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Review

Impact of shade on morpho-physiological characteristics of coffee plants, their pests and diseases: A review

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Traditionally, coffee plant has been considered as a shade demanding species and intolerant of direct sunlight, although it performs well without shade. Still controversy result and recommendation have been reported among investigators in the optimal shading level for coffee growth. This controversy will probably continue endlessly until the effects of shade up on the performance of morphology and physiology of the plant is known better. This review discusses the advantages of shade for coffee production, the responses of coffee plants to shade in morphology, physiology, and effects on coffee pest and diseases and finally, the effect of shade on coffee pest and diseases are discussed.

Key words: Coffee, shade, morphology, physiology, coffee pest, disease.

INTRODUCTION

All commercial coffee species are originated from Africa and belong to the family Rubiaceae which consists of more than 500 genera, of which *Coffea* is economically the most important one (Diby et al., 2016). Of the approximately 124 species, only *Coffea arabica* L. (Arabica coffee) and *Coffea canephora* Pierre ex A. Froehner (Robusta coffee) are economically important worldwide, accounting for approximately 99% of the global bean production (DaMatta, 2017; Bote et al., 2018a). Almost all the coffee species are diploid (2n = 2x = 22) and generally self-incompatible except *C. arabica* which is a natural allotetraploid (2n = 2x = 44) self-fertile species (Diby et al., 2016).

Coffee, a major export commodity, is a tropical crop grown in approximately 80 countries. It is estimated that more than 20 million people throughout the world earn their living from coffee, the majority of them involved in its production (Toledo and Moguel, 2012). The montane rainforests in South-Western Ethiopia are the only place in the world where coffee naturally grows in its original habitat (Stellmacher and Mollinga, 2009). Until today, Ethiopian coffee is mainly produced in traditional coffee production systems. This means wild coffee is simply picked inside the forest, or managed inside the forest by removing competing under growth vegetation and some canopy trees (Demel, 1999). In early plantations, coffee

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bushes were planted under shade canopy in order to simulate their natural habitat accounting for the fact that it has evolved as an understory shrub and showing all physiological and morphological characteristics of a shade adapted plant (Wexler, 2003; DaMatta, 2004; Grades, 2007). But, evidence from different part of the world indicates that satisfactory coffee crops may be produced under shade, as well as without shade, depending up on environmental and cultural practices (Fahl et al., 1994; DaMatta, 2004).

The knowledge of effects of shade (radiation) levels on the growth, morphology and physiology of coffee plants are the most important because, it helps to determine the optimum levels of radiation, as well as to add information on the existing knowledge on the performance of plants grown under shaded conditions. In addition, understanding shade effects on the morphology and physiology of coffee plants is useful for establishing the best management practices as well as for designing coffee production systems (Da Matta, 2004). However, there is still an open controversy among investigators, in what is the optimal shading level for coffee growth. This controversy will probably continue endlessly until the effects of shade up on the performance of morphology and physiology of the plant is known better. This review focuses on impact of both shaded and unshaded coffee on morpho-physiological characteristics and coffee pest and disease. The review is organized into dealing with the advantages of shade for coffee production, the responses of coffee plants to shade (morphological and physiological) and finally about the effect of shade as on coffee pests and diseases.

ADVANTAGES OF SHADE FOR COFFEE PRODUCTION

Production systems of coffee vary from multi-strata agroforestry systems to full-sun monocultures. In agroforestry coffee production systems, coffee trees are planted together with forest trees or within leguminous trees, fruits, timbers, and fire woods. The question of whether the coffee tree benefits or not from shelter trees has not been clear for more than a century (Beer, 1987; Damatta, 2004). Yield potential, competition for water and nutrients, and pest/disease incidence are central issues in this controversy. During the mid-twentieth century, farmers were encouraged to grow coffee in full sun to improve yields and reduce fungal infection; however, widespread acceptance of this practice did not take place until the 1970's (Perfecto et al., 1996).

Shading plantation can provide a number of important benefits to coffee. It has been found to reduce air temperature, soil, and leaf surface temperature as well as the thermal amplitude (Da Silva Neto et al., 2018). It also protects coffee plants from strong winds, rains, or hail and reduces the effect of biennial bearing, and improve and maintain soil fertility by way of returning large amounts of leaf litter to the underneath soil, that is, shade trees can be a valuable source of organic matter, nitrogen fixation, while retaining soil moisture (Beer et al., 1998). Though, its major benefit is the actual reduction in light transmission to coffee crops which softening the effect of biennial bearing and excessive vegetative growth (Beer et al., 1998; DaMatta, 2004). Aranguren et al. (1982) showed that N input from shade tree litter fall alone was approximately 95 kg·N·ha^{-1}·year^{-1}. Fallen leaves from *Erythrina poeppigiana* and the debris provided by pollarding added 330.5, 269.3, and 173 kg·N·ha-^{1}·year^{-1}, depending on whether trees were trimmed one, two or three times a year, respectively (Russo and Budowski, 1986). On the other hand, Babbar and Zak (1995) found that N lost by leaching in modern systems exceeded that in traditional systems by almost three-fold. In addition, shaded plantations have various beneficial features, including less sun scorch damage to the berries, greater natural resource conservation, increased biodiversity and greater stability in coffee production. Likewise, shaded plantations require less input and provide a more stable income due to cash income supplement provided by fruits or timber from the shelter trees (Beer et al., 1998) and a number of initiatives, such as local and national programmes for payment of ecosystem services and coffee certification schemes, have provided incentives for coffee farmers to provide a range of ecosystem services in addition to producing coffee (LeCoq et al., 2011). These characteristics of shaded coffee have stimulated renewed interest in the use of shade trees (Beer et al., 1998) and can significantly increase crop production stability.

On the other hand, unshaded plantations generally require high levels of external inputs to maximize crop yield and are often associated with soil degradation and environmental pollution. In addition, small holder producers of unshaded coffee face serious economic risks related to high variable costs and during unstable market prices. Also, sun plantations typically experience greater run-off and nutrient leaching and remain productive for only one-third to one-half as long as comparable shaded plantations (Perfecto et al., 1996). However, in many situations, coffee grows well without shade and even out yields shaded coffee (Fournier, 1988; Beer et al., 1998). Production of coffee in full sunlight has been highly successful due to the high acclimation capacity of coffee plants to different irradiance regimes, involving changes in physiological, anatomical and ultrastructural characteristics (Fahl et al., 1994; Ramalho et al., 2000; Pompelli et al., 2012).

RESPONSES OF COFFEE PLANTS TO SHADE

Among the many environmental factors, light is the most influential factor involved in the survival, growth and reproduction of tropical species. Light responses usually provoke morphological and physiological alterations, which are determinant for CO_2 assimilation and optimization of gas exchange (Sands, 1995; Gonçalves et al., 2005). When plants grow under either shade or high irradiance, the photosynthesis processes could be inhibited, simply because of the presence of too little or too much light which creates a stressful environment to the system (Goncalves et al., 2005). Some plants show sufficient developmental plasticity to respond to a range of light regimes, growing as sun plants in sunny areas and as shade plants in shady habitats. However, other plant species are adapted to either a sunny or a shaded environment (Valladares et al., 2005) and show different levels of tolerance to high illumination. Generally, sun plants are better able to sustain exposure to high light than shade plants, which experience photo inhibition (Goldstein and Durand, 2001). However, extensive comparative studies indicate that there are few extremely shade tolerant plants and few extremely light-demanding species, with most species having intermediate, and thus overlapping, light preferences (Wright et al., 2003).

Leaves adjust (anatomically, morphologically, and physiologically) to the light environment under which they expand and develop (Abrams and Kubiske, 1990). This ability is a highly important feature of plants because it takes into account, on a spatial and temporal scale, the ability of plants to perceive and respond to different characteristics of different ecosystems. On a temporal scale, this plasticity facilitates survival and a potential specialization of species (Ackerly, 2003). On the individual level, the expression of phenotypic plasticity is accompanied by the potential for discriminating between environmental qualities that are most suitable for growth (Rubio de Casas et al., 2007).

Arabica and Robusta coffees have evolved in the forest as understory trees; therefore, they are considered to be a shade demanding species (DaMatta, 2004). Most cultivars were derived from wild Arabica populations, such as the germplasm collections of Ethiopia, and they become severely stressed when grown without overhead shade and provide low yields (Van Der Vossen, 1985). However, according to van Der Vossen (2005), almost all current cultivars are descendants of early coffee introductions from Ethiopia to Yemen, where they were subjected to a relatively dry ecosystem without shade for a thousand years before being introduced to Asia and Latin America. Most of these cultivars have retained the physiological attributes as shade tolerant plants and can respond to various conditions, such as a mild drought and full sunlight. However, some cultivars (e.g. ‘Typica’) are not suited to the open, showing excessive symptoms of photo-damage when grown at full exposure. In any case, modern high-yielding coffee cultivars have been selected in test trials with high external inputs conducted under full sunlight and wide spacing. Hence the performance of Arabica coffee cultivars in full sunlight is likely to have been improved (DaMatta, 2004). Therefore, under intensive crop management, coffee will often produce much higher yields in sunlight than under shade. However, cultivation of coffee in open sun is common in most coffee producing countries, though its sustainability is questionable (Beer et al., 1998; Kufa et al., 2007; Rodríguez et al., 2001).

According to Fahl et al. (1994), coffee plants are classified as a shade-facultative species, because they have some characteristic features of sun-adapted plants, such as increased growth and photosynthesis capacity, high light saturation under full irradiance and relatively constant quantum yield when coffee is grown in both shade (lower radiation) and full sunlight environments. In addition, coffee displays several shade-acclimation characteristics, including a low chlorophyll a/b ratio and structural change such as higher specific leaf area (Rodriguez et al., 2001).

Generally, different light intensities promote changes in both the physiology and morphology of them; which are features that results from the interaction between gene expression and the environment (Nunes et al., 1993). 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 behavior are adjusted in order to maximize resource acquisition in that particular environment (Dias-Filho, 1997).

Shade effect on anatomical and morphological characteristics of coffee plants

Fahl et al. (1994), Luiza et al. (1999) and Paiva et al. (2003) observed that the highest shading levels reduced the growth of coffee plants. Excessive shading by upper two to three canopy strata of various tree species under forest environment is reported to reduce growth and productivity of coffee plant (Tesfaye et al., 2002; DaMatta et al., 2007). This excessive shading reduces both the quantity (photosynthetic photon flux density) and the quality (e.g. decreased red: far-red ratio) of the transmitted radiation, which affects the morphological and physiological processes of the plant such as photosynthesis and growth (Morais et al., 2003). In such conditions, the plant spends much of its photosynthetic activities for maintenance purposes (DaMatta et al., 2007). Heavy shading due to reduced light penetration by the upper canopy strata can result in increased competition for light for photosynthesis which, in turn, leads to undesirable growth of single stemmed coffee trees with thin leaves and reduced reproductive efficiency. In addition to this, shading reduces flower bud formation and can also reduce the whole tree carbon assimilation (DaMatta, 2004; DaMatta et al., 2007). This may result in reduced yield as a result of death of heavily shaded productive middle and bottom primary branches (Kufa and Burkhardt, 2013). Furthermore, dense shading also results in reduced coffee fruit load through its effects on coffee morphology and physiological changes, such as longer internodes, fewer nodes formed per branch and less flower buds at existing nodes (DaMatta et al., 2007; Kanten and Vaast, 2006). Because the fruit load is the key component of coffee production, its reduction results in decreased productivity (DaMatta et al., 2007).

A study conducted by Baliza et al. (2012) showed that coffee plants grown under 90% shading level (10% solar radiation) showed the smallest mean plant height than plants grown under 35, 50 and 65% shading levels. In addition, the plant diameter and number of plagiotropic branches were also small in the 90% shading level with thinner diameters and fewer branches. Similarly, Braun et al. (2007) observed that there was a higher plant height in *C. canephora* seedlings exposed to 75% shading as compared to coffee plants grown under shade levels of 30% or in full sun. Similarly, Bote et al. (2018a) reported that Arabica coffee plants grown under 70% shade scored the highest plant height as compared to coffee plants grown under 50%, 30% and a coffee plants grown under open sun (0% shade). Moreover, these authors reported that coffee plants grown under open field conditions scored the minimum plant height. Kohyama and Hotta (1990) and Lakshmamma and Rao (1996) also reported that there is a tendency for increasing height by shade adapted species for better exploitation of light penetrating from the higher stories in the canopy. In addition, these authors reported that densely shaded coffee plants undergo inter-plant competition for sunlight and other growth factors, resulting in tall, but slim plants. Generally, these results indicate that the increase in plant height under shade was probably due to a possible adaptation mechanism of the coffee plant for maximization of light interception by individual leaves. And this is evidence that the coffee plants showed shade avoidance syndrome (SAS) which is typically common in sun loving crops that are grown in less than optimum light intensities.

As reported by Fahl et al. (1994), coffee plants possess a fairly high acclimation capacity with respect to the level of irradiance during growth. These authors explained that, coffee plants grown under shade develop thinner leaves and a larger leaf area which allow more efficient capture of light energy. In contrast, unshaded cultivation increases leaf thickness which presumably leads to larger internal volume for CO_2 diffusion and a greater cellular volume to hold photosynthetic apparatus (Björkman, 1981). The increase in leaf thickness is due to larger palisade and spongy cells and to the presence of a second cell layer in the palisade parenchyma. Chloroplast ultrastructure also is affected by irradiance, and chloroplasts from shaded plants possessed a more robust granum system with more thylakoids per granum than those from full sun grown plants. Generally, structural modification of the leaf induced by irradiance would not be physiologically significant unless net photosynthetic rate increased accordingly, a response that does not occur in shade obligatory species (Fahl et al., 1994).

Effects of shade on photosynthesis of coffee

Photosynthetic rate is the rate at which CO_2 is assimilated in order to increase biomass (Gulmon and Chu, 1981). According to these authors, high rates of photosynthesis mean that 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 one. Plants of the same species perform differently if they are grown under different light regimes (Bote and Struik, 2011). It is possible to select the most productive trees based on photosynthetic rates of plants at the initial stage of development (Mazzafera and Warrior, 1991).

The effect of irradiance regimes on photosynthetic gas exchange of coffee trees seems to be contradictory. Cannell (1985) reported that the maximal photosynthetic rates of sun leaves of coffee are lower around 7 µmol CO_2 m^{-2} s^{-2}, but according to the work of Kumar and Tieszen (1980) are higher for shade leaves up to 14 µmol CO_2 $m^{-2}s$-^{2} than for sunlit leaves. Similarly, Bote et al. (2018b) reported that Arabica coffee grown under full sunlight scored a lower rate of photosynthesis as compared to coffee plants grown under shade (50 and 70%). Bote and Struik (2011) discussed that Arabica coffee plants exposed to direct sun light, increased air temperature which resulted in subsequent lowering of stomatal conductance which in turn imposed a large limitation on the rate of CO_2 assimilation. Kumar and Tieszen (1980) and Rodrigues et al. (2018) also reported that Arabica coffee is prone to photoinhibition of photosynthesis when exposed to full solar irradiance as coffee net photosynthetic rate saturates at low irradiance. These authors also discussed that many of the physiological processes of plants are temperature dependent; under high temperature crops have greater difficulty in maintaining photosynthetic activities. Kumar and Tieszen (1980), Kanechi et al. (1995), and Paiva et al. (2003) showed higher photosynthetic rate under shade than under full sun, a lower stomatal conductance for sunlight leaves may at least partially explain that pattern. Kumar and Tieszen (1980) pointed out that shade grown plants photosynthesized at nearly twice the rate of those grown in the sun, with corresponding changes in leaf conductance. Since stomatal aperture is greater under shade or on cloudy/rainy days (Fanjul et al., 1985), it is may be suggested that under full sun photosynthesis would be largely restricted by low stomatal conductance.

There are also considerable information that contradicts the observations of Kumar and Tieszen (1980), Cannell (1985), and Bote et al. (2018b). For example, Gutiérrez and Meinzer (1994) observed in Arabica coffee a higher rate of photosynthesis in sun leaves from the upper canopy than in shade leaves from the middle canopy. Contrary to photosynthetic rate, these authors also reported that stomatal conductance to water vapor (gs) was lower in sun than in shade leaves. As a whole, these results indicate that photosynthetic rate of shade leaves was limited by the low light availability, rather than by stomatal conductance. Friend (1984) and Fahl et al. (1994) also observed higher photosynthetic rate in sun-grown than in shade grown Arabica coffee plants. By contrast, Luiza et al. (1999) did not find differences in photosynthetic rate and stomatal conductance from plants of Arabica and Robusta coffee grown either under full sunlight or under 50% artificial shade, although photosynthetic rate and stomatal conductance strongly decreased in both species when grown under 80% shade. On the other hand, Matos et al. (2009) conducted a study and documented the light responses in coffee by sampling leaves from both sun-exposed and self-shaded leaves on coffee plants under full sun. This allowed for observation of differences between leaves on the same plant growing at different light levels. These researchers observed adaptations under shaded conditions including increased leaf area, lower respiration rates and light compensation points and lower stomatal densities. This study suggests that physiological and biochemical adaptations play an important role in coffee adaptation to shaded conditions, and that morphological or anatomical plasticity may play a secondary role.

Similarly, DaMatta et al. (2007) pointed out that shade can result in net photosynthesis limitations due to insufficient light interception Although, coffee leaves exhibit typical shade acclimation features, theoretically allowing them to maintain net photosynthesis in low light. In addition, Araujo et al. (2008) reported that a low physiological plasticity to low light in coffee leaves located inside the canopy, resulting in reduced net photosynthesis 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 (Beer et al., 1998; DaMatta et al., 2007). Nevertheless, DaMatta et al. (2007) have emphasized that, under optimal or near-optimal edapho-climatic conditions, shade provides little, if any, benefit to the crop.

Generally, these contradictory results might be due to the methodological differences between the conducted works. For studies of this nature, some factors that affect the physiological processes of coffee plants should be considered, such as climatic conditions (temperature and radiation), experimental conditions (pot or field), plant age, genotype and its adaptability to the local climate, shading type (natural or artificial), species that were studied, and shading density (Luiza et al., 1999; Morais et al., 2003).

Effects of shade on stomatal conductance of coffee

Stomatal regulation is a key process in the physiology of *C. arabica,* as well as many other plant species, and hence it is a key parameter in many ecological models (Bote and Struik, 2011). Stomatal conductance is intrinsically linked to photosynthesis and water relations, it provides insights into the plant's adaptive capacity, survival and growth (Craparo et al., 2017). Stomatal movements can be affected by various environmental factors, including plant water status, CO_2 concentration, and light. For example, bright light and low concentrations of CO_2 stimulate opening, while high CO_2 concentration even in bright light, cause closure (Kim et al., 2004). This means that various environmental and endogenous factors control stomatal movements, but from McDonald (2003) observation light is of major importance.

The stomatal limitations in coffee species are associated with a strong stomatal sensitivity to increasing leaf-to-air vapor pressure deficit (VPD) during the day (Vaast et al., 2006) and result in large reductions of photosynthesis, particularly in the afternoon (DaMatta and Ramalho, 2006). For example, when a coffee is grown in suboptimal (hotter and drier) growing conditions, and in full sun, the photosynthesis is lower than in the shade (Kanten and Vaast, 2006); which has been related to the high sensitivity of coffee stomatal conductance to VPD (DaMatta and Ramalho, 2006; Vaast et al., 2006). Shade trees reduce wind speed and leaf temperature while increasing air humidity, and hence reduce VPD and the stomatal limitations of coffee photosynthesis; therefore, agroforestry production systems have been recommended for suboptimal growing conditions (DaMatta, 2004; DaMatta et al., 2007; Vaast et al., 2006).

Barros et al. (1999) reported that the maximum rate of net photosynthesis in coffee was 4.5 mg CO_2 dm^{-2} h^{-1} and photosynthesis rate was decreased at the midday. This is associated to stomatal closure induced by direct action of sunlight, but not by leaf water relations (Franck et al., 2006; Ronquim et al., 2006); and also circumstantially with photoinhibition of photosynthesis and feedback inhibition coupled to an accumulation of soluble sugars in coffee leaves (Franck et al., 2006; Ronquim et al., 2006). Kanechi et al. (1995) also observed that stomatal conductance decreases logarithmically with increasing leaf temperature and vapor pressure deficit. Parallel to this, stomatal and mesophyll conductances are decreased sensitively with decreasing water potential, indicating that both conductances contribute to decline in the leaf photosynthetic rate. Moreover, this species is prone to photoinhibition of photosynthesis when exposed to full solar irradiance as coffee photosynthesis saturates at low irradiance (Ramalho et al., 2000). However, according to Chaves et al. (2008), photoinhibitory limitations of photosynthesis in full sun have been shown to be of secondary importance as compared to stomatal conductance limitations in commercial Arabica coffee varieties and they attributed this feature to an acclimation to high irradiance in order to prevent photoinhibition. Moreover, Cannell (1985) noted that even with the light-adapted sun leaves of coffee, the photosynthetic apparatus seems to be physically damaged by continued exposure to high irradiances, perhaps by disruption of Photosystem II and exposed leaves of coffee exhibit chlorotic symptoms.

Effect of shade in leaf temperature

Caramori et al. (1996), studying frost protection provided by *Mimosa scabrella* Benth*,* showed leaf and air temperatures remained 2 to 4 and 1 to 2°C warmer at night, respectively, in shaded plots and reduced damage from cool temperatures. In Mexico, air temperature was 5.4°C higher and the minimum 1.5°C lower in sun as compared to shade plantations (Barradas and Fanjul, 1986). Soil temperature and vapor pressure deficits also were lower under shade trees. Over story, trees also reduced wind speed below their canopies (Caramori et al., 1996).

The negative effect of temperature on coffee photosynthesis has been reported early in the past century with net CO_2 assimilation decreasing at temperature above 24°C. This temperature effect was confirmed by several authors (Kumar and Tieszen, 1980) in studies where plants experienced a decrease in net CO_2 assimilation due to a reduction in stomatal conductance for temperatures in the range of 25 to 35°C. For this reason, it is assumed that CO_2 assimilation may be reduced in leaves completely exposed to high irradiance due to the high temperatures reached in tropical regions, which are in the order of 10 to 15°C above the air temperature (Cannell, 1985). Generally, shade trees have a pivotal role on creating a favorable ambient micro-climate for coffee plantations in particular and for the integral ecological system of the coffee tracts in general. Tree shades basically help to reduce the amount of heat reaching the coffee plant during the day time and protects the coffee plants from the evening and night low temperatures as the trees will serve as a cover and protection, hence contribute for the creation of an ambient micro-climate, which suits well for the growth and development of coffee bush (Alemu, 2015).

Effect of shade on coffee pest and diseases

Shade trees have been shown to alter the micro-environment around coffee. These changes likely explain why some pests and diseases are less successful under shade (Sarnayoa-Juarez and Sanchez-Garita, 2000). Beer et al. (1998) reported that there is a lack of agreement among farmers and scientists as to whether shade trees reduce or increase diseases and pests of economic importance, such as leaf rust (*Hemilei vastatrix*) and the coffee berry borer (*Hypothenemus hampe*i). Perfecto et al. (1996) reported that shade coffee systems, especially those that maintain a dense natural shade have been found to maintain a high level of biodiversity. Because of the potential of shade coffee as a refuge of biodiversity, coffee producers have been encouraged to maintain a dense, high diversity shade in their plantations. Shade provides an efficient biological management tool for the control of major pests and diseases like coffee white stem borer and leaf rust in Arabica coffee. It is also well documented that white stem borer is active in open patches and these open patches provide ideal conditions for spread of the pest to the neighboring plants. The activity of borer beetles is stifled at cooler temperatures. Thus, providing uniform shade is one of the major mechanisms for the effective management of the white stem borer. Besides providing unfavorable conditions for this pest, the shade trees are also reported to harbor a variety of predatory birds and natural enemies of it, thus contributing towards natural and biological control of the pest (Alemu, 2015).

Similarly, several papers have been reported on effects of shade on coffee beery borer. For example, for the first time, the effects of shade on the coffee berry borer were reported by Hargreaves (1926, 1935, 1940) in Uganda and by Jervis (1939) in Tanzania (Vega et al., 2015). These authors ascribed that the reduced damage was observed in coffee plants grown under full sun and shade; explaining that coffee berry borer damage is higher in unpruned trees and when large trees provide dense shade to the coffee plant. In general, higher coffee berry borer infestation levels have been reported in a coffee grown under shade (Baker et al., 1994). According to these authors, these would be due to two major reasons: first, since the insect evolved in the shade of forests, it is better adapted to that environment and not to the lower to the lower relative humidity (RH) of sun-exposed plantation. The second reason is shade has a negative effect on parasitoids, that is, adult coffee berry borers are very sensitive to high RH with an optimum range for survival and development at 90 to 95% of RH at and 25°C (Baker et al., 1994). These high humidity conditions would be more likely to be encountered in shaded plantations. In addition, Feliz Matos (2004) examined coffee berry borer infestation levels under three shade levels in Nicaragua: no shade, medium shade (40 to 50%) using *Gliricidia sepium* (Jacq.) Walp. (Fabaceae), and dense shade (60 to 70%) using *Eugenia jambos* L. Percent infestation was significantly higher (17 to 25%) in dense shade as compared to <2% under no shade and medium shade. Infestation levels for no shade and medium shade were not significantly different.

Wegbe et al. (2007) in Togo have also reported significantly higher coffee berry borer infestation levels in densely shaded coffee plantations. In Colombia, Bosselmann et al. (2009) reported a trend towards higher infestation levels under shade.

On the other hand, several papers have reported on the effects of shade on different ant species. For example, Armbrecht and Perfecto (2003) reported significantly different levels of litter and twig-nesting ants like *Pheidole, Solenopsis, Hypoponera* and *Wasmannia* in Mexico when distance from the forest was compared for shaded monocultures (that is, coffee under *Inga*, common name Shimbillo) and shaded polycultures (coffee shaded with various tree species). For the shaded monoculture, ant species decreased with increased distance from the forest, while an increase in ant species was reported for the shaded polyculture with increased distance from the forest. Thus, even within one system (that is, shaded coffee), various levels of different ant species can be found. This has important implications for the coffee berry borer, because one particular shaded habitat may be more favorable towards ant species that might potentially prey on the insect when compared with a different habitat. Roberts et al. (2000) and Philpott and Armbrecht (2006) have also reported increased ant diversity in shaded coffee habitats.

CONCLUSIONS

Shading a plantation can provide a number of important benefits to the coffee plant by reducing air and soil temperature extremes, buffer high wind speed and improve and maintain soil fertility by returning large amounts of leaf litter to the underneath soil. It also softens the effect of biennial bearing, but it has to be considered in open plantations. Generally, the overall effect of the different interactions between shade trees and coffee are dependent upon climate and soil condition, and coffee species and varieties. In general, on optimal sites, coffee can be grown without shade using high agrochemical inputs; but at the expense of environmental degradation. On the other hand, shade tree may increase the incidence of some commercially important pests such as coffee berry borer and decrease the incidence of others like coffee leaf rust and coffee white stem borer.

CONFLICT OF INTERESTS

The author has not declared any conflict of interests.

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