, 2004). This result the causes of overbearing which are associated with profuse flower initiation without shading and very sparse compensatory fruit shedding, resulting in a large sink capacity in the seed endosperms (Cannell 1985 cited in DaMatta, 2004). Overbearing exhausts the tree’s reserves and limits both the production and retention of leaves, leading to poor crop the next year. This allows an excessive foliage to form which, in turn, permits a profuse flowering and hence a heavy crop. Furthermore, the study of Vaast *et al.* (2006) proved that the use of shelter trees decreases overbearing and buffer biennial fluctuations of crop yield resulting in reduced exhaustion of the coffee tree, and allow it to

satisfactorily produce for longer. Thus, based on economic grounds, the larger number of more regular crop harvests in shaded plantations compensates the higher yield per harvest in unshaded plantations within given limits (DaMatta, 2004a). This means for coffee growers, this is particularly important, as it limits the need to invest in processing facilities that are oversized every other year and allows them to market a more constant volume and quality of coffee to buyers.

Owing to the current world overproduction, there is a strong interest in producing and marketing coffee of higher quality to alleviate financial difficulties encountered by coffee farmers. Delay in maturation of bean and ripening between the berry pulp and the bean is one of the reasons explaining observed differences in beverage quality between “shade-grown” and “sun-grown” coffee (Adugna Debela, 2007). The beneficial harmonizing effect of shade decreases by half the light intensity and by several degrees (up to 4oC) the temperature around the berries, which slows down the ripening process of the coffee berry flesh (Vaast *et al.*, 2006). This allows more time for complete accumulation of sugar and soluble solids responsible for quality than that of sun-grown conditions resulting to higher quality and larger bean size (Vaast *et al.*, 2006; Adugna Debela, 2007). The study of Vaast *et al* (2006) shows the effect of shade on biochemical composition that attributes for coffee quality. This study shows the presence of high caffeine and fat contents in beans of “shade-grown” plants, whereas high sucrose, chlorogenic acid and trigonelline contents in beans of “sun-grown” plants. Accordingly, the high sucrose content coupled with the low fat content in beans of sun-grown coffee could best signify that bean filling and fat synthesis were incomplete. Meanwhile the higher chlorogenic acid and trigonelline contents in beans produced by “sun-grown” plants point towards incomplete bean maturation and explain the higher bitterness and astringency of the coffee beverage (Vaast *et al.*, 2006).

3.6.2.2. Ecological sustainability

The importance of overstorey trees as a sustainable and financially viable coping strategy for smallholders who have little access to technological improvements to mitigate the current harmful consequences of changing global climate cannot be deprived off (Lin, 2007 cited in DaMatta *et al*, 2007). Shade buffers detrimental diurnal air temperature extremes (day/night) in coffee production systems. It reduces the effect of excessive heat during the day and heat losses

at night on coffee plants (Diriba Muleta, 2007; Adugna Debela, 2007; Vaast *et al.*, 2006; DaMatta and Ramalho, 2006; Beer *et al.*, 1998). Furthermore, shade trees are useful in reducing of wind speed, which in turn minimizes crop desiccation and soil erosion (DaMatta and Ramalho, 2006; Beer *et al.*, 1998). Shade trees also decrease leaf-to-air vapour pressure deficit and would increase decoupling factor (Ω), which in return would allow longer stomatal opening, thus favoring CO₂ uptake, without a proportional increase in transpiration rate so that water loss due to excessive evapotranspiration (DaMatta and Ramalho, 2006). In addition, shade trees not only make a great contribution in reduction of hail damage (Beer *et al.*, 1998), they also protect the coffee from photooxidative damage (Vaast *et al.*, 2006; DaMatta and Ramalho, 2006). On the other hand, in high irradiance conditions there will be inadequate reaction centers to accommodate the light energy and convert into biochemical energy and the coffee plant photorespires excessively and eventually most of the stored carbohydrates get depleted, which ultimate problem of shoot and root die-backs (Taye Kufa *et al.*, 2007). Besides, excessive evapotranspiration and severe water stress, death of actively growing shoot parts, such as branch tips, seasonal crinkling of leaves, frost damages “hot and cold disorder” and subsequent yield reduction are common problems in unshaded coffee stands (Cambrony, 1992 cited in Taye Kufa *et al.*, 2007).

Overstorey trees are also vital in organic matter contribution and nutrient cycling. In shade-coffee growing system, the shade trees maintain the soil fertility by mulching with their fallen leaves retaining soil moisture and stimulating soil organic matter (Vaast *et al.*, 2006; Beer *et al.*, 1998; DaMatta and Ramalho, 2006; Diriba Muleta, 2007). Thus, unlike sun-coffee plants which quickly deplete the natural nutrients in the soil and require massive amounts of chemical fertilizers to survive, shade-coffees grow without requiring such inputs (GUO and CAO, 2004). The coffee agroecosystems also act as potential carbon sink by capturing atmospheric carbon (carbon dioxide) and storing it by one of several mechanisms to reduce this greenhouse gas emissions and accumulation in the atmosphere and its contribution to the current global climate change (Gorsline, 2006). Since tremendous amounts of carbon are stored in aboveground woody biomass of shade trees and leaf-rich soil, the coffee agroecosystem act as a potential carbon sink (Polzot, 2004 cited in Diriba Muleta, 2007).

Furthermore, shade trees minimize soil erosion acting as a physical barrier and reduce the intensity of rain, so that reduce nutrient leaching, specially nitrate which contaminates aquifers (Vaast *et al.*, 2006; Beer *et al.*, 1998; Wexler, 2003). In addition, their deep root system helps in percolation of rain water in to deeper layers of the soil thus minimizing run off of rainwater at the same time contributing to recharging of ground water (Adugna Debela, 2007; Vaast *et al.*, 2006).

In recent years, traditional shaded coffee is one of the diverse agroecosystems that has received considerable attention from conservation organizations. In such traditional production systems, where coffee is grown under a structurally and floristically diverse canopy of shade trees, it serves as a potential habitat for a high diversity of associated flora and fauna (Perfecto *et al.*, 1996; Faminow and Rodriguez, 2001; Perfecto *et al.*, 2005). The wide array of plants on shade-coffee farms provides natural habitat for hundreds of species of migratory birds and beneficial insects, which in turn act as a natural defense against the bugs and pests that can ruin a coffee crop (Adugna Debela, 2007; Faminow and Rodriguez, 2001; Beer *et al.*, 1998). Therefore, they reduce the need for chemical pesticides. Moreover, they form an important refuge for bats, mammals, and reptiles and contain a high diversity of native tree species (Perfecto *et al.*, 1996; Moguel and Toledo, 1999 cited in Peeters *et al.*, 2003; Tadesse Woldemariam Gole and Feyera Senbeta, 2008). Furthermore; shaded coffee might qualify as “better habitat” for forest species moving forest fragments (Armbrecht *et al.*, 2005). Canopy cover in combination with cool and wet weather in coffee production systems also reduces coffee diseases caused by fungus, whilst reducing the incidence of coffee rust as well as they act as weed suppressors, hence reducing the need for chemical pesticides, herbicides and fungicides (Gorsline, 2006).

Additionally, shade coffee plantation system may yield various secondary benefits for small-scale coffee farmers. Their livelihood needs may be better met by multitude of products and services provided by shade coffee production system. Farmers may diversify their diet and sustain their income from the commercial and domestic values derived from associated firewood, timber and fruit trees (DaMatta, 2004; Vaast *et al.*, 2006; Faminow and Rodriguez, 2001; Herzog, 1994 and Escalante, 1995 cited in Peeters *et al.*, 2003).

Therefore, with the removal of these canopy covers, the modern-coffee production system has become prone to stress owing to seasonal fluctuations, water and soil erosion, threatening the long-term sustainability of the production system (Faminow and Rodriguez, 2001; Perfecto *et al.*, 1996). Furthermore, small holder producers of sun-coffee face serious economic risks related to higher variable cost and unstable market prices (DaMatta, 2004). These problems in turn have led to other challenges such as, deforestation and issues related to socio-economic factors, which rendered change in the structure and functions of the forest ecology. It has also threatened traditional production systems particularly most coffee producing farmers in developing countries. (Taye Kufa, 2006; Tadesse Woldemariam *et al.*, 2008).

4. MATERIALS AND METHODS

4.1. Experimental set-up and plant material

Physiological and growth response of two distinct populations from *Coffea arabica* as exposed to differing light intensities were investigated in a greenhouse. The study was conducted between March 8, 2007 and June 27, 2008, in science faculty, Addis Ababa University (AAU). A total of forty eight coffee plants grown in pots of 30cm in diameter and 40cm in depth were used in the study. The coffee seeds were collected from Harennna forest which is located in the Mena-Angetu district (wereda) of the Bale zone in Oromia Regional State (hereafter called Bale) and from coffee forest at Sheko district in the Bench-Maji zone, SNNPRS, in Southwest Ethiopia (hereafter called Sheko). The seeds were germinated and grown in 27 cm high and 25cm wide pots, originally. The pots were filled with sand, soil and compost in a 1:2:1 ratio, respectively. Temperature and humidity of the greenhouse were not controlled but were recorded with a thermohydrograph. The daily mean temperature and relative humidity during the experiment period were 24°C and 76%, respectively. The experimental seedlings were selected based on their height, those achieving ≥ 68 cm. Each plant was separated from the other by 1m distance and all coffee plants were watered to field capacity every other day throughout the study process.

4.2. Experimental design and treatments

The effect of two differing light intensities on two distinct coffee populations was investigated in the present study. The Bale coffee population occurs in the lower altitude of Harennna forest where the share of coffee is 2.1% of which 82.1% is forest coffee. The rainfall pattern of the area is bio-modal with short (March-April) and long (August-October) peak rainy seasons (DoA, 2004 unpublished cited in Taye Kufa, 2006). The annual rainfall and temperature of the forest is also 950 mm and 18°C respectively. Moreover the soil is reddish-brown silty clay, rich in exchangeable cations where its pH is acidic to slightly acidic. Whereas, the Sheko coffee population is found from an area which represents the hot to warm humid low to high altitude, which is transition between the highland rainforests and the lowland forest. It is humid and wet almost throughout the year, except between October and February and the area where Sheko coffee population is located receives the highest amount of rainfall, which can be as high as

2,100mm per annum and with mean annual temperature of 22°C with short drought period (Taye Kufa, 2006). The soils are moderately acidic with high CEC.

In this experiment, two treatments were considered i.e. two light intensities and two populations. The light intensity treatments were set as high solar irradiance (100) % and shade treatment with 20% of the high solar irradiance. The 20% level shade treatment was produced with white shade cloth, with the required light transmittances, positioned at a minimum height of 3m whereas plants left open in the greenhouse were considered as growing under the high irradiance level.

Table 2: The light levels under the shade and high irradiance monitored using a PAR sensor (Li-Cor, Nebraska) for four consecutive days

	Shade		Exposed	
Days	PAR	Time	PAR	Time
17 April, 2007	400 $\mu\text{mol m}^{-2} \text{s}^{-1}$	2:12Pm	70 $\mu\text{mol m}^{-2} \text{s}^{-1}$	2:14Pm
18 April, 2007	402 $\mu\text{mol m}^{-2} \text{s}^{-1}$	2:10Pm	73 $\mu\text{mol m}^{-2} \text{s}^{-1}$	2:12Pm
19 April, 2007	401 $\mu\text{mol m}^{-2} \text{s}^{-1}$	2:08Pm	71 $\mu\text{mol m}^{-2} \text{s}^{-1}$	2:10Pm
20 April, 2007	400 $\mu\text{mol m}^{-2} \text{s}^{-1}$	2:10Pm	72 $\mu\text{mol m}^{-2} \text{s}^{-1}$	2:12Pm

Forty eight coffee plants were used for the study. Twenty four plants from each population were represented and were exposed to two light treatments. Each light treatment included 4 coffee rows of 6 plants each. Each of the population was represented by 12 trees in two of the rows under each light treatment.

Table 3: Location and environmental conditions of the two distant habitats of wild *Coffea arabica*.

Source: Grades (2007)

Habitat	Latitude (N)	Longitude (E)	Altitude (m)	Temperature*		Station
				(max)	(min)	
Harena (Bale)	6°00'	40°00'	1420-1490	34	10	Dolo Mena
(Sheko)	6°59'	35°36'	1040-1180	27	15	Mizan Teferi



Figure 4: Experimental design of the study plants. The four rows of the plants (A) and the six arranged plants in each row (B). The shade treatment produced (C) and the shaded coffee leaves (D)

4.3. Measurements

4.3.1. Growth parameters

Measurement of all growth parameters were conducted 30 days after the establishment of light treatments on and were continued for the next six months, on 8th May 2007 (after 60 days), 8th June 2007 (after 90 days), 8th July 2007 (after 120 days), 8th August 2007 (after 150 days) and 8th September 2007 (after 180 days). The growth rate and pattern were then analyzed from these data.

Height measurement was made from the base of the stem to the highest point of the plants using a measuring tape. Similarly, the number of branches of all the study coffee plants were counted and recorded for six months beginning from the same time as stem height measurement. During the same period, stem girths of all study plants were measured using a caliper about 10 cm from the soil surface. Internode length of all the study coffee plants was also measured using a measuring tape and was recorded. Specific leaf area (SLA) was determined from three randomly selected coffee plants representing each population and light treatments. Two healthy and matured leaves located at the fourth and fifth from the tip were collected from each of selected coffee plant. Then the area of each sample leaf was measured by an area meter (Delta T devices Ltd., Cambridge, England). Then, sample leaves were oven dried at 70°C for 48 hrs (Poorter and Jong, 1999). The dry weight of each sample was then determined by analytical balance (Denver Instrument, XE-50). Finally, the specific leaf area of each sample leaf was determined using the formula:

$$\text{Specific leaf area} = \frac{\text{Leaf area (cm}^2\text{)}}{\text{Leaf dry weight (g)}} \quad (\text{Pierce } et al., 1994)$$

Then, the average SLA of the two leaves of each plant is taken as the result.



Figure 5: Area meter by which the area of the leaves were determined

4.3.2. *Physiological parameters*

4.3.2.1 *Gas exchange*

Gas exchange measurements were carried out by a portable infrared gas analyzer (LCpro, ADC Bioscientific Ltd., Hoddesdon, UK) on 12th, 15th, 18th, 21st and 23rd June 2008. The flow rate, pressure and leaf area were set to 200 cm³ min⁻¹, 100 kPa, and 6.30 cm² for all measurements. Net photosynthetic rate (A_{net} , $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), stomatal conductance to water vapor (g_s , $\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$), transpiration rate (E , $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$) and internal CO₂ concentration (C_i , ppm) were recorded. Instantaneous water-use efficiency (WUE_i) was calculated as the ratio of net assimilation (A_{net} $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) to transpiration (E $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$) (Harrington *et al.*, 1995) for all coffee plants. Measurements were made on three individuals from each treatment. Young fully expanded leaves located on a branch at the fourth node from the tip of each individual were selected and each measurement was taken for five minutes on each leaf sample. Diurnal variation of gas exchange parameters were recorded at 1 h interval from 6:00 to 18:00h. Furthermore, daily integrated values for all important parameters was calculated and shown.

4.3.2.2. Photosynthetic light response curves

Photosynthetic light response curves were measured on the same leaves used for gas exchange measurements with an attached red LED light source (ADC). Measurements of each leaf sample was began by providing low irradiance ($50\mu\text{mol m}^{-2} \text{s}^{-1}$) followed by 9 increments until the irradiance reached $2000\mu\text{mol m}^{-2} \text{s}^{-1}$ with an induction period of 20 minutes. The measurements were restricted to the hours between 9:00am-12:00pm on 26 and 27 June 2008 and sunny days were chosen to minimize diurnal effects on photosynthesis.

4.4. Statistical analysis

All the collected data were subjected to analysis using ANOVA procedure to determine the effects of treatments and the interactions among treatments. When appropriate, the dependency of growth and physiological parameters on different irradiance was evaluated with regression analysis. All the graphs were generated with the Sigma Plot 8.0 (Systat Software, Inc.).

5. RESULTS

5.1. Growth parameters

Beginning from the start of the experiment, and for the next six months of shade adaptation, the data on growth parameters such as stem height, number of branches, stem girth, internode length and specific leaf area were recorded. The result is summarized and presented in the following sub-sections.

5.1.1. Stem height

As indicated in Figure 6, the pattern of height growth rate over the course of the experiment was observed to be similar for both populations under respective irradiance. However, from 30 to 60 days exposed Bale coffee plants showed a decreased value when exposed Sheko coffees showed increment during the same duration and both populations under shade grew in a similar way afterwards. Both populations under high irradiance showed the same pattern, grew more between 30 to 60 days and showed no growth rate afterwards

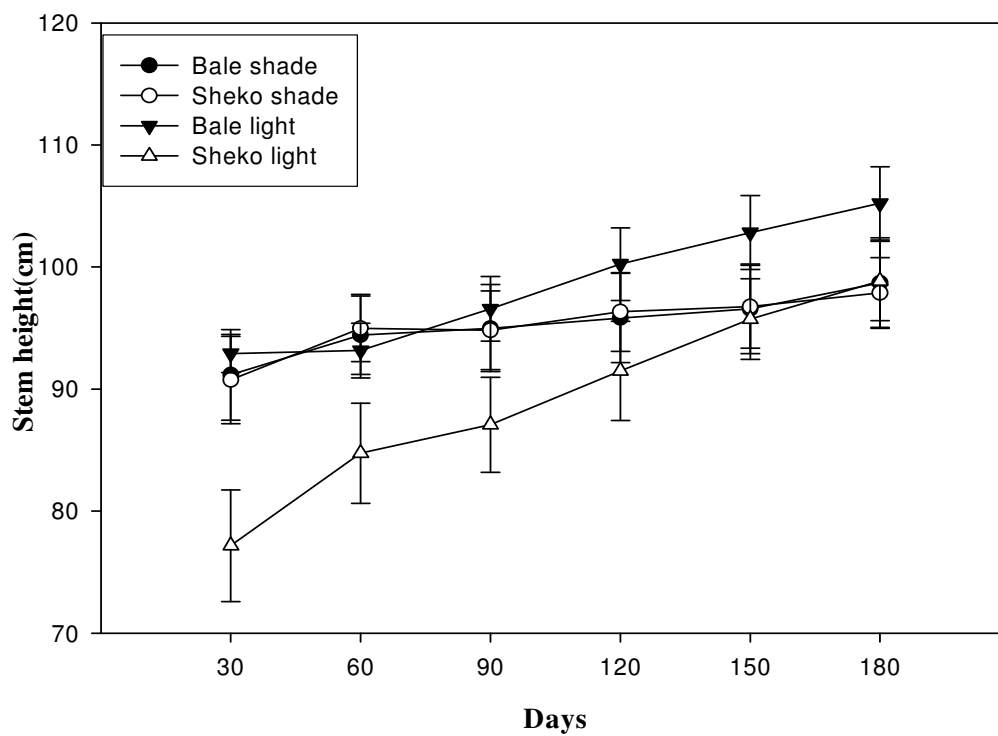


Figure 6: Stem height growth rate pattern in six months of experiment

Stem height increment

SH increment by the end of measurement is found to be greater for coffee trees under full light treatment than shade treatment in both populations. Exposed Bale coffees increased 52 ± 3.5 cm height, while those coffees of the same population under shade grew 46 ± 4.8 cm. Similarly, exposed Sheko coffees grew 50 ± 3.3 cm, while Sheko shade trees increased 24 ± 1.7 cm. Comparing the SH attained between the two coffee populations under light, slight difference in growth rate is recorded and is shown in Figure 7. However, much difference in height increment was observed between the two populations under shade environment, where Bale shade increased more in stem height. Generally, Bale population showed higher increment in stem height than Sheko population under the same light treatment.

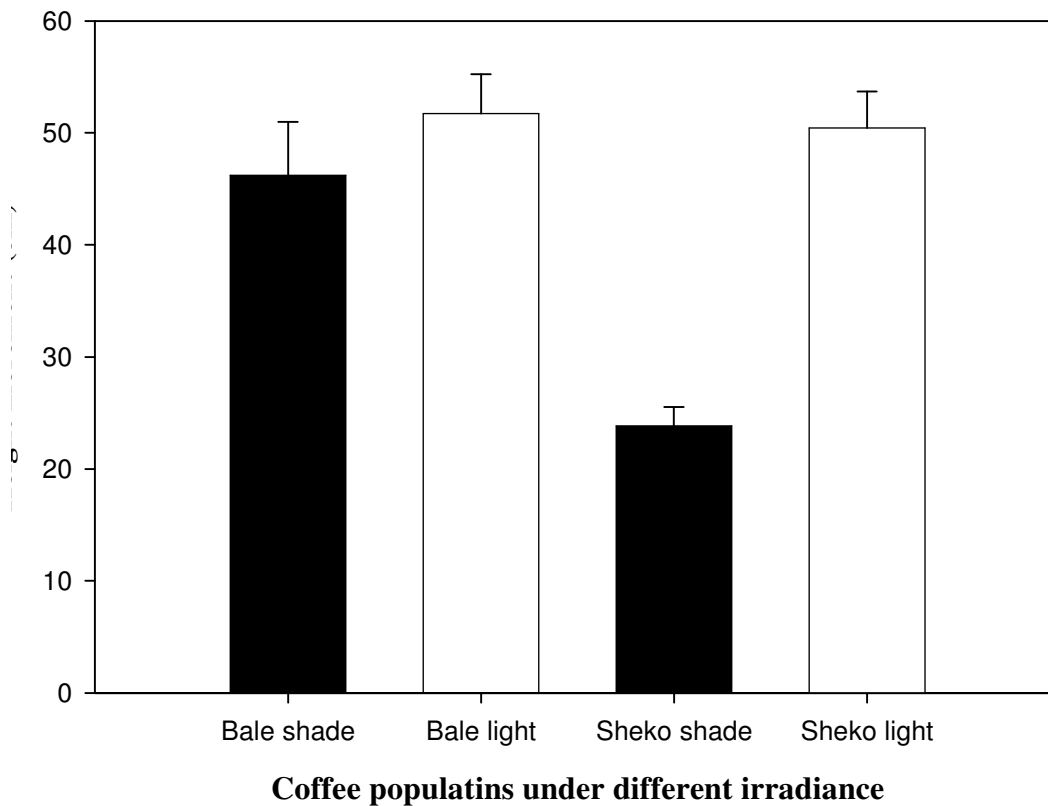


Figure 7: Stem height increment for Sheko and Bale coffee populations under shade and high light treatments. Bars show mean (n=12) and error bars represent $\pm$ S.E

5.1.2. Number of branches

The same as stem height growth rate, number of branches in six months showed similar pattern of growth rate in both populations under respective light treatment. As shown in Figure 8, shaded Sheko and Bale coffee trees showed almost the same growth rate decreasing from 30 to 60 days of the experiment and showed slowly increasing growth rate afterwards. Throughout the experiment period, both coffee populations under high irradiance showed an increasing growth rate.

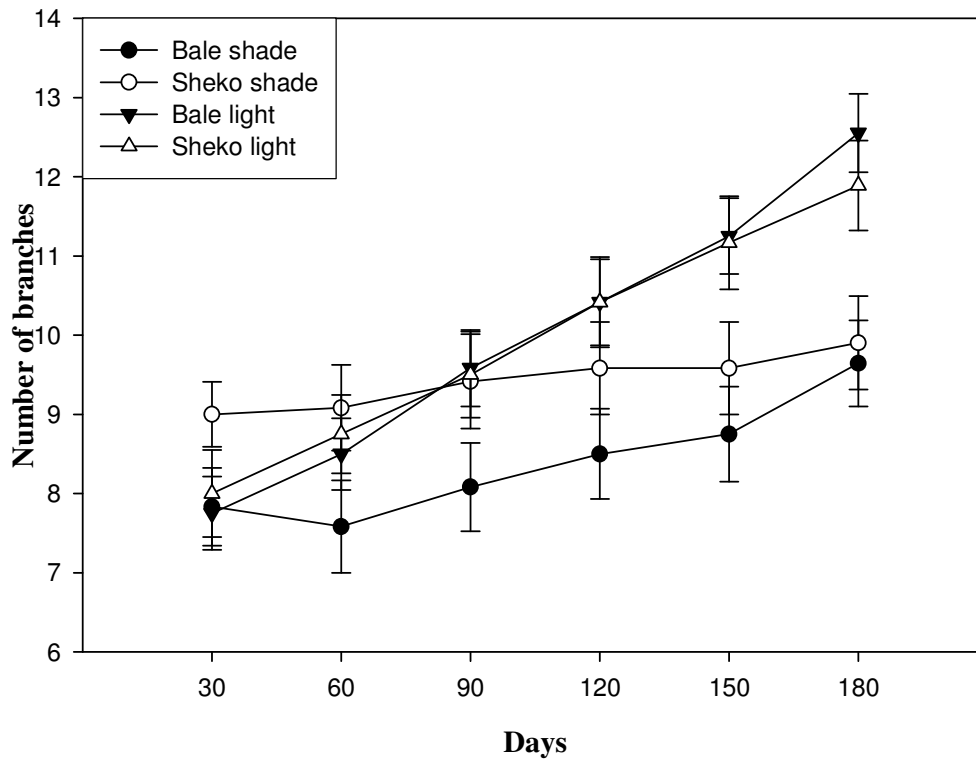


Figure 8: Number of branches growth pattern during six months of experiment

Number of branches increment

There was a difference in NB increment between the two populations under both light conditions from April to December 2007. Exposed Bale population showed 11.5 ± 0.08 of growth in NB, where as Bale populations in the shade achieved 8 ± 0.13 growth rate. For Sheko populations under full light, growth rate of branches was recorded as 7 ± 0.04 while Sheko populations in the

shade increased branches by 5 ± 0.45 . From the result in Figure 9, it is generalized that branch development in Bale population is more affected by light condition than Sheko populations. Under both light conditions, branch increment was higher in Bale populations than Sheko populations. This result also shows that Bale coffees under full light attained the greatest number of branches. Exposed coffees of both populations achieved more branches than shaded coffees.

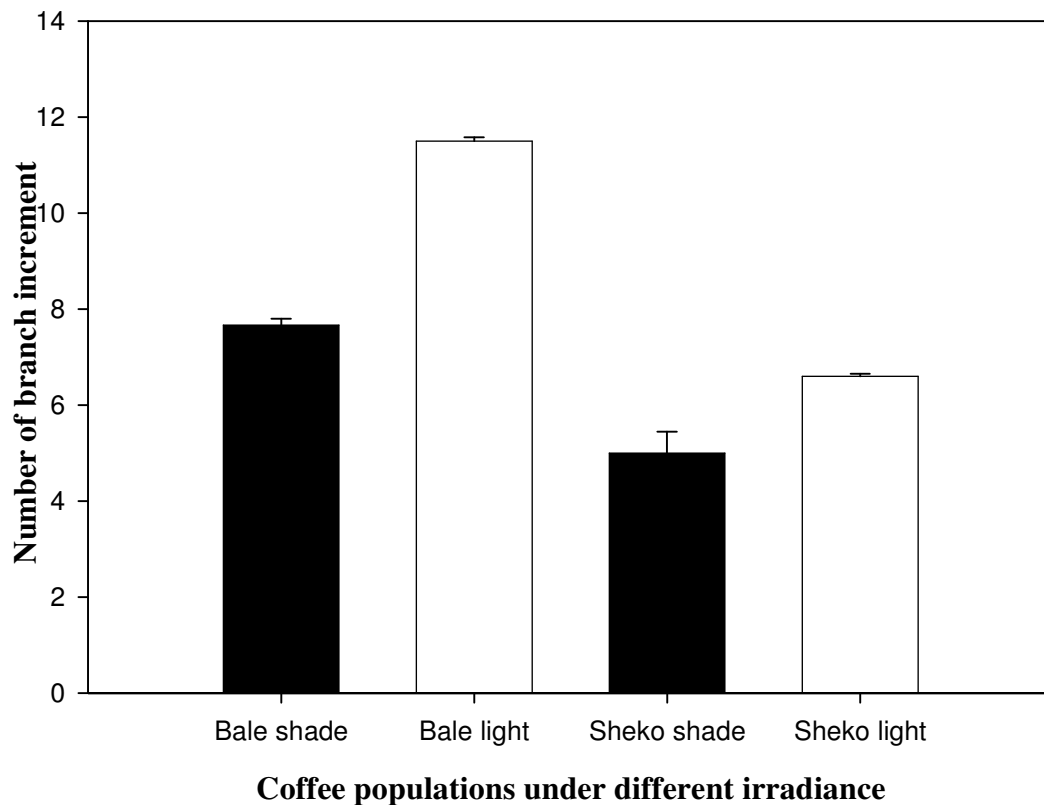


Figure 9: Number of branches development for Sheko and Bale coffee population under shade and high light treatments. Bars show mean (n=12) and error bars represent $\pm$ S.E

5.1.3. Stem girth

As shown in Figure 10, girth growth in both populations had the same growth rate pattern under the same light treatments. Shaded coffees of the two populations increased in their growth rate from 30 till 120 days of the study period and afterwards both coffees started decreasing until the last month of experiment. Exposed Bale coffees grew in constant increment from 30 to 120 days,

but after then increased exponentially. Likewise, Exposed Sheko coffees grew exponentially from 30 to 270 days.

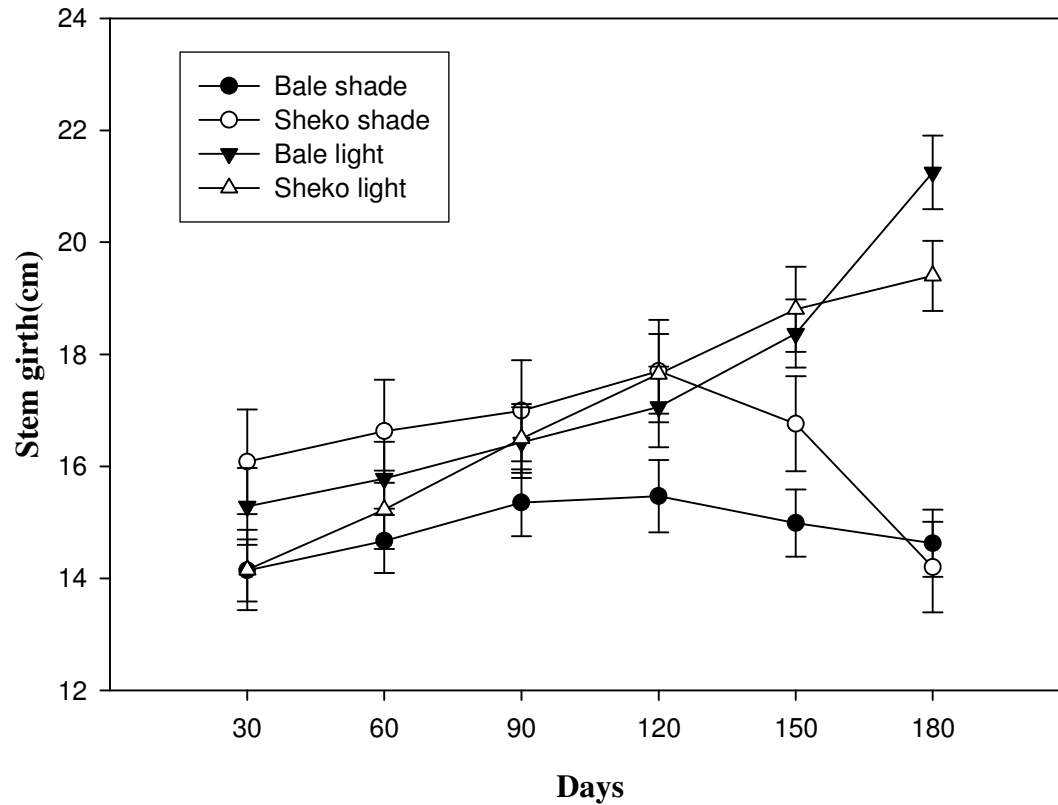


Figure 10: Stem girth growth pattern during six months of experiment

Stem girth increment

Both populations showed similar girth increment, higher values were recorded for plants under full light than for plants under shade, as shown in Figure 11. The impact of shade, however, was not different between the two populations. The result also illustrates that shaded Sheko coffee trees did not show girth increment during the study period, whereas, shaded Bale coffees showed small change.

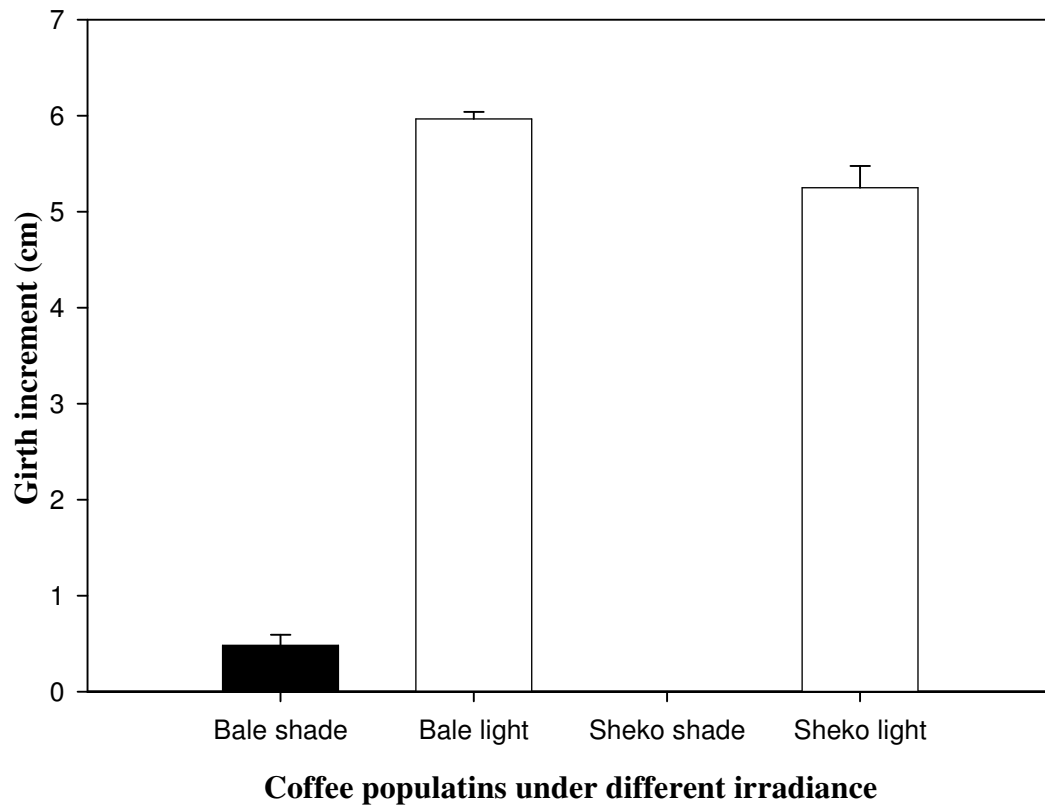


Figure 11: Stem girth increment for Sheko and Bale coffee populations under shade and high light treatments. Bars show mean (n=12) and error bars represent $\pm$ S.E

5.1.4. Internode length

This result as shown in Figure 12, states that population variation in terms of IL. The result indicated that IL is more affected by low light in Bale population than Sheko population. The latter exhibited similar values under both conditions. Exposed Bale coffee plants showed lower IL with a value 5.82 ± 0.9 than Shade coffees of the same population with a value of 6.77 ± 0.95 . However Sheko coffee trees under both irradiances attained almost the same IL growth rate with a value of 6.53 ± 1.19 for exposed and 6.49 ± 0.83 for shaded coffee trees.

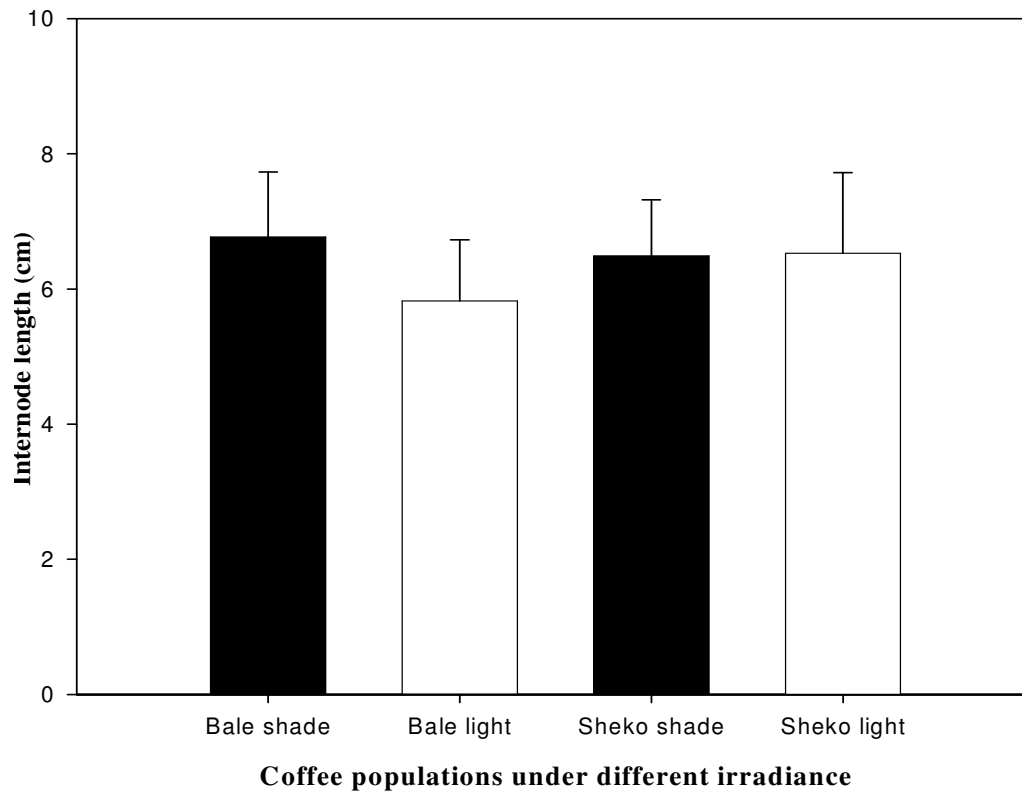


Figure 12: Internode length increment of Sheko and Bale coffee populations under shade and high light treatments. Bars show mean (n=12) and error bars represent $\pm$ S.E

5.1.5. Specific leaf area

Shaded coffee trees of both populations have the same growth rate pattern. In Figure 13 it is indicated that shaded Bale coffees grew slightly from 120 to 150 days of the experiment and then increased in their growth until the end of the experiment. Shaded Sheko coffees grew in the same pattern from 120 to 180 days and showed increasing growth rate afterwards.. Bale coffees under high light decreased in their growth rate from 120 to 150 days and afterwards increased to 180 days of the experiment which finally started to grow constantly. On the other hand, Exposed Sheko coffees increased in their growth from 120 to 150 days and then grew almost the same way until the end of the experiment.

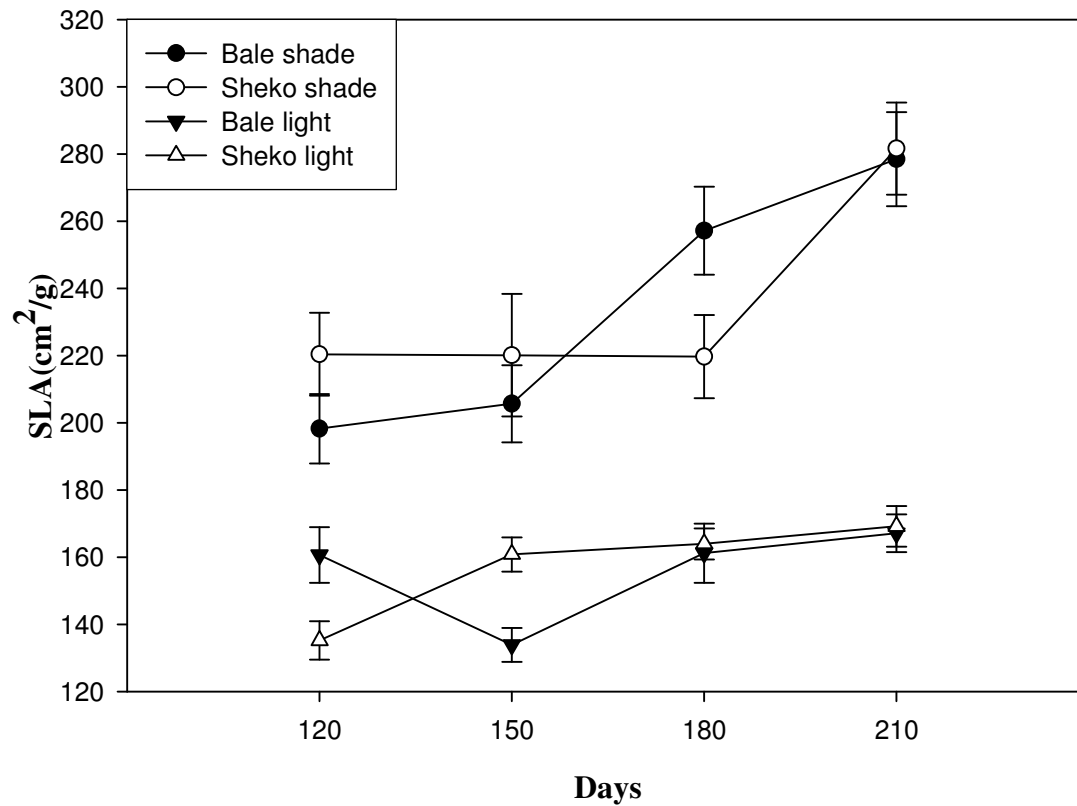


Figure 13: Stem girth growth pattern during six months of experiment

SLA Increment

Both populations showed remarkable change in SLA in response to the two differing light conditions. Figure 14 shows that coffee trees, grown under shade attained twice as high as those grown under full light. But there is considerable variation between Sheko and Bale light populations.

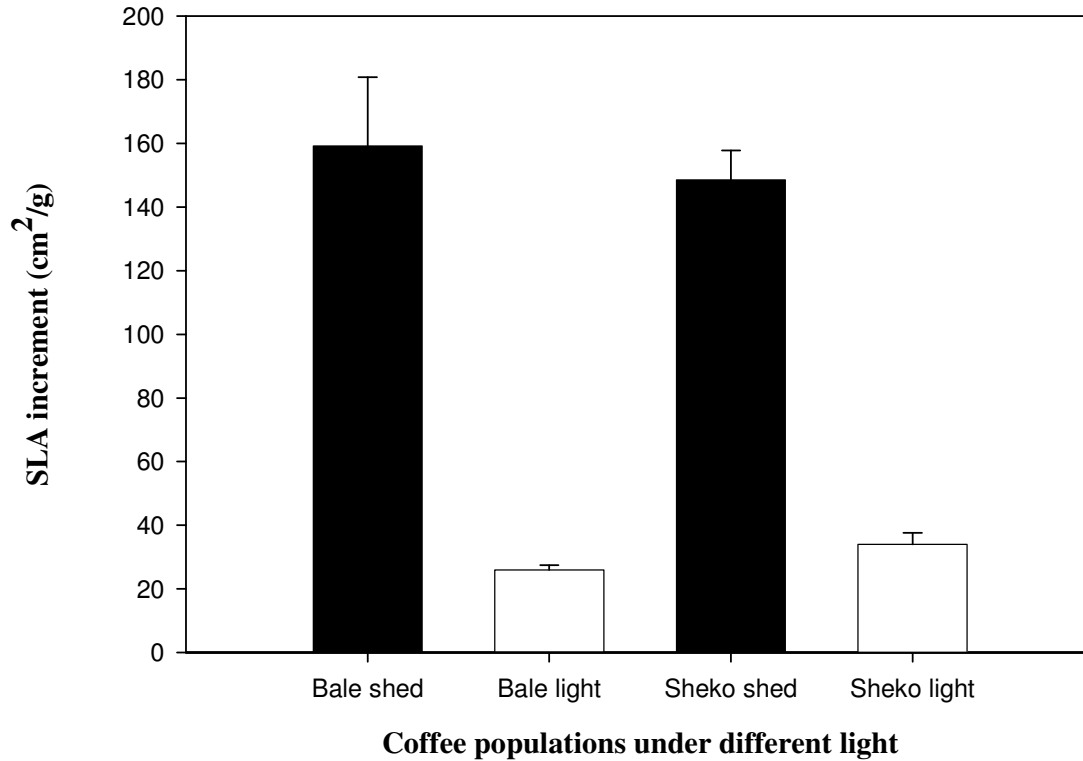


Figure 14: Specific leaf area increment for Sheko and Bale coffee populations under shade and high light treatments. Bars show mean (n=12) and error bars represent $\pm$ S.E

5.2. Physiological parameters

5.2.1. Gas exchange

Assimilation

The highest A_{net} (about $5 \mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$) was recorded in exposed coffee populations. As shown in Figure 15, shade coffee populations had low A_{net} rate than exposed coffees. Bale Shade coffees showed a raised A in the morning at 8:00 am, which afterwards declined in the afternoon. For Sheko shade population, the pattern was the same as for Bale shade coffees. Moreover, Bale light coffees had an increased A that peaked at 10:00 ($4.04 \pm 0.5 \mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$). This was followed by a midday depression rising again until 14:00, declining afterwards. Sheko light coffee trees had highest values of $5.0 \pm 1.0 \mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$ at 8:00am followed by other peaks at

10:00 am and 14:00 pm. There was clear midday depression and declining A in the late afternoon.

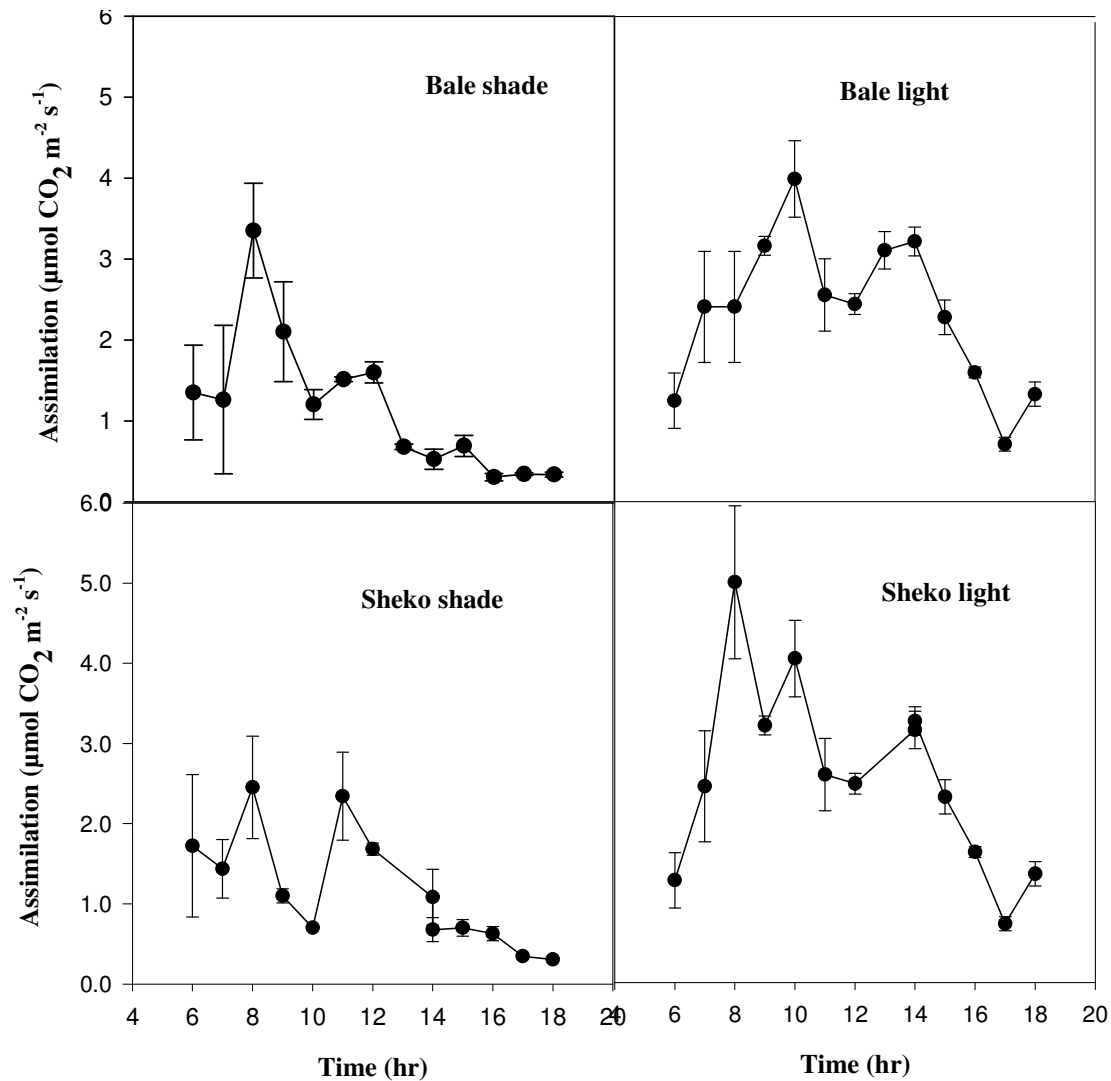


Figure 15: Diurnal CO₂ assimilation rate of two coffee populations under two light conditions

Daily integrated assimilation

The total daily integrated A for exposed coffee population leaves is found higher when compared to shaded coffee leaves. The response of Bale population to high irradiance as well as for shade was higher than that of Sheko. The result presented in Figure 16 is supposed to mean under similar high irradiance and shade growing condition; Bale populations assimilate more CO₂ than

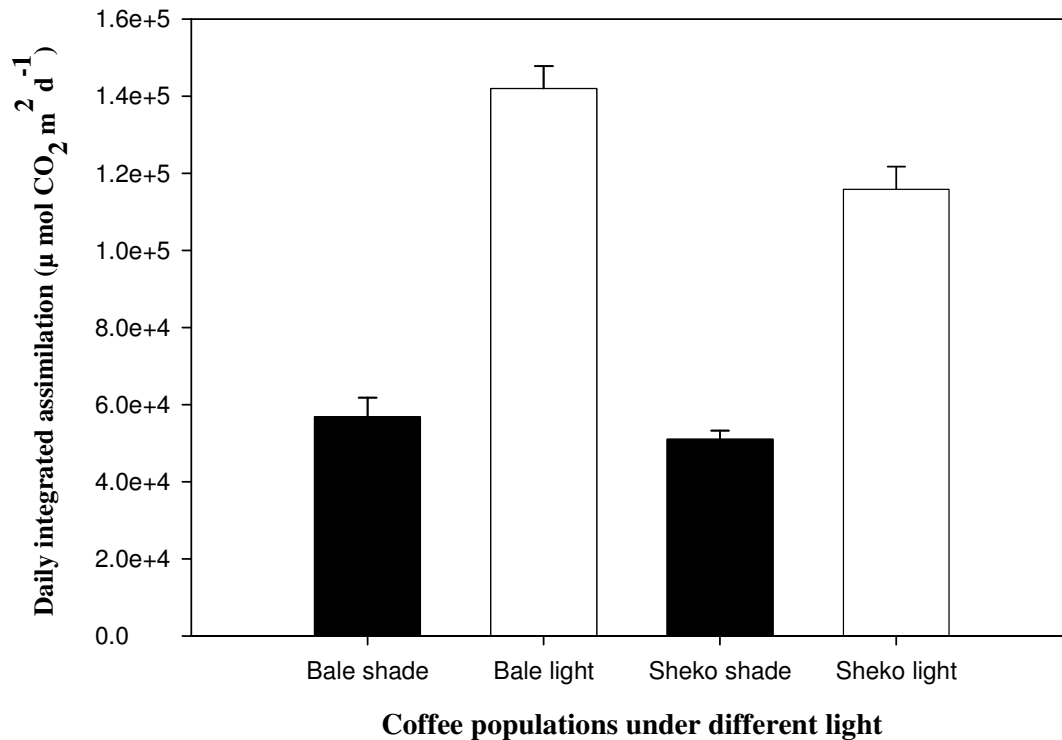


Figure 16: Figure 16: Daily integrated assimilation rate of two coffee populations under two light treatments

Stomatal conductance

gs of the coffee trees under shade and high irradiance is shown in Figure 17. Both populations under both growing light environments showed more or less the same pattern of stomatal conductance. The result shows two stomatal conductance peaks apart from each other by a reduction at mid-day 12:00 to 14:00 hs. The value of stomatal conductance for both coffee populations showed an abrupt decrease on stomatal conductance stating at about 14:00 to 16:00 hs (for shaded) and 14:00 to 17:00 (for exposed) ceasing it early night reaching its minimum afterwards. Moreover, the result obtained from this study shows that exposed coffees of both population performed higher stomatal conductance than the shaded coffees.

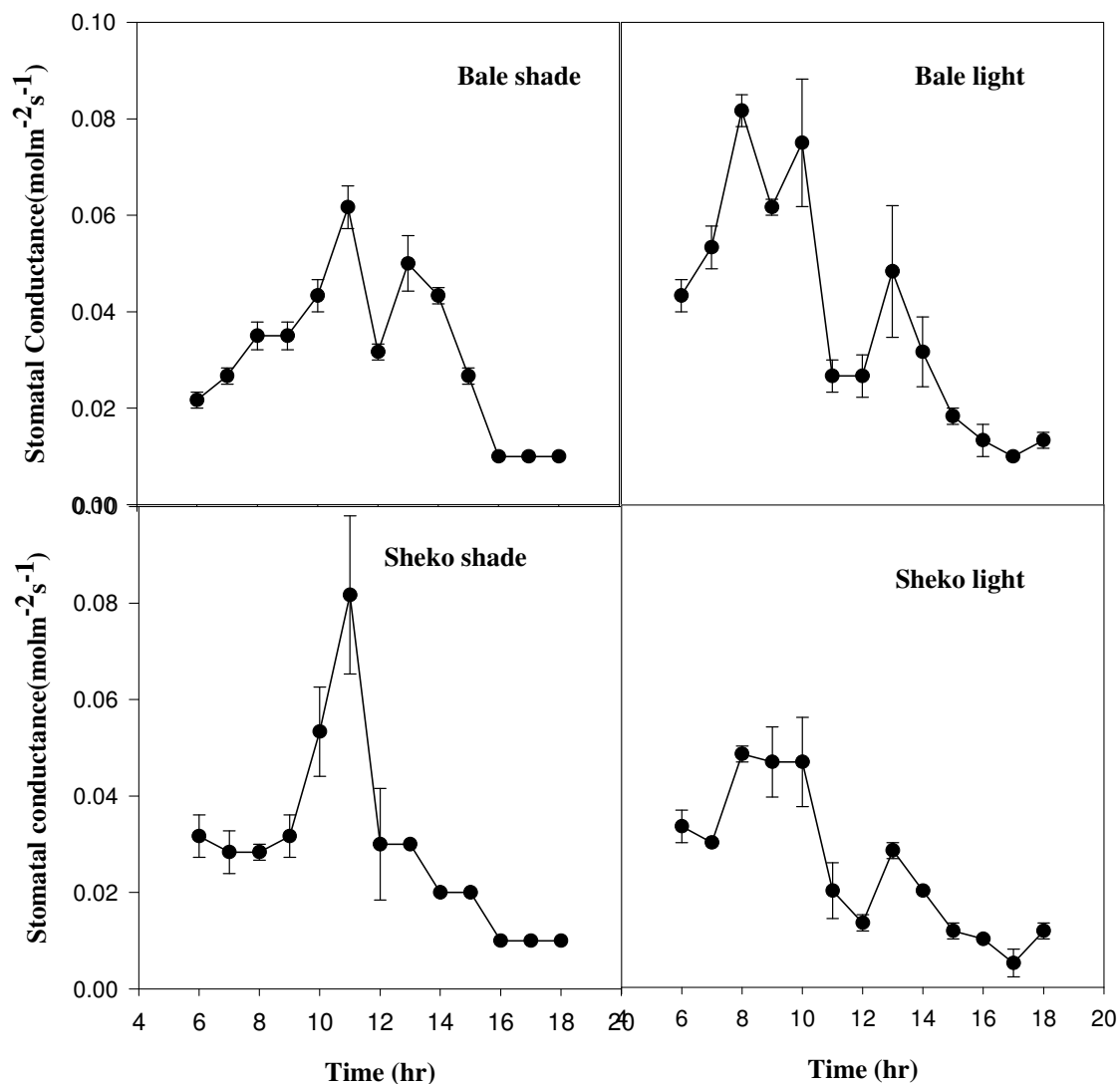


Figure 17: Diurnal course of stomatal conductance of two coffee populations under two light treatments

Transpiration

It is possible to observe on Figure 18 that plants presented two transpiration peaks apart from each other by a reduction at mid-day (12:00 to 14:00 hs).

For both groups of populations under both light conditions E showed more or less the same pattern as gs. In all coffee plants presented an abrupt decrease on transpiration stating at about 16:00 to 17:00 hs ceasing it early night reaching its minimum afterwards. Exception is made for

Sheko Shade plants that presented a slow and continuous reduction on transpiration since 14:00 hrs.

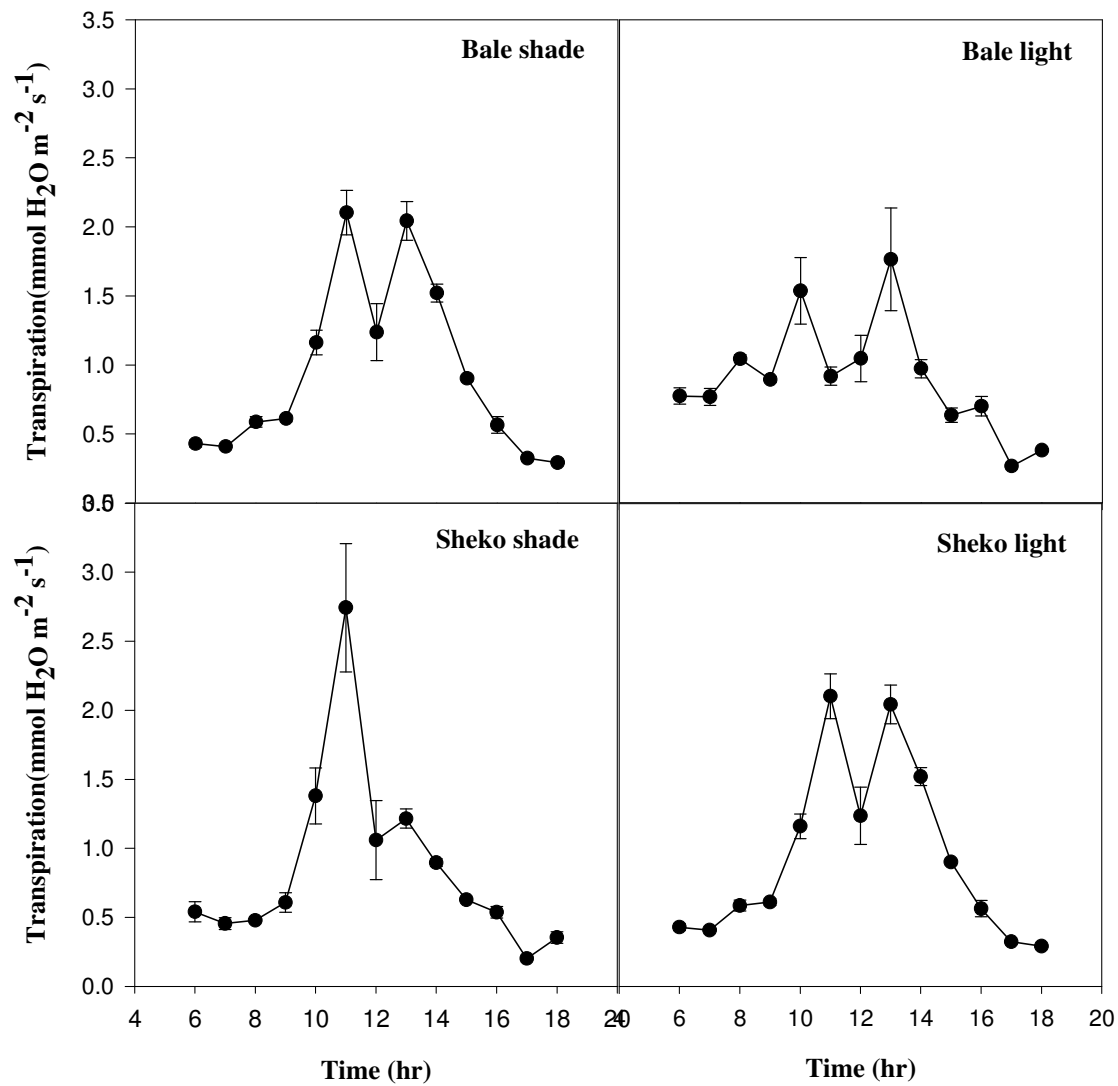


Figure 18: Diurnal course of transpiration rate of two coffee populations under two light treatments

Daily integrated transpiration

The studied populations showed different response in the total daily integrated E to the two different light conditions as shown in Figure 19. Both coffee populations under shade lost much water per day. On the other hand, exposed coffee plants performed the lowest water loss per day

for both populations. Moreover, Bale population showed higher total daily E than Sheko under both light conditions.

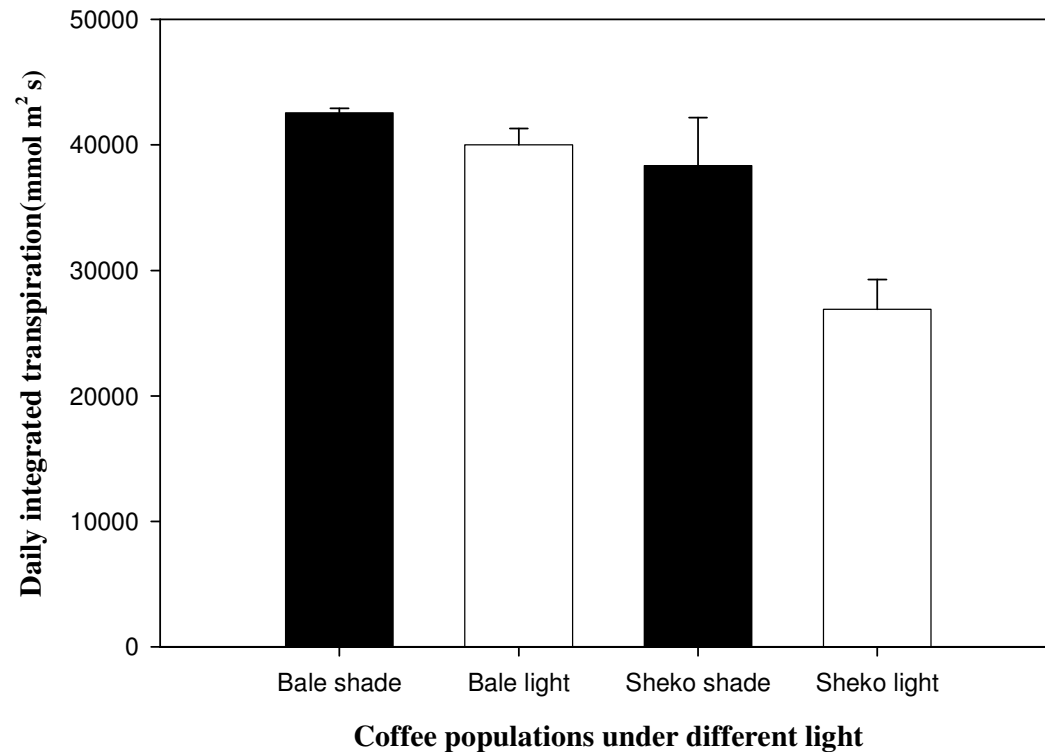


Figure 19: Daily integrated transpiration of two coffee populations under two light treatments

Internal CO₂ concentration

Diurnal course of C_i for both populations under respective light conditions is found almost similar. As indicated in Figure 20, both populations under shade had the lowest value at 8:00 in the morning which afterwards continued to increase along the day except showing lower points at 12:00 and 16:00. In contrast, exposed trees of both populations had highest value at 6:00 in the morning and continued decreasing along the day until 16:00 for Bale and 15:00 for Sheko which afterwards C_i started to raise.

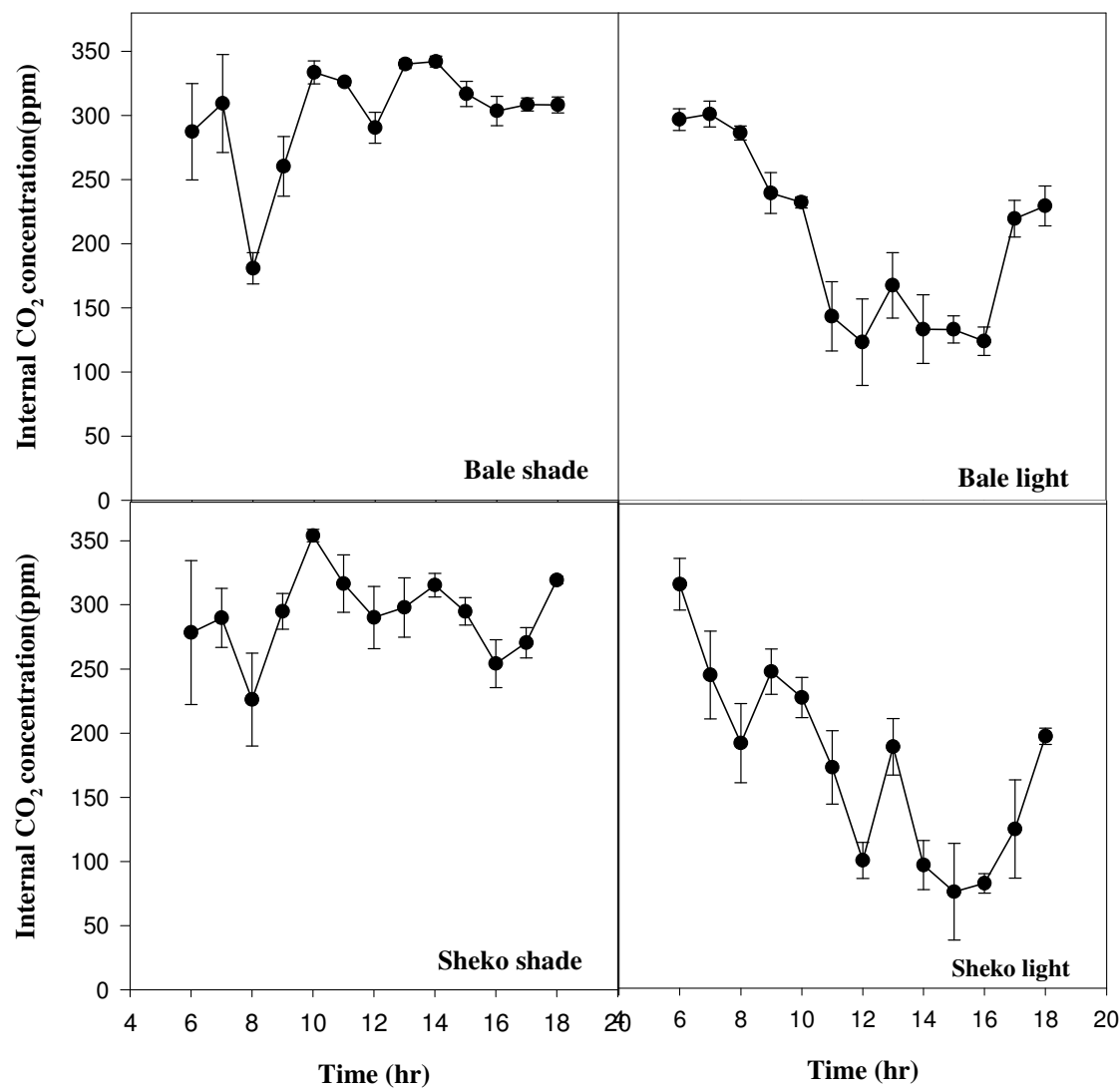


Figure 20: Diurnal course of C_i of two coffee populations under two light treatments

Instantaneous water use efficiency

As shown in Figure 21, WUE_i was found higher for both populations under high irradiance than shade. But both populations under both irradiance levels showed the same pattern of WUE_i . Except for exposed Bale coffee trees, which attained the highest value at 9:00am, shaded Bale and Sheko coffee plants under both irradiance level had the highest WUE_i at 8:00 am. After the stated peak hour, coffee plants of both populations under shade showed a fast declination while those under high irradiance declined gradually throughout the day.

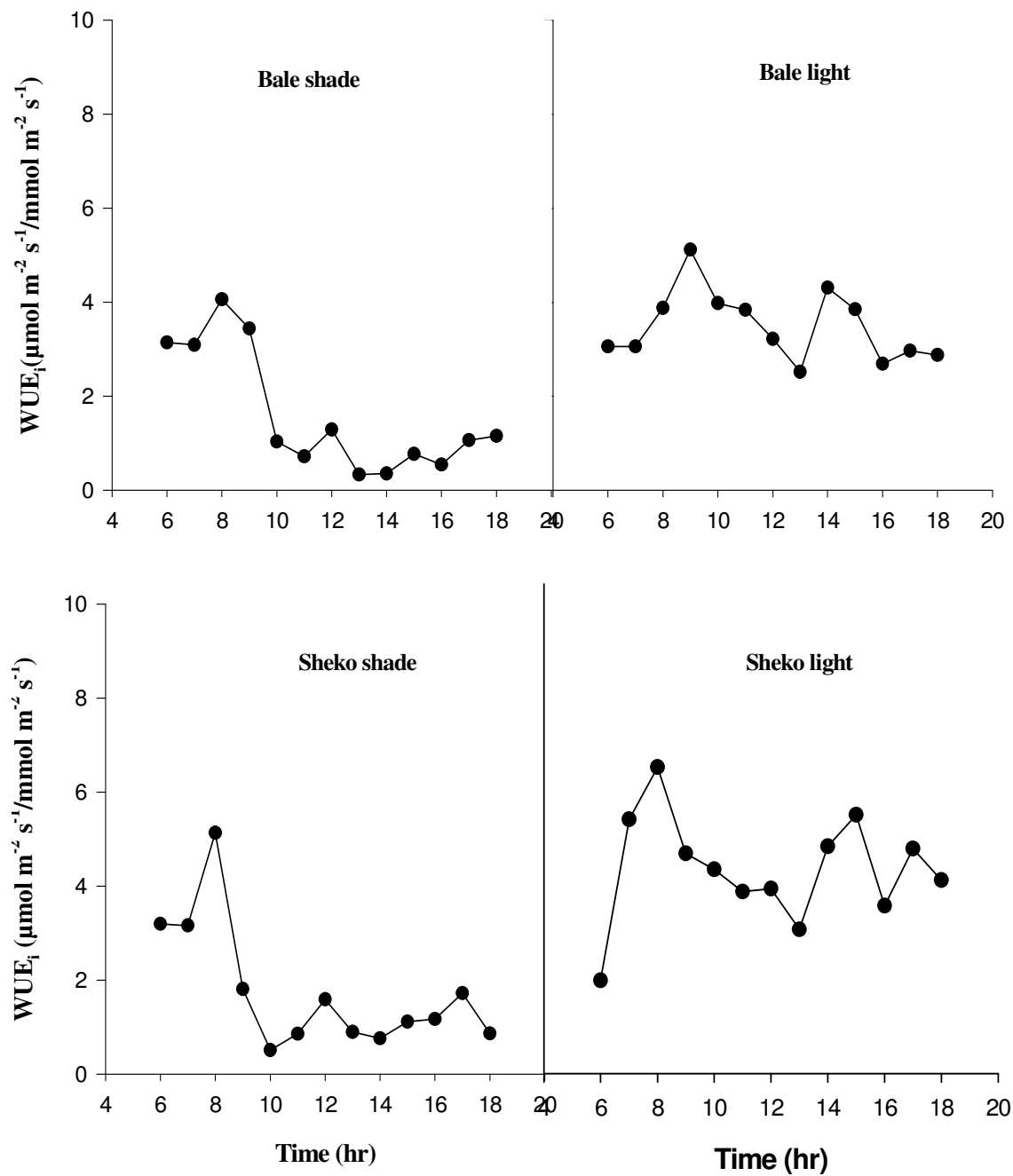


Figure 21: Daily course of water use efficiency of two coffee populations under two light treatments

Daily Integrated WUE

Exposed trees of both populations showed higher total daily WUE than their respective shaded trees. Figure 22 shows that exposed Sheko population attained the highest value than exposed Bale, whereas both shaded populations achieved almost the same total daily WUE.

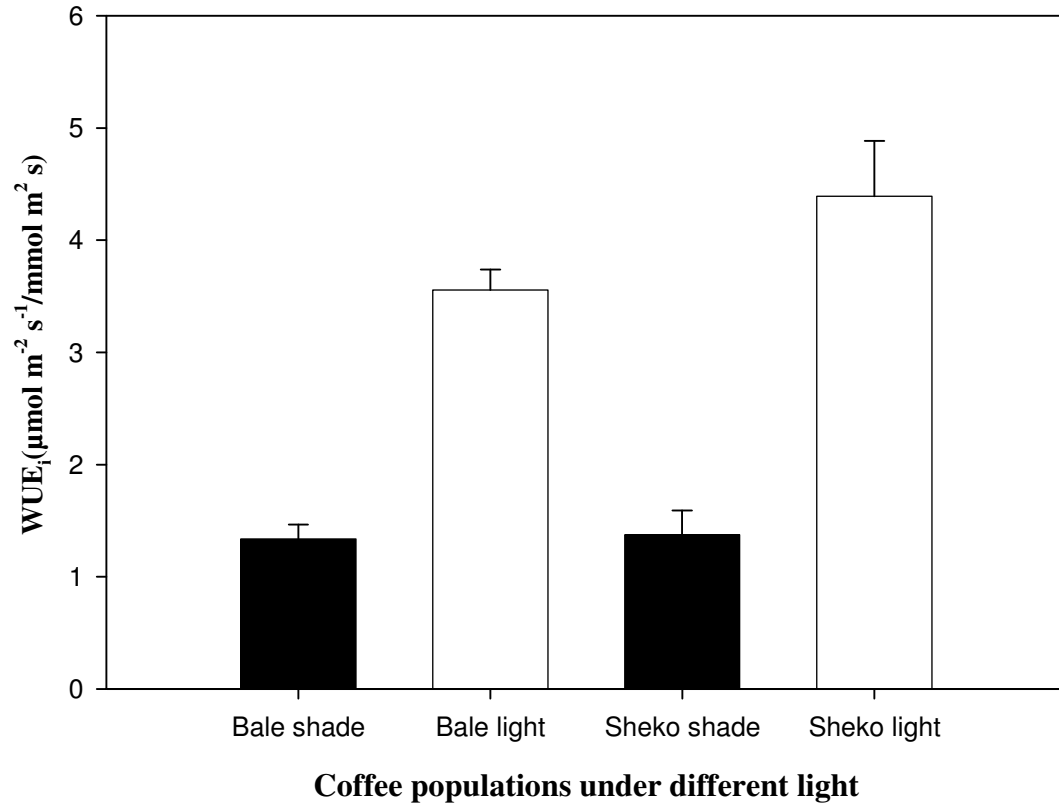


Figure 22: Daily Integrated WUE of two coffee populations under two light treatments

5.2.2 Photosynthetic light response curve

In Figure 23 of this experiment, leaves of Bale coffee population were saturated between 200 μ mol Photons $\text{m}^{-2} \text{s}^{-1}$ and 600 μ mol Photons $\text{m}^{-2} \text{s}^{-1}$. In shade coffee plants light saturation is nearly attained at 200 μ mol Photons $\text{m}^{-2} \text{s}^{-1}$ and in high irradiance plants at 600 μ mol Photons $\text{m}^{-2} \text{s}^{-1}$. On the other hand, shaded Sheko coffee population had the maximum photosynthesis rate at 900 μ mol Photons $\text{m}^{-2} \text{s}^{-1}$, whereas, the exposed coffees reached maximum saturation point at 800 μ mol Photons $\text{m}^{-2} \text{s}^{-1}$.

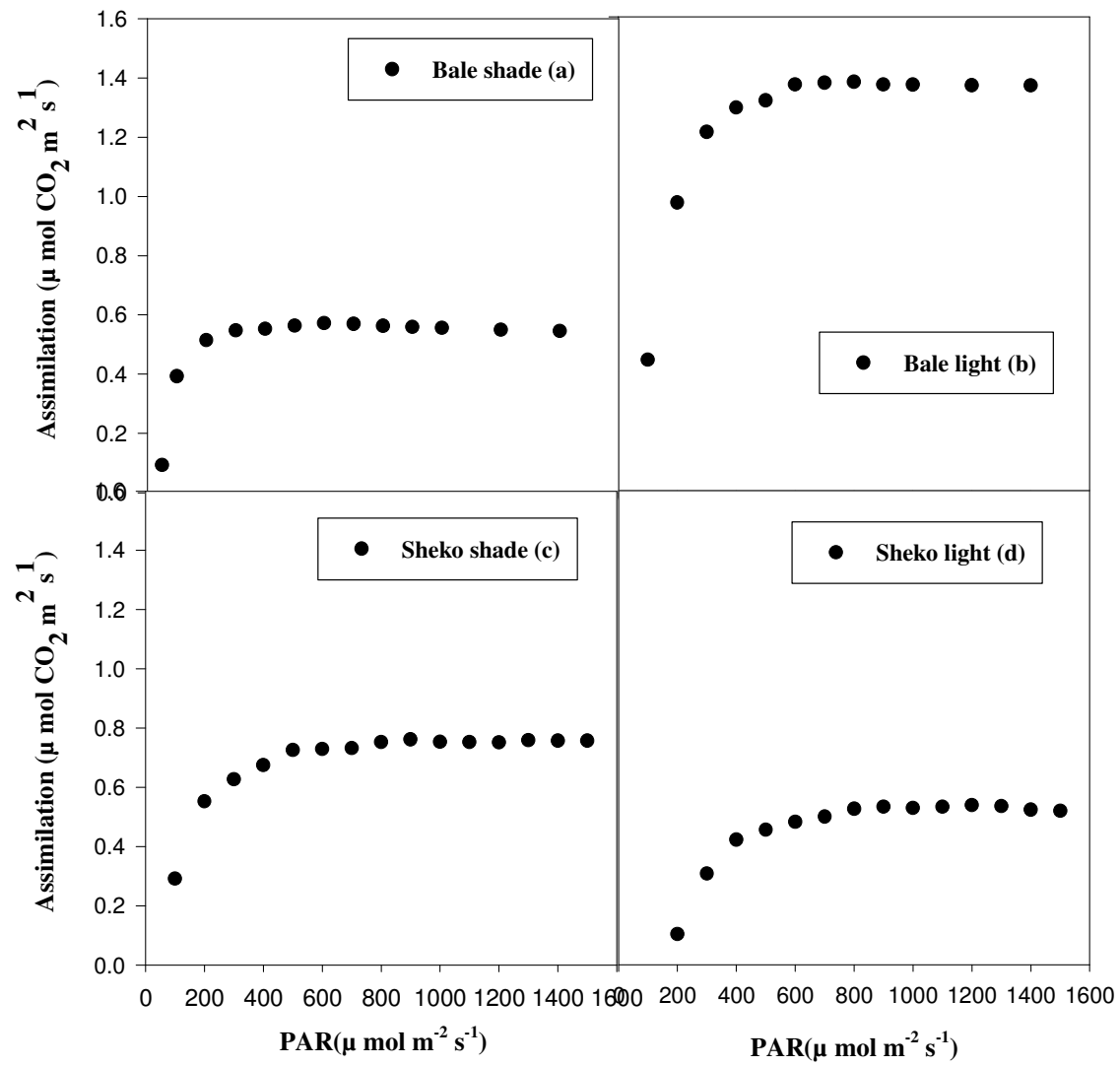


Figure 23: Photosynthetic light response curve of two coffee populations under two light treatments

6. DISCUSSION

6.1. Growth Effects of irradiance difference on *Coffea arabica*

In the present study, growth/morphological traits such as SH, NB, GD, IL, and SLA were different among the coffee populations in response to shade and high irradiance growing irradiance. This study provides information on the dynamic availability of resources and growth adjustment of coffee trees under shade and high irradiance environment. The result in showed that coffee plants grown under high irradiance achieved greater values for the above growth parameters than the shaded coffee trees within the same population. The greater values for most growth variables of coffee trees under high irradiance suggest that high light availability doesn't have a strong influence on the coffee plant morphology and also indicate the plasticity in dry mass allocation to the main stem parts. The negative influence of high light irradiance on the morphology of exposed coffee trees can be explained by the development of relatively higher root mass ratio, stem mass ratio and leaf area index, whereas shaded coffee plants had significantly higher leaf mass ratio which indicates the higher biomass allocation to the leaves than to the other parts. Moreover, the light intensity influenced the coffee plants under high irradiance in enhancing growth of more nodes with short internode length. The increase of leaf density in coffee plants at high irradiance in relationship with more shaded ones seems also to act as a defence mechanism from high temperatures as transpiration costs in highly illuminated environments. Since the exposed coffee trees were not also fruiting so that the carbon demand that could have been used by fruits is utilized for increased vegetative growth. The other reason that may be projected for the reduced growth in SH, NB and SG for shaded coffee trees could be low light availability or dense shade stress. As SH and SG was greater for shaded coffee plants of both populations than the exposed coffee plants during the early days of measurement, where the shading cloth was clean and new, they grew relatively lower than the exposed coffees laterally may be due to the increasingly accumulation of dust on the shading cloth which finally resulted in thick shade level than before. The result of this study is also supported by the work of Kobe (1997) cited in Taye Kufa (2006) who reported that 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. Moreover, Rena *et al* (1994) and Taye Kufa (2007) suggest that the relative growth rate of young coffee plants

decreased with increasing shade. The result of this study doesn't agree with several studies that have shown that young coffee plants grow better and accumulated more dry matter under moderate shade than high irradiance. The work of Franck *et al.*, (2006) states that when coffee grow in high irradiance, lacks a self-thinning mechanism in response to high fruit loads achieved which leads to very high carbon demand by fruits which results in a decreased vegetative growth. From the result of the current study it was also found that the coffee trees of Bale population were taller and thicker stemmed with large number of branches than Sheko population under both respective light conditions. This shows that coffee trees from drier areas adapted to both growing irradiance much more than coffee plants from warm and wet areas.

Specific leaf area (leaf area per unit dry mass) is an important link between vegetation water and carbon cycles. Furthermore, it is associated with many critical aspects of plant growth and survival. The results of this study indicate that plant responses to light are governed by different resource constraints at each end of the light gradient. For both populations under shade SLA was higher than exposed coffee plants. This is attributed to morphological modification of plants growing under shade in order to better adapt themselves to the available low light intensity. Allocation of high biomass to leaves and the formation of thin leaves with a high SLA, results much amount of light intensity to be trapped in to rise up the rate at which CO₂ is assimilated in plants grown under low light. This growth enhancement can be attributed to raising the proportion of photosynthate diverted to the production of leaves rather than the production of non-photosynthetic organs. An increase in SLA is a common response observed in plants under low light conditions and is usually associated with extra layers of mesophyll cells (John *et al.*, 2000; Taye Kufa, 2006; Righi *et al.*, 2008). On other hands, coffee plants under high irradiance reduce transpiration losses and increase carbon gain by making small-sized thick leaves with a low SLA which may be related to the formation of several photo-synthetically active parenchyma layers that can enhance their photosynthetic capacity. Moreover, 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. The same result is reported by Abrams and Kubiske (1990) cited in Adugna Debela (2007) who have arrived at a conclusion that says, "Plants under decreased light increases their SLA" to make use of this available light intensity. In this study, Bale coffee population showed more adaptation characteristics with regard to SLA than Sheko

population under shade environment whilst under high irradiance light Sheko coffee populations showed more adaptation than Bale.

6.2. Physiological effects of Irradiance difference on Coffea arabica

6.2.1. Acclimation of leaf gas exchange to high and low irradiance

Assimilation

Photosynthesis is a process by which plants reduce CO₂ to increase their own biomass and provide for reproduction. Photosynthetic rate of an intact leaf, which is enclosed in a leaf chamber, is measured by detecting the CO₂ concentration as a function of time. That is to mean by measuring the quantity of CO₂. Furthermore, high rate of photosynthesis means there is high biochemical and physiological potential for high carbon fixation capacity. However, different factors affect the photosynthetic rate of a given plant of which light intensity is the one. Plants of some species perform differently if are grown under different light regime. Maximum net photosynthesis of this study was observed greater for coffee leaves grown under high irradiance than shade for both Sheko and Bale populations. This can be explained as coffee leaves under high irradiance may show enough plasticity in order to acclimate themselves to sunny environment, along with the plants optimize photosynthesis. The most important adjustment plants under high light intensity undergo is a reduction in leaf surfaces which may be related to the formation of several photo-synthetically active parenchyma layers that can enhance their photosynthetic capacity. In addition, amongst other morphological adaptations plants under high irradiance develop to the harsh environment are increasing stomatal density, formation of thick cuticle, development of columnar tissue, and change in color of the leaves from glossy dark green to dull light green. Therefore, the higher A_{net} found for coffee plants of both populations under high irradiance is associated with these adaptive mechanisms in such habitats. Moreover, this result may be obtained due to the absence of other stresses such as drought and temperature which is not greater than 25°C. Nunes *et al.* (1986) cited in Kumar and Tieszen (1980) suggested that a rise in temperature resulted in increased internal CO₂, with consequent increased stomatal resistance, since it is known that high internal CO₂ concentration causes stomatal closure. On the other hand, the other suggestion for the effect of shade as A_{net} limitation is projected due to

insufficient light interception by the coffee leaves. Furthermore, a low physiological plasticity to low light in coffee leaves located under shade may result in reduced A_{net} as compared to exposed leaves. This study is supported by the work of DaMatta (2004) and DaMatta *et al.* (2007) who explained lower A_{net} as a result of limitation of light. Kitao *et al.* (2000) cited in Taye Kufa (2006) also indicated that shade plants are more susceptible to photoinhibition than sun plants and that, within the same species, plants grown under a low growth irradiance develop higher susceptibility to photoinhibition. Furthermore, the result of this study is supported by the work of Gutiérrez and Meinzer (1994); Yamaguchi and Friend (1979); Friend (1984) and Fahl *et al.* (1994) cited in DaMatta (2004); Luiza *et al.* (2005) cited in Adugna Debela (2007); Naidu and DeLucia (1998); Marur and Faria (2007); Taye Kufa (2006); Kumar and Tieszen (1980); Weidner *et al.* (2000). Aranda *et al.* (2005) also found higher A_{net} levels for seedlings of the sun plant, *Quercus suber*, growing in high light rather than in low light environments. Bale coffee population showed the higher daily net assimilation under both shade and high irradiance. This shows that Bale coffee trees had more morphological or anatomical plasticity of greater acclimative value in order to respond to the high growing irradiance than Sheko coffee trees. Contrarily, many studies have given explanations that coffee plants under shade achieve higher assimilation than coffees grown under high irradiance light. Furthermore, there was no major difference found in photosynthetic capacity between sun and shade leaves in the work of Araujo *et al.* (2008).

Stomatal conductance

Stomatal conductance is a numerical measure of the rate of passage of either water vapor or CO_2 through stomata. It plays an important role in the plant-atmosphere water exchange and hence it is a key parameter in many ecological models (Chen *et al.*, 1999 cited in Adugna Debela, 2007). The movement of stomata can be affected by several environmental factors, including water status, temperature, CO_2 concentration and light. This movement of the stomata affects the rate at which CO_2 is assimilated and water is evaporated from the leaves. In this study, stomatal conductance was found lower at midday whereas it was shown higher in the morning and low in the afternoon. Under normal condition, such pattern is common in plants growing under tropical conditions. Several times coffee has 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. Stomatal closure while soil water availability has met the plants demand can be explained in relation to the high irradiance and temperature. These factors provoke low local water potential in the leaves by causing a rapid increase in transpiration resulting in stomatal closure (Weidner *et al.*, 2000). Accordingly, in the morning as the irradiance and temperature is lower the stomata of the leaves remain open until the irradiance and temperature reaches higher at midday. As the irradiance and temperature continues strong in the afternoon the stomata of the coffee leaves remains closed. It is also reported that temperature and vapor pressure deficit, and not irradiance, are the most important factors in stomatal regulation, provided that the irradiance level be above the critical value (Nunes, 1988 cited in Righi *et al.*, 2008).

However, self-shading due to overlapped leaves would decrease the calorific load and transpiration costs in highly illuminated environments (Givinish, 1984 cited in Righi *et al.*, 2008). Thus, the increase of leaf density in coffee plants at high irradiance in relationship with more shaded ones seems to act as a defense mechanism from high temperatures, as coffee plants are better adapted to environments with air temperature ranging from 18-22°C (Righi *et al.*, 2008). Therefore, the higher stomatal conductance obtained in this study for exposed coffees of both populations can be attributed to such morphological adaptation.

Transpiration

In this study, transpiration of the coffee leaves also showed the same pattern as the stomatal conductance. It was increasing in the morning until it reached to the lowest value at midday where the irradiance and temperature was higher and decreasing in the afternoon. This might be explained by the stomatal regulation in response to vapor pressure deficit, which increased due to raising leaf temperature when the leaves were exposed to direct sunlight. In this study, shaded coffee plants showed higher daily integrated E than exposed under their respective populations. This is due to the fact the coffee plants present lower total leaf area and higher SLA, with thinner and larger leaves, which makes them to transpire more per leaf mass. Differently, the behaviour of exposed coffee plants was completely opposite, with smaller and thicker leaves, reduced opening stomata due to lesser hydric potential, presenting a higher accumulation of dry matter.

Moreover, the Bale population transpired more than Sheko, due to their leaf characteristics under both irradiance levels. This result is in line with the work of Righi *et al.* (2008) and Taye Kufa (2006). As reported by several authors, changes in SLA values constitute an important plant feature, and are commonly found in species adapted to different luminosity conditions.

Water Use Efficiency

In this experiment, coffee plants of both populations under shade showed greater water loss per unit of incident irradiance. On the other hand, coffee plants under high irradiance had the least water loss per unit of incident irradiance. This fact may be attributed to the higher stomata sensitivity of the coffee plants under more illuminated conditions. Resistance in intercellular spaces (r_i) which is a significant component of stomatal resistance (r_s), becomes higher in thicker leaves than in thin ones and larger in leaves with small intercellular spaces than in those with larger spaces. This resistance allows plants under high irradiance allow them to have a decreased transpiration per unit leaf area. Therefore, the increased photosynthesis rate per leaf area unit divide by the reduced transpiration per leaf area unit for exposed coffee plants would result to increased water use efficiency (WUE). Anet increase in the mesophyll cell surface/leaf surface ratio would certainly lead to higher WUE in that the photosynthesis would be more increased than transpiration .Contrarily; shaded coffee plants had no reason for their stomata to act so as to restrict water loss, in view of the milder environment in which they were, therefore presenting a lesser WUE. Accordingly, this result is in agreement with the work of Kramer and Boyer (1995); Givinish (1988); Jarvis and Slatyer (1966); Nobel (1980) and Ong *et al.* (1996).

6.2.2. Photosynthetic light response curve

The saturating irradiance for Bale exposed coffee plants was found higher showing that their photon flux density requirement was higher than in Bale shade plants. However, for Sheko coffee population an opposite result is observed. Most crops adapted to grow in high irradiance have higher light saturation requirements. The higher light-saturated photosynthetic rates for sun grown coffee plants is expressed as a result of higher maximal carboxylation rate and maximal light-driven electron flux (Araujo *et al.*, 2008). This disparity of result for the two populations may be due to instrumental problem. Different research show that most crops adapted to grow in

high irradiance have higher light saturation requirements (Kumar and Tieszen, 1980; Filho, 1997).

7. CONCLUSION AND RECOMMENDATION

From the results of this study, it is concluded that the growth and photosynthesis parameters of *Coffea arabica* are significantly affected by high and low irradiance levels. It has also been shown that the growth and photosynthesis could be much higher in exposed coffee plants than in shade with little or no effect of damage of high irradiance. This indicates that coffee plants under high irradiance showed higher morphological and physiological plasticity. Therefore, this study can suggest the growth of coffee under high light availability, though it is said to be shade obligatory species. But considering the importance of favourable shade for the production of coffee should not be undermined regarding to its ecological importance. It is also shown that population differ in their response to growth light level. Plants that originated from drier area such as the Bale region show a higher growth under high light availability than shade. The study indicate that the sufficient shade level for good growth and production of coffee needs to be further investigated and related to the natural growth environment of the population. Furthermore, further research on the productivity of the populations under the two irradiance levels including other populations should be carried out.

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DECLARATION

This thesis entitled by “**Growth and Physiological Response of Two *Coffea arabica* L. Populations for Shade and High irradiance Growing Irradiance**” has been submitted for examination with my approval as the work is carried out under my guidance as a major advisor. The work is completed in partial fulfillment of the requirements for the award of Master of Science degree in the field of Botanical Science to the School of Graduate Studies, Addis Ababa University.

Professor Masresha Fetene

Addis Ababa University

Signature _____

Date _____

I, Hiwot Hailu with Id.No. GRS/1917/98 declare that the matter embodied in this work has not been submitted earlier for award of any Degree or Diploma to the best of my knowledge.

Hiwot Hailu

Signature _____

Date _____