Emir. J. Food Agric. 2015. 27 (2): 152-163
doi: 10.9755/ejfa.v27i2.19468
http://www.ejfa.info/

REVIEW ARTICLE

Perspectives on the potential impacts of climate changes on coffee plant and bean quality

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Abstract

The atmosphere CO_2 concentration increased from ca. 280, prior to the Industrial Revolution up to ca. 400 μL CO_2 L^{-1} in our days, rising nearly 2 ppm per year actually. The Intergovernmental Panel on Climate Changes (IPCC) estimates at the end of 21st century the [CO_2] could reach values between 445 and 1130 μL CO_2 L^{-1}, with a potential impact on global temperature and changes in water availability: These changes will have major agricultural and ecological implications. Here are presented some perspectives concerning the potential impacts of these environmental changes on the physiology and, consequently, on the production of *Coffea arabica* and *C. canephora* species, which together account for about 99% of the worldwide yielded coffee bean, considering the coffee plant's requirements mostly focused in temperature.

Key words: Acclimation ability, Climate changes, Enhanced air CO_2, *Coffea arabica*, *Coffea canephora*

Introduction

The concentration of atmospheric CO_2 increased from 280 μL CO_2 L^{-1}, before the Industrial Revolution up to about 390 μL CO_2 L^{-1} in 2009, reached 400 μL CO_2 L^{-1}, measured in Mauna Loa Observatory in Hawaii in 2013, and is continuously increasing at an actual rate of nearly 2 μL CO_2 L^{-1} per year (Nobel, 2009; DaMatta et al., 2010; Ramalho et al., 2013b). Depending on future scenarios of anthropogenic emissions, further increases of [CO_2] are expected, to values between 450 and 600 μL L^{-1} by the year 2050 and between 730 and 1020 μL L^{-1} by 2100. Such increase was predicted to be accompanied by a global warming between 1.4 and 5.8°C by the end of the present century (IPCC, 2007), with most probable implications also on water availability to plants, due to an amount reduction and changes in the rainfall patterns. These environmental variations are expected to have severe ecological and agricultural impacts (IPCC, 2007; Nobel, 2009; DaMatta et al., 2010).

Coffee is one of the world's major crops, being mostly cultivated in Africa, America and Asia, in about 80 countries, generating approximately US $90,000 million per year (Embrapa, 2004), but with a total business impact of ca. $USD 173,400 millions (ICO, 2014). Furthermore, the total coffee sector employment estimated at about 26 million people in the 52 producing countries responsible for 97% of the production (ICO, 2012), although other estimates point to the involvement of more than 80 million people worldwide, considering its cultivation, processing, transportation and marketing (Dereeper et al., 2013) therefore with a huge economic and social importance. Although the *Coffea* genus includes 124 species (Davis et al., 2011), the more important ones for coffee bean production are *C. arabica* L., *C. canephora* Pierre ex A. Froehner, *C. liberica* Bull ex Hiern and *C. dewevrei* Wild and Durand cv. Excelsa, which represents, respectively Arabica, Robusta, Liberica and Excelsa types of coffee (Bicho et al., 2011b).

Received 5 June 2014; Revised 10 July 2014; Accepted 26 July 2014; Published Online 1 February 2015

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Even so, 99% of world coffee bean production relies on *C. arabica* (ca. 65%) and *C. canephora* (ca. 35%), constituting the economic basis of many tropical developing countries (DaMatta and Ramalho, 2006; Partelli et al., 2011; Davis et al., 2012; Martins et al., 2014).

C. canephora generally appears to be more tolerant to biotic stresses, productive and vigorous than *C. arabica*, but the quality of the beverage obtained from its beans has been traditionally considered inferior (Coste, 1992). Yet, that has strongly changed in the last years, particularly in Brazil where the bean quality increased significantly, as a result of better agronomic practices (particularly at the post-harvest stage) and new improved clones from extensive breeding programs.

The conditions of temperature and rainfall amount and pattern (water availability along the year) are considered important factors in defining yield potential of coffee. These factors interfere with crop phenology and hence productivity and quality, but, taking into account the importance of this subject, only a few studies considered the impact on the quality of the grain produced (and in the beverage) under limiting conditions of these environmental variables (Haggar and Schepp, 2012).

Global temperatures increased on average 0.74°C (0.56°C to 0.92°C) over the past 100 years (1906-2005), and this increase appears to accelerate since the 1970s. The 1960 decade was marked by severe drought and high air temperatures, especially during the years 1961 and 1963, which dramatically affect coffee production for the years 1962 and 1964 (Davis et al., 2012). Moreover, recent modelling studies, mostly focusing probable increases in air temperature, also estimated intense effects on the coffee crop for the futur, which included significant yield losses in Mexico (Gay et al., 2006), enhanced vulnerability in Central America growing countries (El Salvador, Guatemala, Mexico, Nicaragua) (Baca et al., 2014), extensive reductions of suitable areas in Brazil, up to 75% in Paraná, and 95% in Goiás, Minas Gerais and São Paulo regions (Assad et al., 2004), and important extinction of wild populations of *C. arabica* in Ethiopia (Davis et al., 2012). In fact, it was argued that *C. arabica* is a climate sensitive species, and that its production will be increasingly influenced by hastened climate change (Davis et al., 2012), therefore, with likely negative consequences for the coffee global supply chain to industry and consumers.

Although important, those modelling approaches did not consider possible mitigating effects of the enhanced atmospheric CO_2 levels. That was so, because only very recently some information became available regarding the long-term effects of elevated CO_2 on the coffee plant, at physiological and biochemical leaf level (Ramalho et al., 2013b; Martins et al., 2014), concomitantly to enhanced temperatures (Ramalho, unpublished data). Therefore, those estimates, together with an almost absence of biological studies relating climate changes and the coffee crop, demonstrates the need for such research considering the in interaction of enhanced growth [CO_2] with environmental contraints (of temperature, water, etc.). These will promote the production of knowledge on the acclimation ability of the actual coffee cultivars to the predicted environmental scenarios, with practical future application, namely by assisting selection and breeding programs to obtain new genotypes (Ramalho et al., 2013b).

For that, it should be recognized that a complex network of biochemical and molecular processes is envolved on plant performance in terms of development, growth, acclimation ability to the environmental changes and stresses, triggering specific mechanisms of tolerance (Wang et al., 2003). Yet, within the numerous metabolisc pathways, the photosynthetic metabolism is a central point in plant sensing of environmental constraints of water, temperature, etc., being frequently used as a proxy for plant stress tolerance evaluation. Besides that, the involvement of enhanced growth [CO_2] promotes, a large number of plant responses. With particular relevance are those related to photosynthesis, as CO_2 is directly implicated as a substract for carboxylation and indirectly by decreasing photorespiration through completion with O_2 at the active sites of RuBisCO. In fact, enhanced air [CO_2] acts both at mesophyll (biochemical, biophysical and molecular) and stomata (opening, density and size) levels in the *Coffea* spp plants (Ramalho et al., 2013b).

Impact and plant responses to extreme climatic conditions

Coffee plants developed a complex network of protection/acclimation mechanisms in order to deal with moderate to extreme environmental conditions (of temperature, water, minerals, irradiance, etc.). As for other plants, in coffee these stressful conditions can cause disturbances, from cellular impairments/imbalances to severe damages, including disruption of ionic and osmotic homeostasis, oxidative stress conditions (as a secondary stress), and degradation of membrane components and proteins. Furthermore, environmental stresses can potentially affect all components of the photosynthetic pathway, namely by restricting CO_2 access to the carboxylation sites due to reductions of stomatal condutance (g^s), by decreasing the rate of chemical and enzyme reactions, by impairing the electron transport chain and the photosynthetic performance, as well as by directly inhibiting key metabolic enzymes (DaMatta and Ramalho, 2006).

At the level of the photosynthetic machinery, the necessary acclimation mechanisms to plant persistence would contribute A) to promote the reduction of energy absorption by leaves (leaf shed and rolling, enhancement of surface reflection, etc., which may reduce energy absorption up to 40%) (Larcher, 1995; Lawlor, 2001; Karpinski et al., 2002); B) to reinforce photosynthetic structures and components, namely the thylakoid electron carriers, in order to achieve a higher photochemical use of energy (Xu et al., 1999; Kornyeyev et al., 2001); C) to promote long-term structural changes at the membrane level (in protein and lipid components) (DaMatta and Ramalho, 2006). For drought and temperature tolerance, the maintenance of fluidity of membranes is essential for their functionality and can be achieved through lipid qualitative changes in the balance of lipid classes and fatty acid (FA) saturation (Nishida and Murata, 1996; Routaboul et al., 2000; Xin and Browse, 2000; Iba, 2002; Partelli et al., 2011; Ramalho et al., 2014). On the other hand, an integrated antioxidative system (based on the ascorbate-glutathione cycle, although not restricted to it) must be in place and has been shown to be a crucial component to plant acclimation. The failure of antioxidative enzymes to protect, namely, lipid membranes, cause a higher root tissue damage and membrane rigidity (Alonso et al., 1997; Queiroz et al., 1998). However, a higher FA saturation level turns the membranes more resistant to peroxidation, changes that are important in acclimation of the coffee tree to high-irradiance exposure (Ramalho et al., 1999). Yet, under cold conditions, in order to maintain adequate membrane fluidity, the saturation of lipid components must be decreased. The presence of a higher number of double bonds would turn these membrane lipids more prone to oxidative damage, demanding a reinforced antioxidative system. In fact, in *Coffea* spp. the control of oxidative stress and a clear dynamic of the membrane lipid components seems constitute common and crucial responses to gradually imposed limiting conditions that provokes an energy overpressure on the photosynthetic apparatus, as for low positive temperatures, water deficit, irradiance and limiting N-nutrition, in which the tolerance degree was linked to the triggering of these (but not only) mechanisms (Ramalho et al., 2000; 2002; 2003; Lima et al., 2002; Campos et al., 2003; Pinheiro et al., 2004; Fortunato et al., 2010; Batista-Santos et al., 2011; Scotti-Campos et al., 2014). Altogether, the above referred mechanisms, functioning complementary in a short-up-to-long term manner, confer stress tolerance and, by reducing the negative effects upon stress conditions, will decrease the stress aftereffects, that is, will promote a better and prompt recovery after the stress ending (Ramalho et al., 2014).

Temperature requirements and stressful conditions to the coffee plant

The different evolutionary history of *C. arabica* and *C. canephora* justifies some variation in temperature tolerance, as these species are considered to have optimum annual mean temperatures of 18-23ºC and 24-30ºC, respectively. *C. arabica* is native to Ethiopian tropical forests at altitudes of 1600-2800 m (DaMatta and Ramalho, 2006). On the other hand, *C. canephora* is native to the lowland forests of the Congo River basin, which extends up to Lake Victoria in Uganda at altitudes up to 1200 m (Coste, 1992).

Exposure to low positive temperature

As for most tropical plants, cold is determinant for coffee geographical distribution. In fact, in regions with a mean annual temperature below 17-18ºC, growth is largely depressed and the occurrence of frosts, even if rarely, may strongly limit the economic sustainability of this crop (Camargo, 1985; Ramalho et al., 2014).

In general, coffee plants may endure temperatures until 7ºC, but problems often arise between 8-10ºC. Furthermore, below 5-6ºC, fruits and leaves are severely affected with photobleaching and burns (Coste, 1992; DaMatta and Ramalho, 2006) and under long periods at 15ºC the leaves and fruits might not withstand (Willson, 1999). Low positive temperatures have an overall negative impact on plant productivity (chloroplast is usually the cell structure most affected) due to the reductions of cell chemical and enzymatic reactions, diffusion rates of molecules and membrane fluidity (Kratsch and

Wise, 2000; Mano, 2002). Also, the sensitivity of coffee's vegetative growth is particularly evident when monthly mean temperatures drop below 15-16ºC. Under such conditions the leaves produced are smaller, yellowish with extended necrosis, having in addition a higher tendency to shed (Barros et al., 1999; Silva et al., 2004a), but lethal damages can also be observed on shoot meristematic cells, seed embryos and roots (lipoperoxidation of membranes and loss of selectivity that provoke a decrease in its fluidity and functionality) when the temperature approaches 0ºC (Alonso et al., 1997; Queiroz et al., 1998).

Moreover, the net assimilation became negligible in the temperature range of 5 to 13ºC (Larcher, 1981; Ramalho et al., 2003; Batista-Santos et al., 2011). Under low positive temperatures, particularly upon chilling conditions, the decrease of photochemical energy use further provoques the overexcitation of the photosynthetic apparatus, which causes photooxidation of chloroplast components, and, in turn, further impairs the photosynthetic structures and promotes photoinhibition (DaMatta and Ramalho, 2006). Such limitations found for the photosynthetic metabolism could be attributed to a large group of effects, including reductions of g^{s}, degradation of pigment complexes and loss of photochemical efficiency, increase of damage and reduction of repair processes at the PSI and PSII level, restrictions of electron transport, enzyme activity, carbohydrate metabolism and increase of chloroplast membrane permeability (Larcher, 1981; Krause, 1994; Adams and Demmig-Adams, 1995; Morcuende et al., 1996; Haldimann, 1998; Allen and Ort, 2001).

Yet, the existence of some genetic variability confers to some plants acclimation ability to low positive temperatures down to 4ºC, for short periods of time (up to 3 diurnal cycles). This lower cold sensitivity was observed only in some *C. arabica* genotypes and the mechanisms that promoted a consistent acclimation included the reinforcement of key enzymes, namely those related to the energy metabolism (e.g., RuBisCO, in the photosynthetic pathway, as well as some enzymes in the respiratory pathway), and differential gene expression capabilities. Moreover, it was found that the acclimation was also closely linked to the triggering and reinforcement of antioxidative molecules, both enzyme (e.g., Cu,Zn-superoxide dismutase, ascorbate peroxidadese) and non-enzyme (e.g., of photoprotective/dissipative pigments, as zeaxanthin, lutein, as well as ascorbate), to an effective dynamic of membrane lipids that undergo qualitative modifications upon cold conditions, and to a higher maintenance of leaf mineral contents and balance (Ramalho et al., 2003; Fortunato et al., 2010; Batista-Santos et al., 2011; Partelli et al., 2009; 2011; Ramalho et al., 2013a; 2014; Scotti-Campos et al., 2014).

Impacts of supra-optimal temperatures

In many parts of the world, as in Brazil, the largest coffee producer, the coffee plants are grown under full sun exposure. Under this management system, the leaves are exposed to high irradiance throughout of the day and absorb much more energy than the one driven to photosynthesis, causing an energy overpressure and, frequently, leaf overheating. The latter would further increase if stomata are significantly closed, limiting transpiration and leading to rises of leaf temperature up to 40ºC or even more (Maestri et al., 2001; DaMatta and Ramalho, 2006) with severe consequences to the photosynthetic metabolism. Again, disturbances in photosynthesis are among the first indicators of stress, because thylakoid membranes are especially sensitive to heat (Lawlor, 2001). In these conditions, strong impacts on the photochemical primary processes of PSII and the electron transport in thylakoids could arise (Nunes et al., 1993; Fahl et al., 1994; Ramalho et al., 2000). Plant metabolism is impaired by high temperatures as reactions kinetic are accelerated, bonds within macromolecules are loosened and membrane lipid layers became more fluid. Furthermore, extensive denaturation and aggregation of cellular proteins, over-production of ROS and inhibition of normal transcription and translation might occur (DaMatta and Ramalho, 2006). Also, under excessive high temperatures leaves and fruits can grow too fast in relation to the available photosynthetic resources, resulting, e.g., in small leaves and shrunken fruits (Lawlor, 2001), what could be accompanied by a stimulation in leaf senescence (particularly in of older ones) if drought stress is concomitantly involved (DaMatta et al., 1997).

The exposure to supra-optimal temperatures, above 23ºC in *C. arabica*, accelerates the development and ripening of fruits, often leading to loss of bean quality (Camargo, 1985). Furthermore, the yellowing of leaves and growth of tumors at the base of the stem may appear if the plant is permanetly exposed to temperatures above 30ºC (DaMatta and Ramalho, 2006), and a relatively high temperature during blossoming may cause abortion of flowers, especially if associated with a prolonged dry season (Camargo, 1985).

Temperature is also an important driven force for other processes. In *C. arabica* the germination will took ca. 3 weeks under temperatures around 30-32ºC, but will require ca. 3 months at 17ºC (Moraes, 1963; IBC, 1985), whereas above 35ºC will be inhibited (Barros et al., 1999). Also, the "optimal" temperature may change along the plant devepmental stages. In the first weeks of life the plant requires temperatures around 30/23ºC (day/night), decreasing to 26/20ºC with the production of the first branches (Moraes, 1963; IARC, 1991; Coste, 1992; Barros et al., 1999). For floral bud initiation temperatures up to 30ºC are needed, but their development, as well as growth of the fruit should occur at values around 23/17ºC (Carvajal, 1984; Camargo, 1985; Barros et al., 1999). Therefore, it is not surprising that, when compared to *C. canephora*, several studies point *C. arabica* as the more affected species by future global warming conditions, and the one that will undergo a more obvious geographical redistribution driven to such temperature increase (Haggar and Schepp, 2012).

On the other hand, *C. canephora* plants are considered to be capable to endure temperatures somewhat higher, but even for those plants high temperatures can be harmful, especially if the air is dry (Coste, 1992). Yet, coffee plants seemed to be more heat tolerant than was traditionally accepted in earlier studies. In fact, an appreciable tolerance to heat (ca. 35-37ºC) was found, if a gradual rising from 24ºC up to 33-35ºC was implemented (DaMatta and Ramalho, 2006). Such maintenance of high photosynthetic efficiency suggests the absence of negative effects on the coffee plant photosynthetic structures (Gascó et al., 2004).

Furthermore, very recent experiments, under environmental controlled conditions, showed that the negative impact of high temperature (40-42 ºC) might be alleviated to a certain degree, and that the plants were capable of maintaining a unaffected photosynthetic performance at temperatures up to 37 ºC when they have been grown under enhanced air [CO_2] conditions (700 μL L^{-1}) for long periods (Ramalho, unpublished data). Such beneficial [CO_2] effects could be related to the higher vigor and physiological performance displayed by the plants grown under increased air [CO_2], when compared to those under normal (380 μL CO_2 L^{-1}) (Ramalho et al., 2013b). These possible mitigating effects are highly relevant to the coffee crop, in a context of expected global warming conditions.

Coffee bean, cup quality and possible effects of environmental temperature

Green bean quality and roasting process

In recent years, coffee markets revealed a growing demand for specialty coffees. Consumers ask for exceptional taste and aroma coffees, as well as balanced characteristics of sweetness, acidity and body (Barbosa et al., 2012), revealing as well an increasing awareness to geographic certification (Rodrigues et al., 2009), fair trade and environmental friendly production issues (Bicho et al., 2011b).

Coffee quality depends on multiple variables, including acidity, moisture content, aroma, sweetness, etc., which are closely linked to bean chemical composition (caffeine, trigonelline, chlorogenic acids, etc.). Coffee acidity depends on a wealth of variables, including the geographic origin of green coffee beans, fruit maturity stage, harvest process, weather conditions during harvesting and drying, and post-harvest processing. Additionally, coffee acidity might also be determined by growth conditions, such as altitude and shading, but Robusta coffees are considered to have low acidity, unlike the Arabica coffees (Bicho et al., 2013b). When pH is lower than 4.9 the drink tastes too acidic, but if that value surpasses 5.2, it might become bitter (Bicho et al., 2013a).

The moisture content in marketable green coffee bean should not exceed 12.5%, otherwise the beans will be easily attacked by fungi, allowing the accumulation of ochratoxin A to prohibited levels (Bicho et al., 2014; Coste, 1992).

Soluble solids correspond to 24-27 and 26–31 g/100 g coffee, respectively and the caffeine levels of green coffee beans might vary between 0.8-2.5 g/100 g coffee. Trigonelline contents (ranges between 0.3 and 1.3% d.b), correspond to about 0.6 g/100 g coffee, but almost 50% of this compound is degraded during roasting with the formation of other compounds, namely nicotinic acid, pyridine, 3-methyl-pyridine, and methyl ester of nicotinic acid. The chlorogenic acids accumulate in the cytoplasm of epidermal cells, but larger quantities can also be found in the periplasm. Caffeoylquinic acids (CQAs), dicaffeoylquinic acids (diCQA), and feruloylquinic acids (FQA) account for about 98% of total chlorogenic acids (CGA) in green coffee and are quite important to final quality (Bicho et al., 2011a; 2013b).

In addition to the chemical composition of the green bean coffee, post-harvest processing (as roasting) also strongly influences the final quality and characteristics of the product (Decazy et al., 2003; DaMatta and Ramalho, 2006). Above 150-160ºC, many exothermic and endothermic reactions will occur; gaseous substances (water vapour, carbon dioxide, and carbon monoxide) are released. The coffee bean becomes light brown and, their volume increases, and aroma formation begins. At 180-200°C, with the disruption of the endosperm, bean cracking occurs, bluish smoke and aroma appears, and caramelization develops (Bicho et al., 2014). In fact, it is known that the chemical reactions responsible for the aroma and flavor of roasted coffee are triggered at such temperatures. The Maillard and Strecker reactions, involving carbohydrates (reducing sugar), proteins, and other compounds, promote the synthesis of, low- and high-molecular-weight compounds, e.g., melanoidins, which are simultaneously degraded and produced (Farah, 2012). Depending on the roasting intensity (in temperature and duration of the high temperature exposure), it follows that roasted coffee can show a brownish colour, yellower in lighter roasts, becoming reddish brown in medium roasting and dark brown in intense roasting (Bicho et al., 2014).

A large number of aromatic compounds result from the thermal decomposition of chlorogenic acids, namely phenolic esters, carbonyl compounds, esters, and polycyclic compounds, which contribute to flavor, acidity, and astringency of coffee drink (Bicho et al., 2011a). Moreover, astringency and metallic taste, which seems to be also associated with diCQA, having a taste threshold ranging between 0.05 and 0.1 mgL, can understate bitterness intensity. Also, in green coffee beans total hydroxycinnamic acids (HCA), synthesized enzymatically or through alkaline hydrolysis of CGA, is further related to the flavor of roasted coffee (Bicho et al., 2012).

Green coffee quality and the relation to some environmental variables

Still, previously to roasting processes, when the fruit is under development and maturation in the plant, there are several environmental variables that contribute to the final quality of the product in a very complex and sometimes uncertain manner. Among those variables, altitude and full sun exposure of the plants were found to be closely related to quality, which are tightly linked to temperature issues. In fact, as stated above, it was found that in *C. arabica* the exposure to temperatures above 23ºC accelerates the development and ripening of fruits, often leading to loss of quality (Camargo, 1985).

In plantation under full sun exposure, beans have higher levels of sucrose, chlorogenic acid (CGA) and trigonelline that was suggested to indicate incomplete bean maturation, resulting in higher bitterness and astringency in cup quality. In other hand, the beans developed under shaded conditions usually presented larger size with a significant reduction in sucrose content and to an increase in reducing sugars (Geromel et al., 2008).

Several studies pointed that altitude and rainfall contributed to the final bean and beverage quality (Rodrigues et al., 2009; Avelino et al., 2005; Decazy et al., 2003; Barbosa et al., 2012). Under higher altitude *C. arabica* takes a longer period to complete the reproductive cycle (Matiello et al., 2005), linked to a delay in the sugar accumulation in fruits. In fact, such sugar increase occurs mostly in the pulp (Geromel et al., 2006) and is related to fruit maturation (Rena et al., 2001).

Coffees produced in between altitudes of 920 to 1120 m showed a weaker body and acidity, together a higher sweetness than the ones produced in the range of 720 to 920 m, leading to the conclusion that higher altitudes promotes a better quality of the produced coffee bean (Silva et al., 2004b). Furthermore, considering three altitude levels (below 1220 m, between 1220 m and 1460 m and above 1460 m) it was observed that, irrespective of the studied *C. arabica* genotype (Bourbon, Caturra and Catuaí), the organoleptic properties, as aroma, body and smoothness, increased while increasing altitude, whereas for acidity there was no clear tendency (Solares et al., 2000). A strong influence of temperature, rainfall, altitude and latitude on the quality of Minas Gerais coffees was also found (Barbosa et al., 2012) and a similar relationship of quality and altitude was also pointed on steeper slopes and different altitudes in the Costa Rica coffee terroirs. In the latter work, it was found a positive relation between altitude (1020-1250 m vs. 1550-1780 m) and taster preferences, although caffeine, trigonelline, fat, sucrose and chlorogenic acid contents were not well correlated with the sensory characteristics (Avelino et al., 2005). Furthermore, a relationship between geographical location and the influence of altitude on coffee characteristics in several coffee producing regions was also depicted (Rodrigues et al., 2009).

These environmental effects were confronted to the chemical compounds trigonelline, caffeine, and especially the acid-5-cafeiolquinic that were found to be also quite relevant to the sensory analysis (Barbosa et al., 2012). The final flavor and aroma of coffee are affected by the presence of various volatile and nonvolatile chemical constituents, namely, proteins, amino acids, fatty acids and several phenolic compounds, and also by the action of enzymes on some of these components (Barbosa et al., 2012). This work pointed that the variables that contributed most to the discrimination of high scores related to quality were temperature, trigonelline and caffeine and the ones that correlated with low scores were rainfall, humidity index and 5-CQA. In fact, trigonelline is an important precursor of the volatile compounds that contribute to the aroma and taste of roasted coffee (Malta and Chagas, 2009), whereas the presence of 5-CQA is associated with coffee beverages of lower quality (Farah et al., 2006), as the reduction in the quality was suggested to be related to the increase of some phenolic compounds (Clifford, 1985; Mazzafera and Robson, 2000; Barbosa et al., 2012).

Considering this set of research works, higher altitude, and therefore, most probably the associated cooler temperature, could enhance coffee bean quality, probably linked to a slower/longer maturation period and to the changes in bean chemical composition. In this view, the predicted scenarios of global warming would point to an acceleration of fruit maturation and loss in the bean quality, what could implicate the migration of the coffee crop to somewhat cooler regions (in altitude and latitude). Still, it should be pointed the complete absence of works relating the concomitant enhancement of atmospheric [CO_2] and temperature to the quality of the obtained bean, considering the actual producing genotypes. Such studies will gather knowledge on the real biological effects and will perspectivate future breeding directions, envisaging the economic and environmental sustainability of this crop in years to come, under the predicted climate changes and global warming conditions.

Concluding remarks

In recent decades, studies have been conducted to understand the adaptation of the coffee plant to various environmental changes, such as cold and high air temperatures, drought, etc., in order to understand the implications to the plant physiology and quality of the yielded coffee bean and, therefore, to the final beverage.

The coffee plants possess a complex network of mechanisms that work in tandem to allow the acclimation within a certain extent of climate variations. These environmental limiting conditions impose stress on coffee plant, affecting morphological and developmental characteristics, by promoting, namely, cellular damage, disruption on ionic and osmotic homeostasis, oxidative stress, and lipoperoxidation of membranes, proteindegradation, etc. which could ultimately lead to lethal damages on the steam, roots and leaves. Some of the first indicators of temperature stress are observed at the photosynthetic pathway level. Therefore, this metabolic pathway can be used as probe to early sensing of stress tolerance/sensitivity, associated to some plant responses related to the reinforcement of the antioxidative system and adequate modifications on the composition of the membrane lipid matrix.

Higher altitude, and probably the cooler temperature associated with it, promote the sensory quality of the coffee beans. That was related with the higher presence of some compounds (trigonelline and caffeine) and the lower presence of others (5-CQA), although some uncertainty still exists due to the range and complexity of variables that determine the coffee quality.

Several modelling studies suggest that the predicted global warming scenarios can threaten the coffee crop sustainability. Therefore, biological studies, that consider concomitant conditions of enhanced air growth [CO_2] and high temperature, are needed to gather knowledge. In this way, the future of this crop closely depend on cutting edge research that envisage the selection and breeding of better adaptated coffee plants to the new predicted climate changes and global warming conditions.

Acknowledgements

The authors wish to thank Novadelta, Commerce and Industry of Coffee, S.A., for technical support. This work was supported by Portuguese national funds through Fundação para a Ciência e Tecnologia, under the scope of the project PTDC/AGR-PRO/3386/2012.

Author contributions

C. A. F. S., A. E. L., F. C. L., J. C. R. and I. P. P. contributed to the writing of the paper. A. E. L., F. C. L. and J. C. R. were involved in the overall planing and supervision of the work (which is part of the referred project) and paper review.

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