

Full Length Research Paper

Effects of shade on growth, production and quality of coffee (*Coffea arabica*) in Ethiopia

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The research work was conducted to evaluate the effect of shade on growth and production of coffee plants. To achieve this, growth and productivity of coffee plants growing under shade trees were compared with those of coffee plants growing under direct sun light. Different physiological, environmental and quality parameters were assessed for both treatments. Shade trees protected coffee plants against adverse environmental stresses such as high soil temperatures and low relative humidity. Shade, however, also triggered differences in physiological behaviour of the coffee plants, such as improved photosynthesis and increased leaf area index, resulting in better performance than possible in direct sun light. Consequently, coffee plants grown under shade trees produced larger and heavier fruits with better bean quality than those grown in direct sun light. Moreover, shaded plants had greater biochemical and physiological potential for high dry matter production which would help them to maintain high coffee yields in the long term. If growing coffee under shade trees would allow other sources of income such as fruits, fuel wood and timber to be produced, it could be socially more acceptable, economically more viable and environmentally more sustainable. Since in Ethiopia people are moving towards replacing coffee by 'chat' and/or growing coffee in an open sun, we support the recommendations of growing coffee in the shade and suggest that the future research should be directed toward deterring the development of fungal diseases and increase of coffee yields under shaded conditions.

Key words: Ethiopia, coffee, photosynthesis, shade, bean quality.

INTRODUCTION

Growing coffee under shade trees is one of the fundamental principles in traditional organic coffee growing systems (Beer et al., 1998). Shade trees reduce excessive light, mulch the soil with their litter, create hostile conditions for pests and diseases, and harbour a variety of predatory animals (Beer et al., 1998). Arabica coffee is a self-pollinated plant initiating heavy flowers that rapidly develop to fruits (Yunianto, 1986). During this period there is increasing carbohydrate absorption from both leaves and wood for flowers initiation and rapid fruits expansion. As a result roots are damaged, leaves are abscised and branches start dying from the tip and go back to the petiole. But, shade trees assist in maintaining coffee yields in the long term by reducing periodic

over-bearing and subsequent die-back of coffee branches. In addition, shading delays the maturation of coffee berries resulting in a better bean filling and larger bean size resulting in better coffee quality (Muschler, 2001).

In Ethiopia, coffee was cultivated in this traditional way following the principles that Lammerts van Bueren and Struik (2004) called 'the concept of naturalness'. Soils were amended by applying compost, farm yard manure and green manure, while no chemical fertilizers, herbicides or fungicides were used. However, as demands for coffee production expanded, many coffee growers abandoned their traditional coffee growing system and started to grow coffee without shade trees. This new coffee production system was accompanied with intensive use of chemical fertilizers, insecticides, herbicides and fungicides resulting in blended and inferior coffee quality. Coffee plants in direct sunlight also showed a

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higher incidence of premature death (Steiman, 2003). In addition, the genetic resources of *Coffea arabica* and its associated biodiversity are disappearing at an alarming rate and environmental degradation, including soil erosion and extreme river discharges, is becoming severe (Gole et al., 2002; Osman, 2001). People in Ethiopia became unable to nourish their families and frequently became dependent on food aid.

However, there is a growing worldwide movement to support and enhance organic coffee production systems under shade trees (Mark, 2005). This requires research into the effects of shade on growth, production and quality of coffee. We therefore carried out on-farm research to assess the effects of shade on physiology, growth, production and quality of coffee.

MATERIALS AND METHODS

Three different coffee farms were selected from Manna district, Jimma Zone, Ethiopia in the 2007 cropping season. The district is 22 km to the west of Jimma town and located between 7°54'N and 36°53'E (Garedew and Tsegaye, 2010) at an elevation of 1820 m.a.s.l with mean minimum and maximum temperatures of 13 and 25°C, respectively. The major soil types of the area are nitosol and comsols and the area receives an average annual rainfall of 1467 mm. *C. arabica* is the economically most important coffee of the area. Manna district is considered as one of the original *C. arabica* producing areas of the country. *C. arabica* produced in Manna has already been certified as organic coffee by the German BCS-Öko Garantie, GMBH (Schmitt and Grote, 2006).

Data on light intensity (lux), air temperature (°C), air relative humidity (%), and soil temperature at a depth of 10 cm (°C) were recorded using a light meter (EXTCH, Model EA30), thermohygrometer (HANNA, HI8564) and soil thermometer (Taylor Bi-Therm), respectively. Photosynthetic rate (A , $\mu\text{mol m}^{-2} \text{s}^{-1}$ of CO_2), transpiration rate (E , $\text{mmol m}^{-2} \text{s}^{-1}$ of water vapour), stomatal conductance (g_s , $\text{mmol m}^{-2} \text{s}^{-1}$ of water vapour or CO_2), Photosynthetically Active Radiation (PAR, $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) and leaf temperature (IT, °C) were determined using a leaf chamber porometer (LCpro+). These parameters were assessed from five intact, young and fully expanded leaves located on the third and fourth pairs from the top of each plant in September and October 2007 between 10:00 and 12:00 a.m. The same leaves were subjected to a period of dark adaptation for 20 min. and then exposed to a light pulse of high (saturating) intensity ($2000 \mu\text{mol photons m}^{-2} \text{s}^{-1}$) using chlorophyll fluorometer (OS-30P) to assess chlorophyll fluorescence, indicating the electron transport efficiency of photosystem II (PSII). Chlorophyll fluorescence is expressed as the F_v/F_m ratio (no dimension) as a measure of relative quantum yield.

Leaf colour was assessed using a colour meter (AccuProbe, HH06) (Lab scale) and leaf area (m^2) was determined by scanning each sampled leaf with a leaf area meter (AM200). These leaves were dried in an oven at 75°C for 24 h to determine their dry weight; nitrogen content (mg per g dry matter) was assessed in the dried leaf material using micro - Kjeldahl Nitrogen apparatus (DK6) and data collected from leaves were averaged per plant per location (replication) for each leaf insertion.

Relative growth rate (RGR, $\text{cm cm}^{-1} \text{ month}^{-1}$) of each plant was estimated from two selected primary plagiotropic branches whose length was measured at the beginning and at the end of the experiment. Fully ripened coffee berries were harvested from the selected individual trees and dried until a constant weight was reached (moisture content 9 to 12%). Coffee weight for each sample was registered on 1000 seed weight base (g per 1000

beans) and beans were made to pass through a series of sieves with round perforations of 0.635, 0.595 or 0.555 cm (hole's diameter) after which weight fractions retained on each sieve were converted to weight percentages of the total sample.

Raw quality (shape and make, colour and odour) was valued on a scale starting from 2, the minimum value (indicating small shape and make, brownish colour and strong/odd odour) to 15, the maximum value (indicating very good shape and make, bluish colour and clean odour). For each sample, 200 g of green coffee were roasted to a uniform light brown colour, at Jimma Agricultural Research Center laboratory roaster. Liquor quality (acidity, body and flavour) was tested by a panel of six experienced judges and values were given from 2, the minimum value (indicating lacking acidity, thin body and poor flavor) to 20, maximum value (indicating pointed acidity, full body and very good flavour (unit for both raw and liquor qualities: percentage of score).

The experimental design was a randomized complete block design with two treatments (shade and direct sun light) in which ten plants (five for each treatment) were randomly selected. This was replicated three times at different sites, resulting in a total of 30 plants (15 plants per treatment). At each measurement five leaves per plant were used for gas exchange and chlorophyll fluorescence. The collected data were subjected to analysis of variance and means were compared by a t-test at 5% probability.

RESULTS

Environmental variables

Soil temperature and light intensity of shaded coffee plants were significantly lower than those of coffee plants grown in direct sun light, whereas the relative humidity of the air of the shaded plants was significantly higher than of plants grown in full sun light. Air temperature did not differ significantly (Table 1).

Photosynthesis variables

Rate of photosynthesis (A) and F_v/F_m were higher for shaded plants than for plants in direct sun light. Treatments did not differ in transpiration rate or stomatal conductance. PAR at leaf level and leaf temperature were obviously lower for shaded plants than for plants in full and direct sun light (Table 2).

Plant variables

Coffee plants grown in the shade had higher values for SLA, LAI and leaf nitrogen content. Shaded leaves were also darker in leaf colour than leaves from plants grown in direct sun light (Table 3). The relative growth rate, however, did not differ significantly between the two treatments (Table 3).

Quality and yield

Bean weight and size assessment made on harvested coffee beans indicated that beans developed under shaded

Table 1. Averages and statistical analysis of various environmental variables for shaded coffee plants and coffee plants in direct sun light.

Variable	Treatment		Significance (two-tailed)
	Shaded plant	Plant in direct sun light	
Air temperature (°C)	25.5	26.7	ns
Soil temperature (°C)	19.7	20.8	0.00*
RH (%)	59.7	55.1	0.01*
Light intensity (lux)	557	1193	0.00**

ns indicates not significant ($P > 0.05$). * indicates significant difference at $P < 0.05$. ** indicates significant difference at $P < 0.01$.

Table 2. Averages and statistical analysis of various photosynthesis variables for shaded coffee plants and coffee plants in direct sun light.

Variable	Treatment		Significance (two-tailed)
	Shaded plant	Plant in direct sun light	
A ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	3.51	2.45	0.03*
F_v/F_m (-)	0.71	0.61	0.01*
Stomatal conductance ($\text{mmol m}^{-2} \text{ s}^{-1}$)	100	60	ns
Transpiration rate ($\text{mmol m}^{-2} \text{ s}^{-1}$)	1090	1140	ns
PAR ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$)	320	2260	0.00**
Leaf temperature (°C)	24.2	28.1	0.00**

ns indicates not significant ($P > 0.05$). * indicates significant difference at $P < 0.05$. ** indicates significant difference at $P < 0.01$.

Table 3. Averages and statistical analysis of various plant variables for shaded coffee plants and coffee plants in direct sun light.

Variable	Treatment		Significance (two-tailed)
	Shaded plant	Plant in direct sun light	
SLA (cm^2/g)	116	98	0.04*
LAI ($\text{m}^2 \text{ m}^{-2}$)	3.8	2.8	0.01*
RGR ($\text{cm cm}^{-1} \text{ month}^{-1}$)	12.3	9.7	ns
Leaf N content (mg g^{-1} leaf dry matter)	288	219	0.03*
Leaf colour (value on greenness scale)	-8.6	-7.6	0.00**

ns indicates not significant ($P > 0.05$). * indicates significant difference at $P < 0.05$. ** indicates significant difference at $P < 0.01$.

Table 4. Averages and statistical analysis of various quality and yield variables for shaded coffee plants and coffee plants in direct sun light.

Variable	Treatment		Significance (two-tailed)
	Shaded plant	Plant in direct sun light	
Coffee weight (g/1000 beans)	148	134	ns
Raw quality (% of maximum score)	85	85	ns
Liquor quality (% of maximum score)	65	50	ns
Bean yield (Mg ha^{-1})	2.13	3.10	ns

ns indicates not significant ($P > 0.05$).

shaded condition were heavier and larger in size and had better liquor taste than those developed on plants grown in direct sun light (Table 4). No treatment difference was observed with respect to raw coffee quality. However,

greater yields were obtained from coffee plants grown in the direct sun than from shaded plants (Table 4), although this difference was also not statistically significant.

DISCUSSION

Soil temperature plays a critical role in the survival of many organisms, but it varies in response to exchange processes that take place through the surface of the soil. The reduction in soil temperature, observed under shade, was mainly caused by the ability of shaded soil to stabilize the local thermal balances and also to reduce the heat flux caused by the accumulated plant based biomass (Morais et al., 2006). Siebert (2002) also reported that shading reduces and stabilizes the soil temperature by reducing the radiant flux reaching the soil and modifying the temperature amplitude at the soil surface.

The reduced air temperature registered for coffee grown under shade was in agreement with the result obtained by (Campanha et al., 2005). As they concluded the reduced air temperature was mainly due to the reduced direct incidence of solar radiation on the coffee canopy. Shading buffers the extreme temperature variations and provides a microclimate which attenuates extreme temperatures of air and soil and preserves surface soil humidity.

High rates of photosynthesis mean, according to Gulmon and Chu (1981), that there is high biochemical and physiological potential for a high carbon fixation capacity. To increase their carbon fixing potential, shaded plants undertake certain modifications such as developing thinner and larger leaves (Friend, 1984) with more thylakoids per granum and more grana per chloroplast (Fahl et al., 1994). These modifications allow them to efficiently capture and utilize the available light energy in order to increase their dry matter production. Plants having higher SLA exhibit higher productivity (Li et al., 2005) and have higher potential relative growth rate than those having lower SLA (Poorter and Werf, 1998).

Robakowski et al. (2003) concluded that SLA decreases as light intensity increases. In our experiment, lower SLA was obtained from coffee plants grown in an open sun condition which is in consistence with the findings of these authors. For shaded coffee plants, the increased SLA and the development of a darker green colour were mainly attributed to the higher nitrogen content found in their leaves. It is likely that the increased SLA and the development of dark green leaf colour under shaded coffee plants partly contributed for the higher rate of photosynthesis observed under this condition. Photosynthetic rate of sun grown coffee plants, on the other hand, was limited by stomata closure, high leaf temperature and low internal carbon dioxide concentration.

Since many of the physiological processes of plants are temperature dependent, under high temperature crops have great difficulty in maintaining photosynthetic activities and growth (Sethar et al., 2002). Coffee is exceptionally sensitive to fluctuations in leaf temperature, especially temperatures above 25°C. For the coffee plants grown in direct sun light, increased air temperature above this level resulted in subsequent lowering of

stomatal conductance (data not shown) which in turn imposed a large limitation on the rate of CO₂ assimilation. Kasai (2008) has also found comparable results: stomatal conductance and photosynthetic rate were found significantly lowered by growing soybean plant under continuous light. High temperatures, according to Farquhar and Sharkey (1982), reduce the electron transport capacity and increase the rates of CO₂ evolution from photorespiration and other sources causing the photosynthetic rate to become lower.

As stomata are highly responsive to the factors that influence the rate of transpiration, their movements can also be affected by leaf-to-air vapour pressure difference (Kim et al., 2004). Under shade, however, reduced air temperature and light intensity increased the percentage relative humidity in the air around coffee plants and subsequently reduced the vapour pressure deficit (VPD) between the interior of the leaf and the atmosphere. This reduced VPD decreased rate of transpiration of the leaf resulting in increased leaf water potential. Under such small VPD, stomatal aperture increases providing better chance for CO₂ to be diffused into the leaf.

Due to the interception of solar radiation by shade trees, the incident solar radiation, PAR, was greatly reduced for coffee grown under shade. But, plants under shade had a higher photosynthetic rate. This paradox can be explained by the fact that plants under shade undertake certain morphological modifications and physiological adaptations, and their leaves are capable of absorbing more than 90% of the energy contained in the wavelengths between 400 and 700 nm (Lee, 1985). In addition, Bartlett and Remphrey (1998) indicated that there are no significant reductions in photosynthetic rate and growth of coffee plants grown under shade unless the level of shade exceeds 90%.

The darker green colour of coffee leaves developed in the shade was most likely associated with the larger amount of nitrogen accumulated in them (Titus and Pereira, 2005). Leaves having such dark green colour absorb more light, have chloroplasts with improved light-capturing capability and are cheap units of photosynthetic area (energetically) as they capture lower light intensity and utilize them efficiently to increase their photosynthetic rate.

The ecological behaviour of plants and their health status can be judged by considering certain parameters. For example, SLA reflect the growing conditions of the plants (Garnier et al., 2001), where as LAI and the F_v/F_m ratio are indicators of the health status of a given crop plant (Kitao et al., 2000; Malone et al., 2002). Higher LAI observed for coffee plants growing under shade indicated that these plants have higher potential for CO₂ assimilation and dry matter production than unshaded plants (McNaughton and Jarvis, 1983). Higher F_v/F_m ratio observed for shaded coffee plants illustrated the fact that these plants are less stressed by high light intensity than those grown in direct sun light. Sethar et al. (2002)

supported this idea indicating F_v/F_m ratio decreases significantly when plants are exposed to heat stress.

For plants grown under higher irradiance, the reduced value of F_v/F_m ratio is an indication of the damage of a proportion of PSII reaction centres, a phenomenon called photo-inhibition. Once a proportion of a PSII reaction centre is damaged, light energy utilization capacity of this centre decreases resulting in a reduced quantum yield of net photosynthesis (Rintamaki et al., 1995; Maxwell and Johnson, 2000). Light, as energy source for photosynthesis, is an essential prerequisite for plant life. Excess light, however, can inhibit photosynthesis and lead to photo-oxidative destruction of the photosynthetic apparatus, thereby decreasing the photosynthetic rate of the plant growing in direct sun light besides affecting its life span (Li et al., 2010). According to Fahl et al. (1994) and Ramalho et al. (2000), higher values of F_v/F_m obtained from shaded leaves can also be linked with higher leaf nitrogen content. Under stressed conditions the availability of more leaf nitrogen triggers photo-protective mechanisms against photo-oxidation by its ability in promoting the activation and backing up of the protective mechanisms (Fahl et al., 1994). Leaf nitrogen was also found to have a strong and positive correlation with carbon assimilation rates (data not shown) allowing shaded leaves to have better photosynthetic performance and greater vegetative growth rate than sun leaves. Therefore, coffee plants found in direct sun light were grown under environmental conditions that are more likely to lead to plants stress responses, compared with the environmental conditions under which shaded plants are grown.

The fact that shade resulted in heavier and larger coffee beans was mainly caused by its effect on temperature and the duration of the ripening period. Muschler (2001), who found comparable results, indicated that coffee bean size significantly and consistently increases even with increasing shade levels. Similarly, the shade effect on liquor taste was also the result of delayed fruit maturation and ripening. Morais et al. (2006) showed that shading enhances coffee quality, in terms of biochemical composition, including the contents of caffeine, oil and chlorogenic acid. The quality and size of coffee beans, and the taste of finished products, are therefore better under shade than in systems without shade trees.

Shade grown coffee gave lower yields than coffee in the direct sun, but this difference was not statistically significant. However, we surmise that a moderate yield will be more sustainable than a maximum yield and the former will be more important for traditional small farmers. Moreover, shade trees are alternative means of income via carbon sequestration, production of fuel wood, timber and fruits. Therefore growing coffee in an agroforestry system is socially more acceptable, economically more viable and environmentally more sustainable than growing coffee in the direct sun.

Conclusions

Coffee plants grown in the shade suffer less from environmental stresses and have higher biochemical and physiological potential for carbon fixation compared with coffee plants grown in the direct sun light. Shade grown coffee plants also produce larger and heavier beans with better cup taste than coffee plants grown in the direct sun. If growing coffee under shade trees would allow other sources of income such as fruits, fuel wood and timber to be produced, it could be socially more acceptable, economically more viable and environmentally more sustainable. We therefore recommended growing coffee in the shade.

In addition, shade trees serve as an alternative source of income for coffee producers. Nevertheless, highest yields per hectare were obtained from coffee plants in the direct sun light indicating the need for further research on determining proper plant density, compatibility between shade trees and coffee plants, as well as extent of competition between them for water and nutrients. Since in Ethiopia people are moving towards replacing coffee by 'chat' and/or growing coffee in an open sun, we support the recommendations of growing coffee in the shade and suggest that the future research should be directed toward deterring the development of fungal diseases and increase of coffee yields under shaded conditions.

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REFERENCES

- Bartlett GA, Remphrey WR (1998). The effect of reduced quantities of photosynthetically active radiation on *Fraxinus pennsylvanica* growth and architecture. *Can. J. Bot.*, 76: 1359–1365.
- Beer J, Muschler R, Kass D, Somarriba E (1998). Shade management in coffee and cacao plantations. *Agroforestry Systems*, 38: 139–164.
- Campanha MM, Silva RH, Freitas GB, Martinez HE, Gracia SL, Fing FL (2005). Growth and yield of coffee plants in agroforestry and monoculture systems in Minas Gerais, Brazil. *Agroforestry Syst.*, 63(1): 75 – 82.
- Fahl JI, Carelli MC, Vega J, Magalhaes AC (1994). Nitrogen and irradiance levels affecting net photosynthesis and growth of young coffee plants (*Coffea arabica* L.). *J. Hort. Sci.*, 69: 161–169.
- Farquhar GD, Sharkey TD (1982). Stomatal Conductance and Photosynthesis. *Annu. Rev. Plant. Physiology*, 33:317–345.
- Friend DC (1984). Shade adaptation of photosynthesis in coffee arabica. *J. Photosynthesis Res.*, 5(4): 325 – 334.
- Garedew W, Tsegaye B (2010). Trends of Avocado (*Persea Americana* M) production and its constraints in Mana Woreda, Jimma Zone: A potential Crop for coffee diversification. *Trends Hortic. Res.*, ISSN 1996 – 0735/ DOI: 10.3923/thr.2010.
- Garnier E, Shipley B, Roumet C, Laurent G (2001). A standardized protocol for the determination of specific leaf area and leaf dry matter content. *Funct. Ecol.*, 15: 688–695.
- Gole TW, Denich M, Demel T, Vlek PLG (2002). Human Impacts on

- Coffea Arabica Genetic Pools in Ethiopia and the Need for its In situ Conservation. In: Managing Plant Genetic Diversity, Rao, R., A. Brown and M. Jackson (Eds.). CAB International and IPGRI, pp: 237 - 247.
- Gulmon SL, Chu CC (1981). The effects of light and nitrogen on photosynthesis, leaf characteristics, and dry matter allocation in the chaparral shrub, *Diplacus aurantiacus*. *Oecologia*, 49:207-212.
- Kasai M (2008). Effect of growing soybean plants under continuous light on leaf photosynthetic rate and other characteristics concerning biomass production. *J. Agron.*, 7: 156-162.
- Kim H, Gregory DG, Raymond MW, John CS (2004). Stomatal conductance of lettuce grown under or exposed to different light qualities. *Ann. Bot.*, 94: 691 – 697.
- Kitao M, Lie TT, Koike T, Tobita H, Maruyama Y (2000). Susceptibility to photoinhibition of three deciduous broad leaf tree species with different successional traits raised under various light regimes. *Plant Cell Environ.*, 23(1): 81 – 89.
- Lammerts van Bueren ET, Struik PC (2004). The consequences of the concept of naturalness for organic plant breeding and propagation. *NJAS-Wageningen J. Life Sci.*, 52(1): 85 – 95.
- Lee DW (1985). Duplicating foliage shade for research on plant development. *Hort. Sci.*, 20: 116 – 118.
- Li H, Yong Y, Li B, Jing R, Lu C, Li Z (2010). Genetic analysis of tolerance to photo-oxidative stress induced by high light in winter wheat (*Triticum aestivum* L.) *J. Genet. Genom.*, 37(6):399-412.
- Li Y, Douglas AJ, Yongzhong SU, Jianyuan Cl, Tonghui Z (2005). Specific leaf area and leaf dry matter content of plants growing in sand dunes. *Bot. Bull. Acad. Sinica.*, 46: 127 – 134.
- Malone S, Herbert DA, Holshouser DL (2002). Relationship between Leaf Area Index and yield in Double-crop and full-season soybean systems. *J. Ecol. Entomol.*, 95(5): 945–951.
- Mark J (2005). Shade grown coffee and bird-friendly coffee. <http://www.thenibble.com/REVIEWS/nutri/matter/organic-coffee4.asp> [Accessed 24 January 2006].
- Maxwell K, Johnson GN (2000). Chlorophyll fluorescence - a practical guide. *J. Exp. Bot.* 51: 659 – 668.
- McNaughton KG, Jarvis PG (1983). Predicting effects of vegetation changes on transpiration and evaporation. In: *Water Deficits and Plant Growth*. Vol. 7, Kozlowski, TT (ed.), pp. 1–47 London Academic Press, New York.
- Morais H, Caramori P, Ribeiro AM, Gomes JC, Kogushi MS (2006). Microclimatic characterization and productivity of coffee plants grown under shade of pigeon pea in Southern Brazil. *Pesq. Agropec. Bras.* 41: 5. 763-770.
- Muschler RG (2001). Shade improves coffee quality in a sub-optimal coffee-zone of Costa Rica. *Agroforestry Syst.*, 51(2): 131 – 139.
- Osman M (2001). Rainfall and its erosivity in Ethiopia with special consideration of the central highlands. –*Bonner Bodenkundl. Abh.*, 37, 249 S. Bonn.
- Poorter H, Werf VA (1998). Is inherent variation in RGR determined by LAR at low irradiance and by NAR at high irradiance? A review of herbaceous species. In: Lambers, H, Poorter, H, Van Vuuren, MMI (eds.). *Inherent variation in plant growth. Physiological mechanisms and ecological consequences*. Leiden, Netherlands, Backhuys Publishers. pp. 309-336.
- Ramalho JC, Pons TL, Groeneveld HW, Azinheira HG, Nunes MA (2000). Photosynthetic acclimation of high light conditions in mature leaves of *Coffea arabica* L.: Role of xanthophylls, quenching mechanisms and nitrogen nutrition. *Aust. J. Plant Physiol.*, 27(1): 43 – 51.
- Rintamaki E, Kettunen R, Tyystjärvi E, Aro EM (1995). Light dependent phosphorylation of D1 reaction-centre protein of Photosystem II: Hypothesis for the functional role *in vivo*. *Physiol. Plant.* 93: 191 – 193.
- Robakowski P, Montpied P, Dreyer E (2003). Plasticity of morphological and physiological traits in response to different levels of irradiance in seedling of silver fir (*Abies alba* Mill.) *Trees*, (Berl.). 7: 431–441.
- Schmitt C, Grote U (2006). Wild coffee production in Ethiopia: The role of coffee certification for forest conservation. Report project 'Conservation and use of wild populations of *Coffea arabica* in the montane rainforest of Ethiopia', Bonn, Germany.
- Sethar MA, Pahoja VM, Chachar Q (2002). Photosynthetic acclimation of cotton genotypes at higher temperatures. *Asian J. Plant Sci.* 1: 261-263.
- Siebert SF (2002). From shade- to sun-grown perennial crops in Sulawesi, Indonesia: Implications for biodiversity conservation and soil fertility. Kluwer Academic Publisher, the Netherlands. *Biodivers. Conserv.*, 11(11): 1889 – 1902.
- Steiman S (2003). Shade vs. Sun Coffee: A review PMicrosoft internet explorer. www.geocities.com/RainForest/Canopy/1290/basics.htm (accessed 24 January 2006).
- Titus A, PereriaG (2005). Nitrogen Economy inside Coffee Plantations in Van Wijk MT Williams M, Laundre JA, Shaver GR (2003). Inter annual variability of plant phenology in tussock tundra: modelling interactions of plant productivity, plant phenology, snowmelt and soil thaw. *Global Change Biol.*, 9:743–758.
- Yunianto YD (1986). Overbearing dieback on Arabica coffee. *J. Pel. Parkebu*, 2(2):60-65.