Climatic Change (2019) 152:167–178
https://doi.org/10.1007/s10584-018-2346-4

Why could the coffee crop endure climate change and global warming to a greater extent than previously estimated?

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Received: 23 April 2018 / Accepted: 3 December 2018 / Published online: 14 December 2018

Abstract
Coffee, one of the most heavily globally traded agricultural commodities, has been categorized as a highly sensitive plant species to progressive climatic change. Here, we summarize recent insights on the coffee plant's physiological performance at elevated atmospheric carbon dioxide concentration [CO_2]. We specifically (i) provide new data of crop yields obtained under free-air CO_2 enrichment conditions, (ii) discuss predictions on the future of the coffee crop as based on rising temperature and (iii) emphasize the role of [CO_2] as a key player for mitigating harmful effects of supra-optimal temperatures on coffee physiology and bean quality. We conclude that the effects of global warming on the climatic suitability of coffee may be lower than previously assumed. We highlight perspectives and priorities for further

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research to improve our understanding on how the coffee plant will respond to present and progressive climate change.

Keywords *Coffea* spp. · Coffee · Crop yield · Elevated [CO_2] · Global warming · Heat · Photosynthesis

1 Introduction

The current rise in atmospheric carbon dioxide concentration ([CO_2]) is one of the major drivers of global warming and climatic change. Atmospheric [CO_2] has increased approximately by 43% from the pre-industrial levels of 280 μL L^{-1} air in 1750 to current levels exceeding 400 μL L^{-1} air, and global mean surface temperature has increased by 0.85 °C over the same period. Depending on the greenhouse gas emission scenarios, projections indicate that, at the end of this century, atmospheric [CO_2] might rise between 421 and 936 μL L^{-1} air, in parallel with a rise in global temperature between 0.3–1.7 °C (best scenario) and 2.6–4.8 °C (worst scenario), relative to 1986–2005 (IPCC 2013; IPCC 2014). These long-term changes, coupled with climate variability, such as longer and unpredictable droughts and sometimes excessive rainfall, are expected to threaten the sustainability of agricultural production on a global scale, with consequences on the amount and quality of harvestable crops for the actual production areas (DaMatta et al. 2010).

Plants sense and respond directly to rising atmospheric [CO_2] through an increase in net photosynthesis rate (*A*) and, frequently, a decrease in stomatal conductance (g_s), and this is the basis for the CO_2 fertilization effect on crops with corresponding increase in yields (Long et al. 2006; Ainsworth and Rogers 2007). Meta-analyses of free-air CO_2 enhancement (FACE) experiments have reported mean reductions in g_s of 22% and increases in light-saturated (*A*) of 31% across a range of C_3 species for an increase in [CO_2] from approximately 366 to 567 μL L^{-1} air (Ainsworth and Rogers 2007). Increases in *A* with enhanced [CO_2] in the chloroplast of C3 plants are associated with a stimulation of the carboxylation rate of ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO), the rate-limiting step in photosynthesis at saturating light and current [CO_2] levels, and a concomitant reduction (or even suppression) of its oxygenation function, and thus the rate of photorespiration (Ainsworth and Rogers 2007). Noticeably, g_s has been systematically, but not universally, demonstrated to decrease at elevated [CO_2] (Engineer et al. 2016); however, increases in g_s with rising [CO_2] have also been reported in a few cases (Purcell et al. 2018). In any case, decreases in g_s often lead to lower transpiration rates and higher water-use efficiency (WUE). However, this also results in less latent heat loss, thus potentially increasing leaf temperatures, which in turn ultimately might impair crop performance in a scenario of global warming.

Coffee, one of the most popular beverages worldwide is consumed by about one-third of the world's population, and is one of the most heavily globally traded agricultural commodities. The world coffee trade is based on two species, *Coffea arabica* L. (Arabica coffee) and *C. canephora* Pierre ex A. Froehner (Robusta coffee), which account for ca. 99% of coffee production worldwide. Coffee is grown in approximately 80 tropical countries and constitutes the economic basis of many of these countries. Furthermore, it is estimated that about 25 million farmer families worldwide produce coffee, with a majority of smallholders and families whose livelihoods largely depend on this crop.

Coffee, particularly *C. arabica*, has been categorized as a highly sensitive plant species to climatic change. Several statistical studies based on projections of rising temperatures and altered precipitation patterns under present and ongoing climate change scenarios have predicted remarkable effects on the coffee crop including extensive reductions in agro-climatic zoning and losses (and drift) of suitable areas in most coffee-producing countries (Zullo et al. 2011; Bunn et al. 2015a; Magrach and Ghazoul 2015; Ovalle-Rivera et al. 2015; Moat et al. 2017). Decreases in crop yields (Gay et al. 2006; Craparo et al. 2015), beverage coffee quality (Läderach et al. 2017), negative impacts on wild populations of *C. arabica* (Davis et al. 2012; Moat et al. 2017), greater pest incidence (Avelino et al. 2015; Magrach and Ghazoul 2015), and increased agricultural, social, and economic vulnerabilities (Baca et al. 2014) have been also foreseen. Nevertheless, these pessimistic findings have not considered the potential positive effects of elevated [CO_2] on coffee photosynthesis (Ramalho et al. 2013; Ghini et al. 2015; DaMatta et al. 2016) and leaf retention (Rakočević and Matsunaga 2018) or the role of CO_2 as a key player in coffee heat tolerance (Martins et al. 2016; Rodrigues et al. 2016) probably because only very recently this information has become available for the coffee crop. Furthermore, the recognized resilience of elite coffee genotypes to acclimate to stressful conditions (Fortunato et al. 2010; Batista-Santos et al. 2011; Cavatte et al. 2012) has also been neglected.

In this study, we summarize recent insights on the coffee performance at elevated [CO_2] in addition to reporting that an increase in air [CO_2] plays a significant role for the success of the coffee crop to endure environmental stresses, e.g., rising temperatures and drought due to climate change. These facets are examined by encompassing multiple plant levels, e.g., physiology (Martins et al. 2014b, 2016; DaMatta et al. 2016; Rodrigues et al. 2016; Rakočević et al. 2018), plant structure (Rakočević and Matsunaga 2018; Rakočević et al. 2018), bean quality traits (Ramalho et al. 2018), and yields (this study). We conclude this review article pointing the gaps in our current knowledge on the coffee crop within the context of climate changes and highlights perspectives and research priority needed to advance our understanding on how this crop will respond to the present and ongoing climate changes.

2 Why is the coffee tree a good candidate to benefit from increased levels of atmospheric [CO_2]?

Insights in coffee behavior at elevated [CO_2] has been gained from growth chamber studies by cultivating plants in large pots in Portugal (both *C. arabica* and *C. canephora*) without restrictions to root growth, as well as in field through free-air concentration enrichment (FACE) trials in rain-fed conditions in Brazil (*C. arabica*). As discussed below, these studies have produced newly unequivocal evidence that elevated CO_2 stimulates photosynthesis and crop yield, and therefore we argue that coffee is a highly suitable crop under elevated [CO_2] more than we could expect as compared with the majority of other C3 crop species.

2.1 Coffee photosynthesis is greatly constrained by diffusive factors

The potential photosynthetic capacity (A_{max}, which is assessed under optimal temperature and light conditions at saturating CO_2 and as such in the absence of diffusion-mediated limitations of photosynthesis) of coffee leaves is relatively high (ca. 30 μmol CO_2 m^{-2} s^{-1}) and could be even greater than that of crops such as wheat and spinach (Martins et al. 2014a). However, their actual A is relatively low (typically in the range of 4–11 μmol m^{-2} s^{-1} at saturating light and current atmospheric [CO_2]) when compared with many other tropical tree crops (DaMatta 2004). Given these facts, it is clear that such a low A is due mainly to large limitations to CO_2 diffusion from the atmosphere to the chloroplasts (Batista et al. 2012). This is good agreement with the low values of

g_s and g_m (mesophyll conductance, i.e., the conductance to CO_2 from the intercellular air spaces to the chloroplast carboxylation sites) displayed by the coffee leaves (see below). Such large diffusional limitations to *A* suggest that coffee might benefit from increasing [CO_2] relatively more than other plant species with low diffusional limitations to photosynthesis.

2.2 Both g_s and g_m do not negatively respond to elevated atmospheric [CO_2]

Coffee trees display an inherently low g_s and g_m (Martins et al. 2014a), and this pattern is barely, if at all, affected by the elevated [CO_2] in plants cultivated under unrestricted conditions for root growth (Ramalho et al. 2013; DaMatta et al. 2016). Thus, provided that water supply is adequate, stomatal closure is not expected in coffee in a high-[CO_2] world, which can be translated into an uncompromised transpiration flow for a given vapor pressure deficit (VPD), which in turn could ultimately play a pivotal role in avoiding increases in canopy temperature (as commonly observed in other crops such as soybeans in elevated atmospheric [CO_2]; Long et al. 2004), in addition to allowing the transport of nutrients through the transpiration flow to be held.

More recently, Rakočević et al. (2018) observed higher g_s values in coffee trees grown at elevated [CO_2] than their counterparts grown at normal [CO_2] during the cool, dry season after 4 years of [CO_2] "fertilization" (FACE trials). These authors suggested that photo-assimilates could be driven to the root system rather than to the plant shoots, which would improve water uptake and leaf turgor, thus allowing higher g_s values (and transpiration rates). These findings should also help to avoid increases in canopy temperature, thereby ultimately contributing to a more favorable plant carbon balance under elevated air [CO_2].

2.3 Photosynthesis enhancement is sustained during the long-term exposure to elevated [CO_2]

Plants that are exposed to elevated [CO_2] often exhibit a stimulation of *A*, although they fail in sustaining their increased photosynthetic potential over long periods (known as photosynthetic downregulation or acclimation) (Norby et al. 2010), a fact that has often been associated with photosynthetic end-product accumulation (Ainsworth and Rogers 2007). Such a downregulation has not been observed in coffee both under adequate or supra-optimal temperature conditions (DaMatta et al. 2016; Rodrigues et al. 2016). In fact, in coffee plants cultivated in large pots in growth chambers during 1 year, *A* increased (on a per leaf basis) by 34–49% at elevated (700 $\mu L\ L^{-1}$ air) when compared to normal (380 $\mu L\ L^{-1}$ air) [CO_2] conditions (Ramalho et al. 2013). A similar response was further observed in coffee trees grown under FACE conditions, with increases in *A* above 40% under elevated (550 $\mu L\ L^{-1}$ air) as compared to normal (390 $\mu L\ L^{-1}$ air) [CO_2] after 2 years of CO_2 "fertilization" (Ghini et al. 2015). Under these same FACE conditions, Rakočević et al. (2018) estimated *A* on a whole-tree basis and demonstrated a sustained higher (> 50%) *A* under elevated [CO_2] after 4 years of CO_2 "fertilization." Lack of photosynthetic downregulation was observed not only during the active growing season, but also during the period of the lowest demand for photo-assimilates when acclimation would be expected to be greatest (DaMatta et al. 2016). A higher *A* under elevated [CO_2] was associated not only with improved carboxylation rates coupled with a higher availability of CO_2 as substrate but also with a relatively higher carboxylation over oxygenation activity of RuBisCO, resulting in decreased photorespiration rates (DaMatta et al. 2016). Also importantly, it has been demonstrated that coffee plants grown at elevated [CO_2] displayed an enhanced investment in key components of the photosynthetic apparatus, namely thylakoid electron transport and RuBisCO activity, although these responses were genotype dependent (Ramalho et al. 2013), in sharp contrast with what has been usually observed in other species (Ainsworth and Rogers 2007; Bader et al. 2010). Taken all of the above information together, it is clear that coffee plants do not show any evident sign of photosynthetic downregulation.

2.4 Coffee plants use more light under elevated [CO_2] and are less prone to suffer from oxidative stress

Light is fundamental for plants since it fuels photosynthesis, but high sunlight can limit plant performance often by exacerbating the occurrence of oxidative stress, particularly when multiple environmental constraints are superimposed. Coffee has evolved in shaded environments and its photosynthetic apparatus becomes saturated at relatively low irradiances (DaMatta 2004). Therefore, when the plant is grown in open fields, leaves can absorb more light energy than can be used in photosynthesis, which could increase the probability of formation of highly reactive oxygen species (ROS) and triplet chlorophyll production. Under elevated [CO_2], more light energy is required to saturate photosynthesis (Ramalho et al. 2013; Rakočević et al. 2018), thus a proportional lower energy level will be available to promote cell oxidative conditions; furthermore, the anticipated lower production of ROS (e.g., hydrogen peroxide) via decreases in photorespiration rates under enhanced [CO_2] should also contribute to decrease oxidative stress and, ultimately, promoting a better physiological and agronomic performance under elevated [CO_2] (see below).

2.5 Mineral dynamic modifications under increased air [CO_2]

It has been suggested that nitrogen (N) availability to plants, more than any other environmental factor, determines their responses to elevated [CO_2] (Ellsworth et al. 2004). This has been associated with the fact that enhanced [CO_2] results in decreased N concentration (typically by 13–16% on a per dry weight basis) which in turn has been usually associated with photosynthetic downregulation (Ainsworth and Long 2005). In coffee, Martins et al. (2014b) reported decreases in leaf N of 7.5–16% on a per dry weight basis in two out of three cultivars raised in growth chambers at 700 $\mu L\ L^{-1}$ air. In contrast, in the above-mentioned FACE trials, leaf N decreased by 5.2% on a per dry weight basis at enhanced [CO_2] in one out of two cultivars (Ghini et al. 2015), but no decrease in N was later observed in these same cultivars (DaMatta et al. 2016). Taken together, this information suggests that a decrease in leaf N under elevated [CO_2] may be genotype-dependent in coffee or that it would occur only at even higher [CO_2], as noted at 700 $\mu L\ L^{-1}$ air. In any case, these decreases have not been associated with a photosynthesis downregulation, as mentioned above. Additionally, a survey of other macro- (P, K, Ca, Mg, S) and micro-nutrients (B, Cu, Fe, Mn, Zn) in a study conducted by Martins et al. (2014b) under environmental controlled conditions showed a pattern that was similar to that shown for N under elevated air [CO_2] and adequate temperature, i.e., a moderate "mineral dilution effect" between 7 and 25% (depending on the mineral and genotype). Yet, such "mineral dilution" (as observed on a per leaf dry weight basis) would reflect qualitative physiological changes rather than a nutrient deprivation, as noted by the higher metabolic activity observed in the coffee plants grown at enhanced [CO_2] (Ramalho et al. 2013). Nevertheless, fertilization management should consider these findings in order to allow the coffee crop to benefit from the enhancement of air [CO_2].

2.6 Plant growth and crop yields are enhanced under elevated [CO_2]

Increased coffee growth has been observed in both enclosure (1-year-old plants; unpublished results) and FACE (3-year-old plants; Ghini et al. 2015) experiments under elevated [CO_2]. Here, we show significant higher crop yields for field-grown, unirrigated *C. arabica* cv. Catuaí plants at elevated [CO_2] over their first three harvests (Fig. 1). Interestingly, crop yields obtained in this FACE trial did not increase over time (from the first to the third/fourth harvests) as usually observed under field conditions due to the growth of the coffee trees. We believe that this fact was, to a large extent, a consequence of the harshest drought event that occurred in the last 28 years in south-eastern Brazil. This drought stress occurred over 2014 and it is likely to have affected crop yields not only in 2014 but also in 2015. In any case, the mean increases of crop yield of 28%, as inferred from Fig. 1, are above the mean stimulation of 17% in FACE experiments with a range of species (Ainsworth and Long 2005), thus demonstrating the suitability of the coffee crop in a high-CO_2 environment even in rain-fed cropping systems. Furthermore, elevated [CO_2], as compared with ambient [CO_2], promoted increased leaf retention and longer thermal time for blade expansion (4- to 5-year-old plants under FACE conditions) during the drought season (Rakočević and Matsunaga 2018), which also helps to positively impact crop yields.

3 Why does an enhanced atmospheric [CO_2] improve coffee physiological performance and bean quality under supra-optimal temperatures?

The single effects of elevated temperatures on the physiological performance of the coffee (*C. arabica* and *C. canephora*) crop have been reviewed elsewhere (DaMatta and Ramalho 2006; DaMatta 2018). Earlier studies pointed out that the *C. arabica* plant is considerably sensitive to

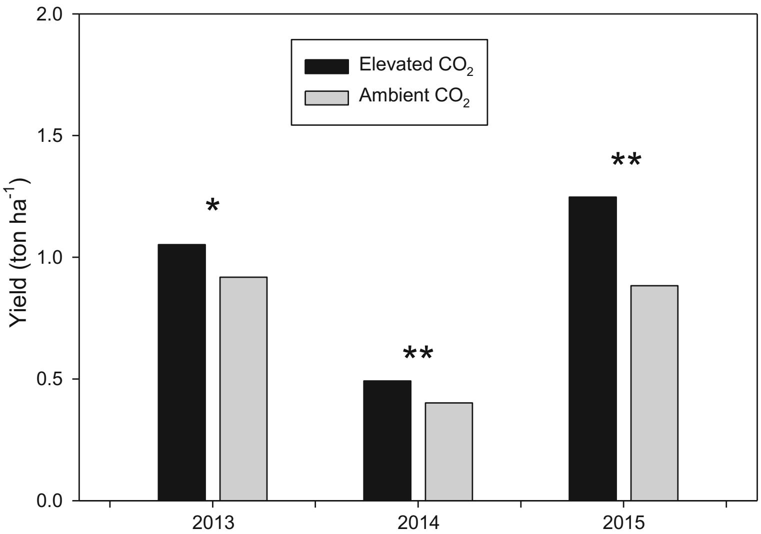

Fig. 1 Effect of elevated (550 μL L^{-1} air) or ambient (390 μL L^{-1} air) [CO_2] on bean yields over three harvests of *Coffea arabica* cv. Catuaí plants grown under FACE conditions in Brazil. See Ghini et al. (2015) for details on growth conditions. The asterisk represents significant difference for the CO_2 effect on crop yields within each harvest (*F* test, $P < 0.05$). $n = 10 \pm$ SE

relatively high air temperatures, as denoted for example by the susceptibility of the photosynthetic apparatus with almost none CO_2 fixation occurring at 34 °C (Nunes et al. 1968). Studies conducted by Drinnan and Menzel (1995) using coffee plants (> 3 years old) grown in relatively small (10 L) pots also agreed with such thermal sensitivity. They found that prolonged exposure to high temperatures of 33/28 °C accelerated leaf loss and induced a general decline in plant health; more floral buds were initiated at 23/18 °C and 18/13 °C (day/night) than at 28/23 °C and no floral initiation occurred at 33/28 °C. However, all of this information was obtained under conditions of restricted root growth, which are known to negatively affect the overall physiology of the coffee plant (Ronchi et al. 2006). In any case, there appears to be no doubts that supra-optimal temperatures impair coffee beverage quality (see DaMatta et al. (2012) for a review).

3.1 Physiological performance

In recent studies, plants from three widely-cropped genotypes from both *C. arabica* and *C. canephora* were grown for 1 year in large pots under conditions of unlimited water supply (at ambient or enhanced [CO_2]) at 25/20 °C (day/night) and then subjected to temperature increases (0.5 °C day^{-1}); evaluations were performed at 25/20 °C, 31/25 °C, 37/30 °C, and 42/34 °C (Martins et al. 2016; Rodrigues et al. 2016). Overall, it was demonstrated that these coffee genotypes performed better at supra-optimal temperatures (at the leaf scale) than previously estimated. In fact, many photosynthetic-related parameters and components, including A, A_{max}, photosystem efficiency, thylakoid electron transport, and the activity of enzymes (RuBisCO) displayed only a small, if any, impact under the exposure up to 37/30 °C, independently of air [CO_2] at which the plants were grown (Rodrigues et al. 2016). Such responses reflect a tolerance to temperatures well above what might be expected considering classical reports of negative impacts on *C. arabica* photosynthesis above 20–25 °C (which are currently considered experimental artifacts), but fully agrees with the field conditions frequently found in coffee tropical cultivation areas (see DaMatta and Ramalho 2006). For higher temperatures (up to 42/37 °C) a damage threshold was clearly reached for all genotypes and most photosynthetic parameters (particularly at the enzyme level, including RuBisCO). However, the plants grown under elevated [CO_2] maintained a higher metabolic/functional photosynthetic activity for all temperature treatments. This was the case of photosystem functioning, which showed a high heat tolerance considering both the physical (energy capture) and photochemical (electron transport) processes (Rodrigues et al. 2016), leading to a much lower photoinhibition status (Martins et al. 2016). It should be also emphasized that, in these studies, no signs of leaf loss or plant degeneracy were noted up to temperatures of 37/30 °C, and floral initiation was apparently uncompromised although most flowers that were produced at high temperature were abnormal ("starlet" flowers) (unpublished data).

The control of oxidative stress has proven to be decisive to stress acclimation in coffee (DaMatta and Ramalho 2006). In fact, protective and antioxidative mechanisms were found in response to supra-optimal temperatures in coffee plants, helping them to support photosynthetic functioning up to 37/30 °C (irrespective of air [CO_2]), but with a higher prevalence of those mechanisms at 42/37 °C in the plants grown under high [CO_2], with some cultivar-dependent responses (Martins et al. 2016). The control of oxidative stress might have been achieved via a reinforcement of several protective mechanisms including antioxidant enzymes (e.g., Cu, Zn-superoxide dismutase, ascorbate peroxidase, glutathione reductase, and catalase), heat shock protein 70 (HSP70), energy dissipation pigments (lutein, carotenes), α-tocopherol, and raffinose family oligosaccharides. This would reflect a cross-talk between several abiotic stress response mechanisms to control reactive oxygen species formation and scavenging in coffee, and was further linked to a significant upregulation of genes related to other protective molecules as early-light induced proteins (*ELIPs*) and chaperonins (*Chape 20* and *Chape 60*) (Martins et al. 2016).

3.2 Coffee bean quality

It is well known that elevated [CO_2] can impair the food quality of several crops (DaMatta et al. 2010). However, in *C. arabica* plants grown in large (80 L) pots under controlled conditions (unlimited water supply), Ramalho et al. (2018) observed that elevated [CO_2] per se did not promote noticeable changes in bean quality traits. Most importantly, enhanced [CO_2] remarkably altered the heat promoted patterns of variation on most physical and chemical bean traits in a way that would not be expected from the single effects of heat or [CO_2]. Among the observed impacts in fruits exposed to high temperature (30–40 °C) in their final stages of maturation, elevated air [CO_2] increased acidity but decreased 5-caffeoylquinic acid (CQA) and caffeine, which all can be associated with an improved bean quality (Bertrand et al. 2012). Additionally, elevated [CO_2] canceled (soluble solids, total CQAs, caffeic acid), attenuated (4-CQA, trigonelline), or reversed (*p*-coumaric acid) the biochemical modifications driven by heat (Ramalho et al. 2018). Given these facts, it is tempting to suggest that enhanced [CO_2] can have the potential to modify and mitigate the heat impact on bean quality traits, that is, to keep bean composition, and concomitantly its quality, closer to the actual standards. In addition, the faster fruit development due to elevated temperature results in malformed beans with poorer cup quality (Vaast et al. 2005; Läderach et al. 2017), which is at least in part a consequence of excessive demand for resources from the seed endosperm in a compressed timeframe. This negative effect is likely to be, at least in part, offset by the increased photo-assimilate availability due to an improved *A* in a high-[CO_2] environment, reinforcing the positive role of enhanced [CO_2] on coffee bean quality.

The impacts of supra-optimal temperatures on coffee bean quality traits reported by Ramalho et al. (2018) were lower than what are commonly observed in the field. Nevertheless, prevalence of high temperatures in the field often coincides with decreased water availability and high atmospheric VPD (compared to the controlled conditions in the study of Ramalho et al. (2018)). Given that water supply per se might affect coffee bean quality (Vinecky et al. 2017), it is anticipated that a negative interaction between water supply and temperature could occur under field conditions, which would ultimately exacerbate impairments on coffee bean and beverage quality.

4 Predictions on the future of the coffee crop based on rising temperatures and the mitigating role of CO_2

Coffee production systems will have to be adapted to (i) mean rising temperatures and shifts in mean precipitation rates and patterns, (ii) extreme events (e.g., heat waves and precipitation) and on a more short-term horizon increased climate variability overall.

Optimal mean annual temperature for *C. arabica* has been traditionally assumed to range from 18 to 23 °C (DaMatta and Ramalho 2006). Until 20–30 years ago, unsuccessful growth and production of *C. arabica* was thought to be the rule above 23 °C. Notably, however, *C. arabica* cultivars selected under intensive management conditions have spread to and performed well in areas that were previously considered to be inadequate because of average mean annual temperatures as high as 24–25 °C (DaMatta 2018). Furthermore, empirical observation from the field suggests that there is some genetic variability in terms of tolerance to relatively elevated temperature, particularly some *C. arabica* cultivars that were introgressed with *C. canephora* (DaMatta 2018).

Previous predictions of the impact of climate change on coffee production have proved suitable for characterizing broad agro-ecological zones (Bunn et al., 2015b) and generating first hypotheses on suitable climatic conditions for coffee (Magrach and Ghazoul 2015; Ovalle-Rivera et al. 2015). These predictions were based on currently cultivated coffee systems using species distribution models. Therefore, they are constrained by the available observation data of where coffee is currently grown. Furthermore, they did not take elevated [CO_2] or adaptation options such as improved coffee genotypes or shade management into account. However, recent research has substantially improved our understanding on these aspects, enabling the use of process-based models (e.g., Rahn et al. 2018b) to update the estimate of likely climate change impacts.

Rahn et al. (2018a) adapted a mechanistic model that processes spatially-explicit soil and climate data and applied it to two African sites (Uganda and Tanzania). These authors showed that elevated [CO_2] could potentially mitigate the negative impact of rising temperatures and drought stress depending on site conditions; they also showed that elevated [CO_2] should increase coffee crop yields particularly at higher altitudes. Similar conclusions were also reported by Verhage et al. (2017); based on five global climate models, these authors found that elevated [CO_2] might fully offset the negative effects of increased temperatures and water deficit by 2050 assuming growing locations and irrigation use remain the same for the actual Brazilian coffee-producing areas. Taken together, these studies suggest lower negative impact of climate change than previously expected, although it should be noted that extreme events are not yet well represented when using downscaled global climate model data, suggesting that further improvement could be achieved in future studies, for example, by following Hazeleger et al. (2015). Furthermore, while the physiological response to elevated [CO_2], temperature and drought stress has received some research attention, responses of reproductive processes (e.g., floral bud initiation, flowering success), as well as pest and diseases and coffee quality to climate change have received insufficient consideration so far. It is likely that the positive effects of enhanced [CO_2] could be more evident in intensive farming systems (i.e., adequate fertilization, pruning and pest and disease control or including irrigation). Hence, sustainable intensification of low input smallholder farmers will be required for them to benefit from the CO_2 fertilization effect. Thus, this is an important part of climate change adaptation next to the selection of appropriate coffee genotypes and shade tree management for advantageous microclimates (Craparo et al. 2017; Rahn et al. 2018b).

5 Concluding remarks

We here emphasize the role of CO_2 as a key player for mitigating some of the harmful effects of supra-optimal temperatures. Unpublished results (R.T. Ávila and F.M. DaMatta) also suggest that elevated [CO_2] may allow a better endurance of coffee plants against drought stress. Therefore, to provide accurate estimates regarding the success of coffee farming under future climate change scenarios, [CO_2] must be taken into account.

Nevertheless, several crucial questions, in terms of the responses of the coffee crop to climate change, remain to be fully elucidated and are, therefore, priority needs for future research. For example, increased temperature could alter the plant-pest/diseases equilibrium, but how an elevated [CO_2] might affect this equilibrium is fully unknown. There is no information on the real, scientific-based impact of elevated temperatures, and their interaction with [CO_2], on key crop aspects such as abnormal flower formation, fruit development and cup quality under plantation conditions. It is also unknown how an increase of VPD (which is expected to become increasingly important particularly in warmer and drier regions) may affect coffee growth and yields, and how this might be mitigated by the elevated [CO_2]. Finally, while elevated [CO_2] could mitigate negative effects of rising mean temperatures on coffee productivity, the predicted increases in extreme rainfall, drought and overall climate variability bring large uncertainties on how all of these environmental factors will ultimately affect the coffee yields and quality. Notably, some information suggests that there is intraspecific variability in terms of tolerance (e.g., photosynthetic performance) to both elevated temperatures and drought, while varying genotypic responses to elevated [CO_2] appear also to exist (Martins et al. 2016; Rodrigues et al. 2016). Therefore, future research should also be directed toward selecting promising genotypes for a changing global climate.

The overall information presented in this review could point toward a more optimistic scenario than the previous catastrophic estimates of the impact of climate change on coffee production. Nevertheless, a strong and continuous engagement to research efforts will be decisive to agriculture in the years to come, since in-depth scientific knowledge will be crucial to ensure an improved sustainability of the entire coffee-value-chain in a changing climate. These challenges certainly constitute difficult and daunting tasks and will require unparalleled transdisciplinary research teams with collaborative research to integrate insights gained at different scales (plant, plot, regional scale) in distinct environmental contexts with different cultivars and management conditions. After all, proper knowledge regarding the impact of CO_2, and its interaction with other environmental factors, on growth, production and cup quality will remain a key to understand the performance of the coffee crop in a changing world.

Acknowledgments This work was supported by European Union, Program Horizon 2020, call H2020-SFS-2016-2, action RIA, project BreedCAFS, proposal 727934, as well as through Portuguese national funds from Fundação para a Ciência e a Tecnologia through the research units UID/AGR/04129/2013 (LEAF) and UID/GEO/04035/2013 (GeoBioTec), and through the project PTDC/ASP-AGR/31257/2017. This work was also implemented as part of the CGIAR Research Program on Climate Change, Agriculture and Food Security (CCAFS), which is carried out with support from the CGIAR Trust Fund and through bilateral funding agreements. For details please visit https://ccafs.cgiar.org/donors. The views expressed in this document cannot be taken to reflect the official opinions of these organizations. Research fellowships from the National Council for Scientific and Technological Development (CNPq, Brazil) that were granted to FMD are also acknowledged.

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