

Mitigation of the Negative Impact of Warming on the Coffee Crop: The Role of Increased Air [CO₂] and Management Strategies

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Abstract

Crop sustainability can be threatened by new environmental challenges regarding predicted climate changes and global warming. Therefore, the study of real biological impacts of future environmental conditions (e.g., increased air [CO₂], supra-optimal temperature and water scarcity) on crop plants, as well as the re-evaluation of management procedures and strategies, must be undertaken in order to improve crop adaptation and promote mitigation of negative environmental impacts, thus affording crop resilience. Coffee is a tropical crop that is grown in more than 80 countries, making it one of the world's most traded agricultural products, while involving millions of people worldwide in the whole chain of value. It has been argued that this crop will be highly affected by climate changes, resulting in decreases in both suitable areas for cultivation and productivity, as well as impaired beverage quality in the near future. Here, we report recent findings regarding coffee species exposure to combined supra-optimal air temperatures and enhanced air [CO₂], and impacts of drought stress on the crop. Ultimately, we discuss key strategies to improve coffee performance in the context of new environmental scenarios. The recent findings clearly show that high [CO₂] has a positive impact on coffee plants, increasing their tolerance to high temperatures. This has been related to a better

plant vigor, to the triggering of protective mechanisms, and to a higher functional status of the photosynthetic machinery. Even so, coffee plant is expected to suffer from water scarcity in a changing world. Therefore, discussion is focused on some important management strategies (e.g., shade systems, crop management and soil covering and terracing), which can be implemented to improve coffee performance and sustain coffee production in a continually changing environment.

Keywords: coffee crop sustainability, climate changes, mitigation, heat stress, drought

1. Introduction

Global emissions of the main greenhouse gases in the Earth's atmosphere raised in the mid-eighteenth century during the industrial revolution associated with the use of fossil fuels. Since then, the CO₂ concentration [CO₂] has increased from 280 to 400 $\mu\text{L CO}_2 \text{ L}^{-1}$ in 2014, and it is expected to rise to values between *ca.* 730 and 1020 $\mu\text{L CO}_2 \text{ L}^{-1}$ by 2100 [1]. Agricultural activity has also directly contributed to this process, being responsible for 1/3 of the CO₂ emissions but also with additional N₂O and CH₄ production, intensified mainly by inadequate management of crops and pastures [2], especially in low- and middle-income countries with predominating family farming [3].

Increased greenhouse gas emissions are expected to cause a temperature rise between 0.3 and 4.8°C by 2100, depending on future emissions and adequate measures to strongly limit them. Altered temperature may further promote extreme weather events, alter intra- and inter-annual precipitation patterns with long periods of drought and/or heavy rainfalls, partial melting of glacial ice, and consequently rising of the sea level [1]. Climate changes, particularly global warming, has a severe impact on the Earth's ecosystem and pose serious threats to agricultural sustainability [4–6], which is one of the human activities most vulnerable to climatic variation, since plants require optimal growing conditions to produce desired quantity and quality products [7, 8]. On the other hand, global demand for food is increasing as it is linked to the rapidly growing populations, which together with climate constraints, may compromise world food security [9]. In addition, increase in [CO₂] can affect the fundamental plant processes, such as photosynthesis and respiration, and, therefore, growth is also anticipated to be affected accordingly [10–12].

With regard to the coffee crop, it is known that plant growth, development, and productivity, as well as bean quality, are highly sensitive to climatic conditions [3, 13–16]. Accordingly, recent modeling studies have predicted important reductions of suitable areas for coffee cultivation in several producing regions [7, 16–19], with severe productivity losses in Mexico [20, 21], Nicaragua [3] and Tanzania [22], and extinction of wild populations of *C. arabica* in Ethiopia [23]. Although world coffee production has increased significantly in recent decades [24], studies state that climate change has caused substantial production losses [18], associated with periods of extreme droughts combined with supra-optimal temperatures [22, 25, 26], reducing coffee yields and bean quality as well as increasing the incidence of pests and diseases [16, 27]. In fact, it is believed that the recognized present climate changes have already caused yield losses in several coffee-producing countries, including Brazil, Ethiopia and Tanzania [22, 28, 29].

The negative estimates of future impacts on coffee crop were based on modeling approaches mostly focusing on increased air temperatures. However, these studies have only taken into account the current cultivars [30], and did not consider the considerable ability of some genotypes to endure various environment constraints, through metabolic adjustments and morphological and anatomical changes. Additionally, it was recently reported that coffee plants can respond positively to increased air [CO₂] [31–33], improving plant physiological and metabolic performance, and mitigating warming impacts [11, 33–35]. Such beneficial effect could even overcome these impacts, allowing some yield increase under adequate water availability to the crop [36], particularly at higher altitudes [37]. Nevertheless, given that coffee is one of the most important agronomic products, and that possible implications of ongoing climate changes may affect the sustainability of this crop in many actual areas, with potential dramatic economic, social and environmental implications, there is an urgent need for improving our knowledge regarding the plant performance under a wide range of environmental conditions. It is also equally important to identify adequate mitigation and adaptation strategies to be implemented, such as shading system crop management and soil cover and terracing, together with breeding new cultivars, in order to alleviate the impacts of climate changes on coffee plants.

Studies dealing with water stress in coffee species and genotypes have provided a detailed picture of biological mechanisms involved in drought tolerance [38–48], whereas recent works also showed that some genotypes of both *C. arabica* and *C. canephora* can endure temperatures much higher than what was traditionally accepted [11, 35]. As referred, plant resilience can even be improved under the exposure to high atmospheric [CO₂] [11, 34–37, 49]. In this context, the objective of this review chapter is to report the recent findings regarding the coffee plant responses to the single and combined exposure to atmosphere-supra-optimal temperatures and [CO₂], as well as to drought stress, together with the envisagement of some important crop management strategies (e.g., intercropping/shade systems, soil covering and terracing), which can be implemented to improve coffee performance and to mitigate the impact of environmental constraints, aiming at sustaining coffee production in a permanent changing environment.

2. General aspects of production, origin and favorable environmental conditions for *Coffea arabica* and *C. canephora*

Coffee, one of the most traded commodities in the world, is supported by *C. arabica* L. and *C. canephora* Pierre ex A. Froehner species [14]. It is estimated that the coffee chain of value generates a global income of *ca.* US\$ 173,000 million [50], having as well great social implications. In fact, this tropical crop is grown in approximately 80 countries [51], and about 25 million farmers, mainly smallholders, depend on this highly labor-intensive crop [52], with a worldwide involvement of *ca.* 125 million people in the entire chain [53]. Brazil, Vietnam, Colombia, Indonesia, Ethiopia, India, Honduras and Uganda are the major coffee producers, for a world annual production of green coffee beans which has been increasing steadily in the last decades, being consistently near or above 9 million tons since 2011/2012 [54]. This supports over 2.5 billion cups of coffee consumed every day around the world [55], with promising prospects for increased consumption in the coming years, especially among young people in Asia.

The coffee plant is characterized as a perennial woody shrub that belongs to the Rubiaceae family. Although there are at least 125 species within the *Coffea* genus [56], *Coffea arabica* L. (Arabica coffee) and *Coffea canephora* Pierre ex A. Froehner (Robusta coffee) are responsible for approximately 99% of the world coffee production [23, 57], with the former accounting for ~65% of total coffee production [55, 58]. Besides differences in origin, these species present important ecological differences in plant traits, as well in bean chemical composition, among them aroma precursors. In fact, the levels of these compounds have implications on sensory attributes, namely on astringency, taste, aroma, and flavor after roasting. Such chemical composition is not only genetic related but also strongly depend on environmental conditions (e.g., soil, shade, temperature), bean maturation stage, and to agricultural management and post-harvest procedures [59–64].

C. arabica are originated from the tropical forests of Ethiopia, Sudan and Kenya, at altitudes of 1500–2800 m, annual averages air temperatures between 18 and 22°C, precipitation from 1600 to more than 2000 mm distributed throughout the year, with a well-dry season (3–4 months), coinciding with the cold annual period. Currently, *C. arabica* coffee is grown in areas with cooler temperatures (18–23°C), at altitude mostly between 400 and 1200 m [7, 30, 65, 66], although cultivation up to 2000 m can be found in some countries in Central America. In contrast, *C. canephora* originated from the lowland forests of the Congo River basin, which extend to Lake Victoria in Uganda at altitudes up to 1200 m, are subjected to annual averages air temperatures between 23 and 26°C with minor fluctuations, and average precipitation exceeding 2000 mm distributed along 9–10 months [67–69]. Currently, cultivation occurs predominantly in lower altitude areas and higher temperatures, showing satisfactory development when the daily average temperature is above 22°C so that minimum is above 17°C and the average maximum air temperatures are below 31.5°C, with regular pattern of precipitation [70–74].

3. The impact of climate changes on coffee crop: warming and water scarcity

Coffee plants require both adequate water supply and optimal temperature, which are considered the most important environmental variables, since water and temperature-limited conditions cause negative impacts on growth, yield and productivity [14, 16, 30, 75]. Although in many coffee producing areas water scarcity occurs in the cooler season, climate modifications has increased the situations where low water availability and elevated temperature occur concomitantly under field conditions, which, as observed in other plants, will have the potential to exacerbate the limitations to the photosynthetic functioning [76].

In plants, photosynthesis and respiration are among the most sensitive metabolic processes to increasing temperatures [77]. High temperatures can cause protein denaturation and aggregation, increased production of reactive oxygen species [14], and ethylene synthesis [78]. Moreover, supra-optimal temperatures can reduce stomatal conductance and light energy use as well as alter thylakoid ultrastructure and diffusion of gas through mesophyll [15, 79–81] with a direct impact on net C gain. The latter will be even more amplified due to the increase of O₂ solubility in relation to CO₂ under higher temperatures, favoring the oxygenase activity of

RuBisCO over its carboxylation activity, thus increasing photorespiration rates [82, 83]. Altogether, this ultimately may lead to the decline in the availability of carbohydrates for energy supply as well as carbon skeletons to support plant growth [77]. Thus, warmer temperatures can affect crop yield at any time from sowing to grain maturity, but it is the time around flowering, when the number of grains per land area is established, and during the grain-filling stage, when the average grain weight is determined, that high temperatures causes major impacts on the final harvestable crop [9, 73, 84]. In addition, it causes a reduction in the production of leaves and consequently alters the photosynthetic activity [85].

Coffee trees presented a remarkable tolerance to temperatures relatively high (up to 37/30°C; day/night) when air humidity was maintained at 75%, occurring relevant physiological/biochemical impairments only at 42/34°C, associated, namely, to large activity reductions of RuBisCO and Ru5PK [35], despite large accumulation of RuBisCO transcripts [86]. The reported heat tolerance was related with increases in protective molecules, namely, enzyme and non-enzyme antioxidant molecules, heat shock protein 70 (HSP70) reinforcement, and altered gene expression [11, 86]. However, under field conditions, rising temperature may lead to increase in air vapor pressure deficit (VPD_{air}), what may result in decreased stomatal and canopy conductance in *Coffea* spp., due to a high sensitivity of coffee stomata to VPD_{air} values above 2 kPa [87–89]. In addition, elevated temperatures can contribute to a gradual increase in soil water depletion, particularly in areas lacking sufficient precipitation, resulting in water stress, which further exacerbates the adverse effects of high temperatures.

Stomatal closure is one of the first responses to water deficit in coffee plants, aiming at limiting water loss through transpiration flow. However, this directly decreases the CO₂ availability in the chloroplasts, reducing the photosynthetic rates [14]. In this context, irradiance reaching the chloroplasts may exceed the light energy needed to saturate photosynthesis, which in turn can lead to the formation of reactive oxygen species (ROS). ROS can cause oxidative damage to multiple cell and chloroplast components, namely to the D1 protein, lipids, RNA and DNA molecules, associated with increased cellular and metabolic disorders, resulting in cell death [47, 90, 91]. Moreover, ethylene synthesis often increases under drought stress conditions, promoting leaf senescence and slowing growth [10]. However, coffee plants display a noticeable metabolic plasticity to cope with environmental stresses [14, 51], as referred above for supra-optimal temperatures. Additionally, air [CO₂] enrichment improved both coffee antioxidant defense system and photosynthetic performance regardless of temperatures, but maintaining a relevant photosynthetic functioning at temperature as high as 42°C. This prevented an energy overcharge in the photosynthetic apparatus, eventually reducing the need for energy dissipation and PSII photoinhibition [11, 35].

Considering water stress, a large number of early studies have reported that coffee plants can cope with drought stress through morphological, biochemical, and physiological modifications [14], as discussed later in this chapter. However, prolonged drought events associated with elevated temperatures can lead to very severe conditions, with a general impact on cell metabolism, associated as well to increased oxidative stress, altogether resulting in intense defoliation and yield losses (**Figure 1**), although genotypic difference in stomatal sensitivity to water stress among *C. canephora* genotypes have been reported [43, 45]. Furthermore, drought



Figure 1. Intensive defoliation and yield losses due to prolonged severe drought (A), together with high temperatures (B) in *C. canephora* cultivations in Espírito Santo State, Brazil.

should be envisaged as contributing to a multidimensional stress, exacerbating the negative impacts of elevated irradiance and supra-optimal temperatures [13, 14, 42]. Therefore, drought-resistant coffee genotypes are a useful strategy for improving coffee performance in regions that are predicted to face moderate to severe drought [49].

Overall, drought-sensitive *C. canephora* genotypes show a shallow root system and ineffective stomatal control, whereas drought-resistant coffee genotypes show considerably deeper root system, the strengthening of antioxidant defense system, and higher stomata sensitivity to reduced water availability (both in soil and atmosphere) [43, 92]. Increased wood density reinforcing vessels and, in turn improving resistance to cavitation, was correlated with tolerance to hydraulic dysfunctions [45]. On the other hand, *C. canephora* genotypes with specific traits conferring drought tolerance generally show reduced yield under optimal environments conditions due to their increased stomata sensitivity to VPD_{air} . This is related to hydraulic limitations to water flow from roots to leaves [43, 45]. Therefore, coffee genotypes displaying increased phenotypic plasticity as, e.g., deep root system, substantial hydraulic conductance, intermediate stomatal control and strengthening of antioxidant defense system, could be used in regions which are predicted to face moderate water deficit, while drought-resistant genotypes could be used in regions predicted to face severe drought.

In addition to the traits outlined above, leaf size as well as canopy architecture should also be considered as important traits associated with drought tolerance. For example, although the leaf hydraulic conductivity (K_{leaf}) values found in *C. arabica* plants are typically low, probably linked to their native shade habitat [44, 93], *C. arabica* coffee genotypes with smaller leaves displayed higher vein density, higher K_{leaf} , increased gas exchange and reduced drought vulnerability [40, 44]. Drought tolerance was also found to be higher for *C. canephora* genotypes displaying smaller leaves [42]. In fact, it is known in other plants that smaller leaves allow for more rapid convective heat loss, resulting in lower transpiration and water loss likely due to smaller boundary layer [94]. Furthermore, a more compact crown structure may result in reduced VPD_{air} within the coffee canopy, decreasing the transpiration demand [14], besides allowing to increase plant density coupled with improved soil covering and reducing the negative impacts of elevated temperatures, and high wind speed on coffee trees. On the other

hand, *C. arabica* genotypes displaying open architecture crown show high transpiration rates (as measured by the sap flow technique) depleting accessible soil water more rapidly [40]. Therefore, although the water use efficiency in coffee genotypes is associated with the hydraulic capacity of the soil and stem to supply the leaves with water [95], coffee traits linked to water safety, e.g., a more compact crown structure and to greater extent an effective stomatal control, seem to play an important role in drought tolerance.

A recent study by [48] reported that both drought-sensitive and drought-tolerant *C. canephora* genotypes showed a drought stress “memory,” with plants exposed to multiple drought events showing better recovery than those submitted to drought events for the first time. This performance was mainly associated with substantial metabolic reprogramming, involving key processes such as photosynthesis, respiration, photorespiration, and the antioxidant system. In this sense, it would appear reasonable to suggest that multiple moderate water stress in coffee seedlings at nursery stage may improve to some extent the initial coffee performance under field conditions in areas prone to water scarcity.

4. Can elevated [CO₂] help the mitigation of the negative impacts of high temperature and water deficit?

Although climate models point CO₂ as the major greenhouse gas responsible for global warming due to its high accumulation rate in the atmosphere [6], the impacts of increased air [CO₂] at plant physiological and biochemical levels should not be neglected, namely in coffee metabolism [11, 31, 32, 35], as well in yield [36, 37].

The current [CO₂] in the atmosphere is still below the optimum for photosynthesis of C₃ plants; therefore, leaf photosynthetic rates are predicted to increase in response to future increase in air [CO₂], due to increased carboxylase activity of RuBisCO [82, 83, 96]. This C-fertilization may eventually reinforce plant vigor (and the defense systems), which, in turn, could reinforce the plant ability to endure environmental stresses [97]. On the other hand, elevated CO₂ levels will especially benefit plants with strong sink capacity to use such increased amounts of photoassimilates. Otherwise, an accumulation of soluble sugars may occur which in turn will decrease the net photosynthetic rate through negative feedback mechanisms, that is, will provoke *downregulation* of photosynthesis, not allowing the plant to fully explore the positive effect of [CO₂] increase [83].

In the case of coffee, significant increases of net photosynthesis, between 34 and 49%, were observed for *C. canephora* (Clone 153) and *C. arabica* (Icatu and IPR 108) genotypes [31], when comparing plants grown subjected to elevated [CO₂] (700 μL L⁻¹) or normal [CO₂] (380 μL L⁻¹) under environmental controlled conditions. Furthermore, under such high [CO₂], plants also showed a better water-use efficiency, reinforcement of photosynthetic components and increased activity of key enzymes involved in photosynthesis and respiration, without noticeable leaf sugar accumulation. Therefore, these coffee genotypes were able to cope with enhanced [CO₂], maintaining the consumption of photosynthates and regeneration of RuBP associated with continuous investment in vegetative and reproductive structures. The evidence of improved

coffee performance under enhanced $[\text{CO}_2]$ was further obtained with other *C. arabica* genotypes (Obatã IAC 1669–20 and Catuaí Vermelho IAC 144) under field conditions using free-air CO_2 enrichment (FACE) system, showing increased photosynthesis and decreased photorespiration, without changes in stomatal and mesophyll conductance, for an air $[\text{CO}_2]$ of $550 \mu\text{L L}^{-1}$ [33]. Additionally, coffee plants grown under elevated $[\text{CO}_2]$ were more vigorous, with increased leaf area, growth rate at height and stem diameter, showing as well increased grain yield by 14.6 and 12.0% for Catuaí Vermelho 144 and Obatã IAC 1669–20, respectively, [8, 32], although average yield increases of 28% were also reported after three harvests [37] when compared to plant grown at ambient $[\text{CO}_2]$. Another study also demonstrated that coffee trees grown under $550 \mu\text{L CO}_2 \text{ L}^{-1}$ presented increase in photosynthesis of leaves from upper and lower canopy layers, inhibition of photorespiration, and no apparent sign of photosynthetic *downregulation*, when compared to plants grown under ambient $[\text{CO}_2]$ ($390 \mu\text{L L}^{-1}$) [98]. Finally, recent studies based on modeling approaches accounting with high air $[\text{CO}_2]$ positive impact reported that coffee yield losses associated mostly with high temperatures can be offset by the CO_2 fertilization effect, with a probably yield increase by 2040–2070 [36], or 2050, particularly at higher altitudes [37].

The simultaneous occurrence of various environmental constraints is the most common situation under field conditions, and therefore, it has been argued that a positive plastic response from plant experiencing a single stress can be increased, canceled or even reverted under the combined action of multiple stresses [6]. Regarding the coffee plant, responses to the combined effects of increased $[\text{CO}_2]$ and supra-optimal air temperature started to be investigated quite recently, whereas the simultaneous exposure to elevated $[\text{CO}_2]$, heat and water deficit have never been studied. The exposure to increased air $[\text{CO}_2]$ revealed interesting implications to plant physiological response to supra-optimal conditions. This was the case in both *C. arabica* (cvs. Icatu and IPR 108) and *C. canephora* cv. Conilon Clone 153 plants exposed to elevated $[\text{CO}_2]$ and temperatures up to 42°C [11, 34, 35]. Notably, a remarkable heat tolerance was observed up to $37/30^\circ\text{C}$ (day/night) irrespective of air $[\text{CO}_2]$. The tolerance (and high physiological performance) to such temperature was somewhat surprising as it is above what is traditionally accepted to be tolerated by coffee plant [35]. Furthermore, enhanced $[\text{CO}_2]$ greatly mitigated the negative impact of the temperature, especially at $42/34^\circ\text{C}$, with higher water-use efficiency (WUE) at moderately higher temperature ($31/25^\circ\text{C}$). Increased CO_2 was observed to strengthen the photosynthetic apparatus, improving light energy use and biochemical functioning. These results were linked to the maintenance or increase in the content of several protective molecules (neoxanthin, lutein, β -carotene, α -tocopherol, heat shock protein-HSP70, raffinose), the activity of antioxidant enzymes (superoxide dismutase, SOD; ascorbate peroxidase, APX, glutathione reductase, GR; catalase, CAT) and the upregulation of some genes related to stress-protective molecules (ELIP, HSP70, Chaperonin 20 and 60), and antioxidant enzymes (*CAT*, *CuSOD2*, *APX Cyt*, *APX Chl*) [11]. In the same experiments, overall leaf mineral macro- and microelement contents have remained within a range that could be considered largely adequate for coffee plants, with no changes in macronutrient profile ($\text{N} > \text{K} > \text{Ca} > \text{Mg} > \text{S} > \text{P}$), that is, satisfactory mineral content was maintained in the context of warming, under high $[\text{CO}_2]$ [34].

Climate changes are also predicted to affect intra- and inter-annual rainfall patterns, and the decrease in precipitation amounts in conjunction with increased air temperature may reduce

net photosynthesis at current [CO₂]. Still, under increased air [CO₂], a partial relief of negative impacts of water deficit may occur [99]. Indeed, arabica coffee plants grown under severe drought conditions and increased biotic pressure showed strategies which allow the maintenance of structural and physiological integrity in the fourth period of winter growth [98]. This occurs because of the dichotomous responses of net photosynthesis and stomatal conductance to high [CO₂], which lead to improved WUE, reducing soil moisture depletion during periods of drought [9]. Studies by [10, 76] on *Agropyron cristatum* L. and *Perilla frutescens* var. japonica Hara, respectively, reported positive results of elevated-CO₂ mitigation of drought stress, verifying increase in photosynthetic capacity and decrease in stomatal conductance with lower transpiration rates. Consequently, increased intrinsic water-use efficiency (WUEi) and total water-use efficiency (WUEt) were observed. Furthermore, high [CO₂] can also alleviate oxidative stress conditions, and photoinhibition status, likely associated to a higher photosynthetic functioning (as also observed for high temperatures [11]), even under significant stomatal closure. Altogether such responses may result in improved tolerance to drought stress, as found in other plants [6, 10, 12]. Nevertheless, it is important to note that under severe drought, such positive results might not be obtained, and that mitigation associated with high [CO₂] does not always occur [6].

In addition to the positive effects on the impacts of abiotic stresses, elevated [CO₂] can also reduce to some extent the incidence and severity of coffee pests and diseases. In fact, decrease in leaf rust (*Hemileia vastatrix*) severity, number of lesions, leaf area injured, number of sporulating lesions, percentage of damaged leaf area and area under disease progress were observed in *C. arabica* cv. Catuaí IAC 144 grown under elevated [CO₂] [8]. Reduced incidence of leaf miner (*Leucoptera coffeella*) during periods of high infestation was also observed at elevated [CO₂] [32].

In summary, enhanced [CO₂] can have a positive mitigation effect on the negative impacts of high temperature and, probably, low water availability, as well as by reducing the severity of some pests and diseases. However, since responses are highly species (and even cultivar) dependent, it is urgent to implement long-term studies in coffee considering single and, especially, combined stresses, with the simultaneous exposure to elevated [CO₂], supra-optimal temperatures and drought, relating them to phenological stages (e.g., flowering), therefore, to increase knowledge on this crop in a context of climate changes.

5. Mitigating the impacts of climate changes through management practices

To promote crop sustainability in the context of climate changes and global warming, adaptation and mitigation measures must be implemented. Regarding adaptation, plant screening and breeding are essential to provide new improved and stress-tolerant genotypes, but their implementation are somewhat delayed due to the time needed to obtain new varieties. As an example, the use of improved genotypes with an optimized architecture is a valuable tool. It is known that small-size plants, with denser canopies, are prone to display lower transpiration

rates [13, 14]. Additionally, plants with larger and deeper root systems would have an ability to explore increased soil volumes, reaching water resources that other plants with a more superficial root system do not [14]. Still, several years will be needed until such new genotypes can be available and, therefore, ready-to-use strategies should be implemented, namely those regarding an effective mitigation of the environmental negative impacts on the actual cropped genotypes. This can be even more important when dealing with tree crops that have a productive lifespan of several years or decades, as it is the case of coffee, which can last for more than 30 years [18].

A significant range of management techniques can be used to minimize the impact of different stresses that can affect the performance of agricultural systems. For coffee crop, several different agronomic tools stand to that purpose, e.g., the use of shade systems with tree species, as well as other intercropping associations, to improve an efficient water use and minimize warming at the plant level, maintaining a more suitable microenvironment concerning both temperature and air humidity. Improved soil covering with other intercropped species, and terracing under conditions of significant slopes, are also quite useful techniques to minimize soil water loss (or to increase its infiltration), therefore, helping to maintain water resources available to the plants for longer periods.

5.1. Fertilization management under high air [CO₂] and warming conditions

Minerals have a wide number of roles in plant cell. Therefore, as in other plants, an adequate mineral fertilization is recognized as crucial to allow the triggering of acclimation mechanisms in face of environmental constraints in the coffee plant. This is the case of nitrogen (N) supply, which is of utmost importance to allow the recovery from high irradiance impact, through the triggering of repair mechanism, and the reinforcement of leaf defense mechanisms, including the control of highly reactive molecules of chlorophyll and oxygen, whose production is exacerbated under high irradiance/full sun exposure [100–102]. Additionally, the presence of adequate contents of other minerals allows the plant to maintain high metabolic performance due to their specific roles. For instance, copper, iron and manganese, which were shown to promote the activities of, respectively, superoxide dismutase, ascorbate peroxidase, and photosystem II under cold exposure [103], as well as calcium, which is essential to the stabilization of chlorophyll and the maintenance of photochemical efficiency at PS II level [104].

Changes in mineral contents may affect plant development, but may also have other important consequences, namely as regards the quality of agricultural products for food and feed, herbivory, litter decomposition rates, etc. [105, 106]. It is known that mineral contents often decline in the leaf biomass under high air [CO₂] conditions. This was related to higher growth rates, accumulation of non-structural sugars (mainly starch), lower transpiration rates, or to changes in the nutrient allocation patterns under enhanced air [CO₂] [107–109]. This mineral “dilution” effect on leaves can affect the photosynthetic apparatus (e.g., through N, S and Fe), enzyme activity (e.g., through K, P, Mn and Fe), alters redox reactions (e.g., through Fe, Zn and Cu), and modifies the structural integrity of chloroplast membranes (e.g., B) [105, 110–113]. However, this so called “dilution effect” may frequently reflect qualitative physiological changes rather than a lack of nutrients [108], since in many cases, these plants did not present

mineral nutrition disturbances. This seems just to be the case in *Coffea* spp., since it was observed that under adequate temperature, long-term exposure to enhanced [CO₂] (700 $\mu\text{L L}^{-1}$) net photosynthetic rate was increased by between 40 and 49% [31], concomitantly to a moderate mineral reduction that ranged from 7 to 25% in N, Mg, Ca, Fe in *C. canephora* cv Conilon Clone 153, and in N, K and Fe in *C. arabica* cv. Icatu [34].

Most important was also the observation that contents (on a per leaf mass basis) of several minerals increased under supra-optimal temperatures, largely offsetting the dilution effect observed under control temperature (25°C), keeping the large majority of minerals and their ratios within a range that is considered adequate, therefore, suggesting that coffee plant can maintain its mineral balance in a context of climate changes and global warming [34]. Even so, taking into account the importance of mineral dynamics to virtually all biological processes, studies under field conditions must be implemented to better understand the possible CO₂ implications for coffee fertilizer management in a context of climate changes and global warming in a near future.

5.2. Reducing irradiance at the leaf level

Both *C. arabica* and *C. canephora* have been cultivated under full sunlight in many regions around the world, particularly in Brazil. In fact, coffee plant can successfully adjust its photosynthetic metabolism to high light conditions, namely if adequate mineral nutrition is provided [100–102]. Effective acclimation to other environmental constraints (e.g., cold, heat, drought) was also reported [14]. Such acclimation ability depends on the presence and/or reinforcement of several mechanisms, among them leaf antioxidants, and qualitative modifications on the lipid matrix of cell membranes, particularly in the chloroplast. This allows the plant to maintain high metabolic activity, namely as regards the photosynthetic pathway, depending on stress severity and on species and genotype capabilities [11, 41, 57, 93, 101, 114]. However, these coffee species have evolved and grow naturally under shaded understory [14, 68, 69]. Not surprisingly, *Coffea* sp. presents some leaf traits usually associated with shade plants, namely low light saturating point (*ca.* 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$) [115], therefore, quite below the irradiance values occurring under field conditions. This increases the probability of photoinhibition under high solar radiation [13, 14, 100, 116, 117]. Taking into account predictions of a global warming and lower water availability along the present century, the implementation of coffee cultivation under shaded conditions (e.g., under agro-forestry systems) may be recommended as a cultural management practice to alleviate the combined impacts of drought and elevated temperatures [118], while improving nutrient cycling, soil fertility and soil organic matter accumulation [119–122]. Additionally, shade crops can improve ecological aspects including increasing bio-diversity of flora and fauna [123, 124].

Traditionally, coffee trees grown under shaded conditions show reduced yield, since shade trees may compete with coffee for essential requirements such as light, water and nutrient depending on tree density [13, 119, 125], with less nodes per branch and fewer flowers at existing nodes must be also considered. Additionally, coffee plants show limited light distribution within their own canopies [88], thus leading to the further reduction of the light availability at whole canopy scale. However, increased light-use efficiency can compensate

the low availability of photosynthetically active solar radiation in coffee trees grown under shaded conditions [126]. Also, shade trees can increase the proportion of diffuse light under their canopy by 60–90%, what may lead to increased penetration of radiation inside the coffee canopy [126]. In fact, *C. canephora* Clone 02 (clonal variety “EMCAPA 8111” [127]), grown under an irradiance retention of 70% promoted by Australian cedar (*Toona ciliata* M. Roem) in southeastern region of Brazil showed similar yield to unshaded counterparts, although for a study considering only one crop season [128] (**Figure 2**). Similar yield and leaf nutrient content were also found in shaded *C. canephora* cv. Verdebras G35 plants intercropped with rubber trees (*Hevea brasiliensis* (Willd. ex A. Juss.) Müll. Arg.) in the same region, with a reduction of ca. 70% in total irradiation [129], while similar yield were reported for *C. arabica* cv. Caturra intercropped with *Erythrina poeppigiana* (reduction of ca. 70% in total irradiation) in the central Valley of Costa Rica [126] and in six *C. arabica* genotypes shaded by *E. verna* and *Musa* sp. (shade up to 80%) [130].

As referred above, coffee trees show increased stomatal sensitivity to VPD_{air} , so that increase in air temperature and/or decrease in air relative humidity (RH) can result in reduced stomatal



Figure 2. *Coffea canephora* cv. Conilon under shading conditions promoted by A) Australian cedar (*Toona ciliate* M. Roem. var. *Australis*), B) papaya (*Carica papaya* L.), C) rubber tree (*Hevea brasiliensis* Willd. ex A. Juss), and D) African mahogany (*Khaya* spp.), in northern Espírito Santo state, Brazil.

aperture. In this sense, shaded systems with trees, including rubber [129] and Australian cedar [128], can reduce air temperature, maintain higher air humidity, and decrease low wind speed near the coffee plants, thus resulting in decreased VPD_{air} between the leaf and the atmosphere, and a lower water loss through transpiration [13]. Therefore, shade will promote a better WUE, reducing plant transpiration and soil evaporation, while contributing to improve plant physiological performance [117].

In addition to the impacts on photosynthetic machinery, rising temperature causes increases in plant respiration rates, mainly associated with “maintenance respiration” to support protein turnover and to maintain active ions transport across the membrane [81]. Recent studies have reported decreases of 2 up to 6°C in air temperature surrounding coffee canopy under shaded condition [125, 128, 129, 131]. Such reduction in air temperature can therefore reduce maintenance respiration [126], as *C. arabica* cv. Caturra plants in the Central Valley of Costa Rica that showed a 40% decrease in peak maintenance respiration under a 4°C decrease in maximum temperature [125].

Coffee growers need to obtain high yields, while maintaining bean quality in order to guarantee their income. Rising temperature may decrease coffee bean yields due to bud abortion or development of infertile flowers, particularly when associated with prolonged dry periods [65]. Additionally, increased temperature may accelerate fruit maturation and ripening, reducing the accumulation of sucrose and altering the content of several compounds that are known precursors of taste, flavor and aroma after roasting [15, 60, 62, 64]. Shade trees may provide a milder microclimate, attenuating temperature rise on coffee beans, and by lowering air temperature close to the coffee plant can extend the maturation period so that the bean filling period will be enlarged [132, 133], what can contribute to higher sucrose accumulation.

Besides the importance of shade in reducing thermal stress, other important benefits arise as well. For instance, coffee trees grown under full sunlight show a typical biennial pattern, e.g., during one crop season, a heavy fruit load will constitute a major sink at the expense of new leaves and branches, reducing productivity in the following year [134]. Moreover, high fruits load may result in reduced bean size due to the carbohydrate competition among berries during bean filling [133]. In this sense, depending on density, shade trees can reduce coffee flowering intensity, resulting in a better coffee bean quality, as well as in higher yield stability along the years. Although the central purpose of coffee cultivation under shaded conditions is alleviating the impacts of both high irradiances and supra-optimal temperatures, it is worth to mention that cultivation of trees of economic importance, such as *Inga* sp. [125], Australian cedar [128], rubber tree (**Figure 2**) [129], can constitute important complementary sources of income to coffee farmers.

The application of kaolin particles can also reduce the irradiance at leaf surface, increasing radiation reflections, and, consequently decreasing leaf temperature [135]. Kaolin particle film can as well improve light distribution inside the canopy, leading to increase in photosynthetic rates, increasing crop water use efficiency at whole-canopy scale, as reported for apple (*Malus sylvestris*) [136, 137] and grapevine (*Vitis vinifera* L.) [137]. Moreover, kaolin particle film protected apple fruits from damage caused by excessive heat linked to high light conditions, besides avoiding the direct impacts of ultraviolet radiation on fruits as well [135]. Additionally,

some works have demonstrated that particle film technology can alleviate the negative impacts of water stress, particularly associated with increase in light reflection and decrease in canopy temperature [137, 138]. In coffee, kaolin particle film was observed to increase C-assimilation and bean yield, linked to improved light distribution within the canopy, since sunlight is essential to floral initiation [139], and can, therefore, constitute a promising alternative technique to reduce the thermal energy at leaf level.

Considering the effects of supra-optimal temperatures, high density planting system can alleviate the negative impacts of heat stress, because under such conditions, the air surrounding the coffee plants becomes more humid due to plant transpiration and low wind speed, decreasing VPD_{air} [14]. Additionally, in areas facing strong winds, the use of windbreaks or tree shelters is recommended as both can avoid an extensive removal of boundary layer, leading to decreased demand for water from the atmosphere. However, under high density planting systems, coffee crop management through pruning is fundamental for renewal, revitalizing and yield stability in coffee plantations [140], what can improve soil coverage.

5.3. Soil covering and terracing

The distance between coffee rows allows for growth of other plants, which may compete for water and nutrients, depending on species involved. Overall, weed control aims at removing the invasive plants, exposing soil to intense solar radiation which can result in increase in water evaporation directly from the soil as well as facilitating the surface water runoff, leading to erosion losses, especially in areas with a pronounced slope. Depending on weed species, invasive plants are allowed to grow naturally between coffee rows without any management strategy. Although such plants may reduce erosion losses and direct solar radiation, as well as improve the infiltration of water into the soil stratum [141], they lose water during the day through transpiration, decreasing soil moisture [142]. Therefore, weed management strategies (for example, cut using a mower) can contribute for organic matter accumulation and, in turn, increase the water retention capacity of the soil, improving water productivity.

Also, the use of some leguminous species, correctly managed between coffee rows, can protect the soil, providing N to the coffee plants. Furthermore, soil coverage with herbaceous plants between coffee rows increases soil moisture and reduces both soil temperature and weed incidence, improves the physical and chemical soil properties [143, 144], promotes water infiltration, reduces rainfall impact and erosion, stimulates microbial activity, and improves organic matter in the soil [145]. Improved ground cover can be further obtained from weeds control, and by keeping biomass from coffee plants pruning, a common practice used to promote crop productivity [140] and soil microbiota diversity.

Coffee straw/husks, a by-product generated during coffee processing and discarded in many farms, can also be used for soil covering, reducing water losses through soil evaporation. In addition, coffee straw/husks can provide essential macro and micronutrients, namely N, P, K, Ca, Mg, S, Fe, B, Mn, Zn and Cu [72], lowering the need of chemical fertilization regarding these nutrients, and increasing coffee yield up to 25% [146]. Moreover, these coffee by-products can improve the soil physical associated with increase in CTC and soil pH [147], and inhibit seed germination of many weed species such as *Amaranthus retroflexus*, *Bidens pilosa*, *Cenchrus*

echinatus and *Amaranthus spinosus* [148]. Therefore, coffee straw/husks can increase soil water retention and reduce to some extent costs associated with weed managements and fertilizers.

Other strategies for areas with a high slope are terracing, contour plowing terrace and rectangular ditches. Such practices contribute for preventing rapid surface runoff, allowing rain water to percolate into the soil, contributing for soil conservation [149–151]. Therefore, the establishment of terraces, although expensive, could constitute a worthwhile alternative to reduce water losses through runoff and soil erosion, while promoting infiltration [152]. Rain water storage in reservoirs should also be implemented. This will allow future water use during periods of negligible rainfall, constituting an important mitigation strategy to avoid drought stress. Therefore, increasing the water retention/storage capability in the farm can delay or even prevent coffee water stress.

6. Future perspectives

Climate changes are expected to negatively affect the coffee crop, causing serious social and economic impacts. Supra-optimal temperatures and water scarcity may decrease coffee yields and some studies state that these stresses are already occurring in some coffee-growing countries. However, coffee plants show a potential ability to cope with several environmental stresses and enhanced [CO₂] can improve such ability and mitigate to some extent the negative impacts of supra-optimal temperatures. Even so, some mitigation strategies will be necessary to alleviate the impacts of elevated temperature and/or drought stress on coffee trees. We have reviewed some strategies that can be implemented depending on main environmental stresses occurring in specific regions, such as those based on coffee traits (root systems, size leaf, canopy architecture and stomatal sensitivity) and crop management (nutrient managements and pruning system), as well as those aiming at reducing excessive light at coffee tree level (shaded systems, kaolin-based particle film and plant density), and at improving soil water retention (soil covering and terracing). Notably, however, a single mitigation strategy may not be enough to face severe stress conditions; thus, multiple strategies should be undertaken.

Future studies considering simultaneous exposure to the main environmental stresses (e.g., high temperatures and drought), taking into account as well elevated [CO₂], will be necessary to elucidate the mechanisms underlying plasticity and vulnerability of coffee plants under conditions that are expected to occur in the fields in a near future. Such studies are a fundamental basis for plant breeders to obtain new/more adapted genotypes. Finally, these strategies appear to be useful tools toward maintaining the coffee chain production.

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