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Physiological and Agronomic Performance of the Coffee Crop in the Context of Climate Change and Global Warming: A Review

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ABSTRACT: Coffee is one of the most important global crops and provides a livelihood to millions of people living in developing countries. Coffee species have been described as being highly sensitive to climate change, as largely deduced from modeling studies based on predictions of rising temperatures and changing rainfall patterns. Here, we discuss the physiological responses of the coffee tree in the context of present and ongoing climate changes, including drought, heat, and light stresses, and interactions between these factors. We also summarize recent insights on the physiological and agronomic performance of coffee at elevated atmospheric CO_2 concentrations and highlight the key role of CO_2 in mitigating the harmful effects of heat stress. Evidence is shown suggesting that warming, per se, may be less harmful to coffee suitability than previously estimated, at least under the conditions of an adequate water supply. Finally, we discuss several mitigation strategies to improve crop performance in a changing world.

KEYWORDS: *Coffea spp., coffee, crop yield, drought, elevated [CO_2], global warming, heat, light stress, photosynthesis*

■ INTRODUCTION

The atmospheric CO_2 concentration (C_a) has increased by approximately 50% since preindustrial times to values currently exceeding 400 ppm. Over the same period, the global mean surface temperature has increased by 0.85 °C. By the end of this century, C_a is predicted to rise to values as high as ∼1000 ppm in parallel with temperature increases of up to 4.8 °C.[1,2] These climate changes are also predicted to be accompanied by shifts in the frequency and severity of extreme events including increasing heat waves, floods, and prolonged drought episodes. Therefore, plants are expected to face abiotic stresses to a greater extent than in the environments in which they naturally evolved.[2] These stressful conditions represent significant challenges for the sustainability of agricultural production on a global scale, quantitatively and qualitatively impacting harvestable crops within their current production areas.[3]

Coffee, a C3 woody species, is one of the most important global crops and provides a livelihood to millions of people living in developing countries. Coffee is a highly popular beverage that is consumed by about one-third of the world's population. From among the 125 species of the *Coffea* genus,[4] only two of them, *C. arabica* L. (Arabica coffee) and *C. canephora* Pierre ex A. Froehner (Robusta coffee), are economically important, accounting for approximately 99% of global production. In the last few decades world coffee bean yields have been increased steadily, and presently they are approximately nine million tons,[5] with an estimated income close to U.S. $173.000 million for the entire coffee value chain.[6]

The natural habitat of virtually all *Coffea* species is the understorey of African tropical forests.[7] The natural populations of *C. arabica* are restricted to the highland forests of Ethiopia at altitudes of 1600−2800 m above sea level. In this region, the air temperature fluctuates minimally between seasons, averaging approximately 20 °C. Rainfall is well distributed, varying from 1600 to more than 2000 mm annually, with a dry season of three to four months coinciding with the coolest months[8] when vegetative growth is restrained. On the other hand, *C. canephora* is native to the lowland forests of the Congo River basin, which extend to Lake Victoria in Uganda. The altitude of this region varies from sea level up to 1200 m in Uganda with average temperatures between 24 and 26 °C without wide oscillations; rainfall, above 2000 mm, is abundantly distributed throughout a 9−10 month period.[9] Taken together, these observations largely explain why the optimum mean annual temperature range for *C. arabica* (18−23 °C) is lower than that for *C. canephora* (22−26 °C) under plantation conditions. Importantly, *C. arabica* trees are generally less vigorous and productive with higher production costs than *C. canephora*, while the former generally yields a higher-quality beverage and dominates the high-quality specialty coffee market.[10,11]

The production of the coffee crop is confined to the intertropical zone, which extends from a latitude of 20−25° N in Hawaii to 24° S in Brazil. Within this zone, rainfall quantity

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and distribution, temperature, sunshine, and CO_2 and the interactions between these conditions are key environmental factors affecting coffee growth and production. Notably, drought is the major environmental stress affecting coffee production in most coffee growing areas, as illustrated by marked decreases in yield, as much as 80% in very dry years, in some marginal regions with no irrigation.[10] Indeed, global coffee yields and their sustainability are believed to be potentially threatened by present and ongoing climatic changes,[11] and therefore coffee species have been described as being highly sensitive to climate changes.[12,13] Given that the two commercial coffee species have evolved in shaded habitats, it is believed that the harmful consequences of these climate changes will be exacerbated by high levels of irradiance.[14] Regardless, recent modeling studies, based largely on projections of increasing temperatures and changing rainfall patterns, have predicted marked consequences on the coffee crop, including changes in the areas suitable for cultivation,[15−20] reductions of bean yields,[12,15,19,21] and impacts on natural biodiversity coupled with the extinction of wild populations of *C. arabica*.[13] Taken together, these factors are expected to result in major environmental, economic, and social problems in the main areas where coffee is currently grown.[22] Nevertheless, the anticipated negative effects of climate change on the coffee crop could be, to some extent, mitigated by elevated C_a. Elevated C_a is associated with enhanced photosynthetic capacity,[23−26] metabolism, and antioxidant protection[27] coupled with changes in gene transcription and the maintenance of mineral balance.[27,28]

In this review, we discuss the physiological responses of the coffee tree in the context of present and ongoing climate changes including drought, heat, and light stresses and some of the interactions between these factors. We also summarize recent insights on the physiological and agronomic performance of coffee at elevated C_a and highlight the role of CO_2 as a key player for mitigating the adverse effects of heat stress. Evidence is shown suggesting that the effects of warming on coffee suitability may be less harmful than previously estimated. Finally, we discuss several mitigation strategies that are expected to improve crop performance in a climate change scenario.

Drought Stress. Although coffee production is strongly affected by drought events, a significant portion of the world's coffee has been cultivated in drought-prone regions where the use of irrigation is the exception.[29] Where irrigation is used to guarantee adequate crop yields, coffee growers in some regions have faced serious problems in the availability of water for irrigation, a situation that is expected to be aggravated due to (i) predicted increases in the frequency and severity of drought episodes and (ii) increased temperatures which in turn are expected to augment the air evaporative demand and thus affect soil water availability.[14] Therefore, the selection of drought-tolerant coffee cultivars that can withstand severe drought spells and produce acceptable yields under conditions of water scarcity is of utmost importance.[30]

The native home of *C. arabica*, and particularly that of *C. canephora*, are characterized by relatively low water deficit conditions.[7,31] However, virtually all modern cultivars are descendants of early introductions of coffee from Ethiopia to Arabia (Yemen), where they were subjected to a relatively dry, unshaded ecosystem for a thousand years before being introduced to Asia and Latin America.[32] Most of these cultivars can tolerate mild drought and full sunlight, suggesting that modern cultivars are significantly different from their wild relatives in terms of drought tolerance. Indeed, some coffee cultivars display moderate tolerance to hydraulic dysfunction,[14] and plant death is predicted to occur at a water potential (Ψ_w, a key water relation parameter that describes the energy state of water; low Ψ_w, is associated with a greater extent of plant dehydration) as low as −7 to −8 MPa.[33] For additional information on water relations and other responses of the coffee crop to drought stress, the reader is referred to comprehensive reviews by DaMatta[14] and DaMatta and Ramalho.[29]

There is marked variability in drought tolerance among *C. arabica* and particularly *C. canephora* genotypes.[34−36] Nonetheless, to the best of our knowledge, the most drought tolerant genotypes of *C. canephora* endure prolonged drought spells better than their *C. arabica* counterparts, as empirically observed under plantation conditions. From an ecophysiological perspective, drought tolerant coffee cultivars are able to sustain better water status than their drought-sensitive counterparts during long-term drought spells, which has been ascribed to a combination of deep rooting and adequate stomatal control of transpiration.[37,38] The ability to cope with oxidative stress (a complex chemical and physiological phenomenon that accompanies virtually all types of stresses in higher plants and develops as a consequence of the overproduction and accumulation of reactive oxygen species, ROS) also seems to explain some of the differences in drought tolerance among coffee cultivars.[39,40] Ultimately, these traits facilitate leaf area maintenance, which is supposed to save resources that would otherwise be diverted toward the restoration of leaf area upon the resumption of watering.[37] Regarding drought tolerance indicators, recent results by Menezes-Silva et al.[34] with *C. canephora* clones suggest a promising role for wood density in selecting drought-tolerant coffee genotypes. However, attention must be paid to the trade-off between drought tolerance and hydraulic efficiency, as genotypes that successfully thrive under low water supply may have compromised fitness under ample irrigation.

Drought stress stimulates earlier leaf senescence, particularly in physiologically older leaves,[10] which may represent a much more direct consequence of hydraulic failure.[35,37] Even so, decreases in total leaf area are not necessarily accompanied by decreases in the net photosynthetic rate per unit leaf area (A), but strong decreases in A are observed as drought progresses further, as has been found in *C. arabica*.[41] These decreases are strongly associated with stomatal factors, as coffee stomata are quite sensitive to both soil water availability and air evaporative demand.[42] In fact, stomatal conductance (g_s) decreases curvilinearly with decreasing leaf Ψ_w, with no apparent threshold value of Ψ_w triggering stomatal closure.[38,43] With regard to the air evaporative demand, we have found in seven coffee cultivars that under well-watered conditions and constant temperature, g_s decreased by 60% (with a mean decrease in A of 40%) as the leaf-to-air vapor pressure deficit (VPD) sharply increased from 1.0 to 3.0 kPa (unpublished results). Given that the VPD increases with increasing temperature, caution should be exercised in separating the effects of VPD per se from the effects of elevated temperatures (see below) on photosynthetic gas exchange.

Drought effects are often believed to be intensified under full sunlight conditions. The rationale is that drought-induced stomatal closure decreases the availability of CO_2 to ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO) and, given that CO_2 reduction is the main sink for photochemical energy, this ultimately causes an excess of energy within chloroplasts.[25,44] Inasmuch as drought spells are often accompanied by high irradiance, a proportionally greater energy level will be available to produce high levels of ROS, which can potentially increase oxidative stress and impair the plant's physiological and agronomic performance. Nevertheless, Cavatte et al.[45] reported that the effects of light and water supply on the growth of young coffee plants are independent; the combination of drought and shade did not alter the negative effects caused by drought stress on several photosynthetic traits. Therefore, in contrast to what has been previously suggested,[46] shading may not significantly alleviate the impacts of drought on young coffee plants, unless they are grown in areas with a combination of drought and elevated temperatures.

Drought stress impairs coffee plants at all phases of their growth cycle, but these impairments are much more pronounced during the bean-filling phase. In this phase, there is a strong carbon imbalance between photoassimilate production (due to overall decreases in *A* and total leaf area) and photoassimilate requirements (because fruits are the strongest and highest priority sinks for coffee assimilates).[29] As a rule, drought-induced impairments are exacerbated as the fruit burden increases. Empirical observations from the field suggest that these responses are more pronounced in early maturing cultivars, probably because these cultivars require photoassimilates in a compressed time frame. Therefore, the exhaustion of tree reserves is aggravated in heavily bearing trees suffering from drought stress, a condition that is further aggravated under the elevated temperatures that usually accompany drought spells. As a consequence, extensive defoliation, branch death, and malformed fruits are usually observed under drought with negative consequences on cup quality. Under these conditions, shading can minimize these negative consequences, especially by decreasing fruit loads and improving the microclimate within the coffee canopy,[47−49] ultimately avoiding tree degeneracy (see below).

Light Stress. Although light is a fundamental environmental resource that drives photosynthesis and ultimately influences plant growth, both low and high sunlight can limit plant performance. Despite being considered to be a shade-dwelling species, commercial coffee species have been cultivated worldwide under varying light regimes, ranging from full sunlight (as in Brazil) to relatively deep shade (as in some parts of Central America where *C. arabica* is grown). Coffee has a marked phenotypic plasticity to cope with light availability at both the leaf and whole-plant levels.[44,50] For example, as irradiance was reduced by 60% under the crowns of shade trees, coffee light-use efficiency increased by 50%, leaving net primary productivity fairly stable across all shade levels.[50] In any case, coffee cultivated under full sunlight often outyields shaded coffee in suitable environments under intensive management conditions.[51] This is likely because elite coffee cultivars have been selected in test trials with high external inputs, under full sunlight, as in Brazil. Therefore, shading has been abandoned as a regular cultural practice (or its extent has been markedly decreased) in several regions worldwide.[14,46] Increased bean yields with increased light availability are often accounted for by (i) higher whole-tree carbon assimilation; (ii) greater stimulation of flower bud development; and (iii) more flower buds at existing nodes, and more nodes formed per branch.[46] Increased production under open conditions, however, may be accompanied by extensive defoliation, branch die-back (death of twigs starting from the apex and progressing downward) and root death,[12,52] especially when heat and drought stresses are superimposed. These disorders may accentuate the biennial production cycle, as coffee trees usually require two (sometimes three) years to recover, while also contributing to a reduction in the commercial lifespan of trees.[14]

An excess of light energy in the photosynthetic apparatus can occur when the fraction of energy used for photosynthesis is decreased (e.g., under drought conditions), while the absorbed energy remains unchanged (or even increases). However, in many cases an excess of energy is related to high sunlight, which can limit plant performance, largely by exacerbating oxidative stress. The combination of low *A* in coffee leaves with high irradiance levels frequently results in linear electron fluxes several times greater than those required for the observed *A*.[53] Nonetheless, photoinhibition and photodamage are not commonly observed when coffee plants are grown in suitable climate conditions, even in leaves that are highly exposed to direct solar radiation.[54−56] Indeed, coffee leaves fully exposed to sunlight are well protected against oxidative stress by a range of energy-dissipating pathways[45,49,56] (e.g., pigments, pseudocyclic electron transport, and photorespiration), by increases in the activities of antioxidant enzymes (e.g., Cu, Zn-superoxide dismutase, ascorbate peroxidase, glutathione reductase, and catalase) together with the complementary action of non-enzymatic molecules, such as hydrophilic (e.g., ascorbate and glutathione), lipophilic (e.g., zeaxanthin, β-carotene, and α-tocopherol), and phenolic compounds (e.g., caffeoylquinic acids).[27] In general, these protective mechanisms can be triggered quickly, in a matter of minutes to days, with leaf acclimation observed a few days after the transfer from shade to full sun, although this process is dependent on an adequate availability of nitrogen.[57−59] Nevertheless, when the plant is grown at full light exposure in conjunction with other stresses (e.g., heat waves), excess energy could arise to the point of causing leaf overheating (by as much as 15−20 °C above air temperature). Overheating may occur more readily on sunny days during dry spells, when there is a minimal stomata aperture and negligible evaporative cooling. In these conditions, leaf chlorosis and burning due to chlorophyll photobleaching and extensive damage to the photosynthetic apparatus are often observed,[14] leading to extensive leaf shedding.[57] Fruits can also be burnt, with negative consequences on cup quality. These conditions lead to tree degeneracy and strongly reduce tree lifespan.[46] In marginal areas (warm and dry conditions), successful cultivation of coffee without shading has proven to be unfeasible.

Heat Stress. Early information obtained in a number of studies conducted from 1950 to the 1970s suggested that coffee photosynthesis is highly sensitive to temperatures above 20−25 °C[29] with almost none occurring at 34 °C.[60] This observation may largely be explained by the failure to examine the effects of high temperature in isolation, thus allowing other limiting conditions such as high VPD to be superimposed. In fact, increasing evidence suggests that the coffee plant is able to increase its *A* up to temperatures of 30−35 °C if g_s is held in check in response to the increasing VPD.[46] More recently, by exposing coffee plants to a gradual temperature increase, significant thermal tolerance has been found at temperatures as high as 37/30 °C (day/night),[26,27] in good agreement with field conditions that frequently occur in several coffee cultivation areas.[29] Such tolerance was conferred by resilience of the photosynthetic machinery, i.e., maintenance of the performance/integrity of the photosystems, chloroplast electron transport and enzyme activity (*e.g.*, RuBisCO), in both *C. arabica* and *C. canephora*[26] genotypes.

In the event of global warming, *C. canephora* will have a relative advantage over *C. arabica* because the former grows and produces well in warmer regions, where the cultivation of *C. arabica* trees has proven to be unsuccessful.[11] This has been explained by the observation that the optimum mean annual temperature range for *C. arabica* is lower than that for *C. canephora* (see Introduction). In any case, until recently, the growth and production of *C. arabica* were thought to be unfeasible above 23 °C. Nevertheless, some *C. arabica* cultivars (especially those with some degree of introgression with *C. canephora*) selected under intensive management conditions have spread to and performed well in areas that were previously considered to be inadequate due to their average temperatures of up to 24−25 °C.[29] Even so, coffee growth is reduced in warmer climates, while the development and ripening of berry pulp are accelerated, often impairing beverage quality due to incomplete bean filling.[13,61] Also importantly, supra-optimal temperatures can reduce the accumulation of sucrose in the beans and modify the levels of several compounds that are known to contribute to taste, flavor, and aroma after roasting.[62−65] Additionally, relatively high temperatures during blossoming, especially during a prolonged dry season, may often cause abnormal flower development ("starlet flowers"),[11] whereas short, sudden simulated heat waves (49 °C for 45 or 90 min) completely inhibit flowering.[66] The consequences of these treatments, as analyzed via measurements of gas-exchange and photosystem II functionality, were intensified by full sunlight, and the recovery of photosynthesis after heat stress was faster in mature leaves than in their expanding counterparts.[66] Notably, mature leaves, but not expanding ones, have been shown to acclimate to sharp transitions from low to high light via reinforcement of their protective systems,[58,59,67] which may partially explain why mature leaves are better able to cope with heat stress at full sunlight.[66] Indeed, *Coffea* spp. plants have been observed to rely on antioxidative/protective mechanisms to successfully cope with environmental limitations, which is a common response to several environmental stresses, including nitrogen starvation, high irradiance, cold, and drought.[40,45,58,68−71]

Protective and antioxidative mechanisms have been shown to be generally up-regulated in *Coffea* spp. in response to supra-optimal temperatures (up to 37 °C), but not at 42 °C, when a strong deleterious impact has been observed.[27] The response at 37 °C is largely supported by increased activities of a range of antioxidant enzymes (ascorbate peroxidase, glutathione reductase and catalase), lutein, α-carotene, β-carotene, α-tocopherol, and raffinose, and heat shock protein 70 (*HSP70*) but not zeaxanthin or ascorbate. Additionally, increased temperatures promote a concomitant up-regulation of genes encoding protective proteins (*HSP70*, *Chape 20* and *60*, *ELIP*) and antioxidant enzymes.[27] These mechanisms act in concert to control the formation and scavenging of ROS and constitute a common line of defense against heat in *Coffea* spp. Moreover, higher expression of genes associated with protective molecules has been reported in *C. canephora* at the highest temperature studied (42/34 °C), in agreement with its better tolerance of high temperatures.[27]

It has also reported that *C. arabica* and *C. canephora* genotypes display maximal leaf mineral contents when grown at 37/30 °C, or even higher at 42/34 °C, relative to plants grown at 25/20 °C.[28] This reflects relevant mineral dynamics, with implications for coffee thermotolerance related to the specific roles of minerals in cell metabolism. As stated above, coffee acclimation to environmental stresses is strongly related to the triggering of antioxidative mechanisms. However, the reinforcement of these mechanisms greatly depends on N,[58,59] Cu, Zn, Fe, and Mn[71] availability at the leaf level, with Mn having an additional important role in photosystem II performance. In fact, oxidative damage may be aggravated by mineral deficiencies.[72] In summary, despite the countless gaps that still exist in our comprehension on how heat stress impacts coffee physiology, it is suggested that the coffee plant can cope with supra-optimal temperatures to some extent. With regard to coffee's mineral dynamics, attention should be paid to fertilization management under future global warming and enhanced C_a conditions (see also below).

Elevated C_a Improves Gas Exchange and Crop Yield. As summarized in Table 1, most information suggests that elevated C_a positively impacts the photosynthetic performance of coffee leaves with at most minor effects on g_s and related traits. For example, stomatal size and density, which are key determinants of maximum g_s, do not apparently respond to elevated C_a (700 ppm in enclosure studies[25] or 1000 ppm in somatic embryogenesis-derived coffee plantlets[73]). This observation supports findings that g_s responds little, if at all, to

Table 1. Trait Responses to Elevated C_a (550 ppm,[18,19] 700 ppm,[20−23] or 1000 ppm[62]) Relative to Ambient C_a (385 ppm on Average)[a]

traits	response to rising CO_2
SI	unresponsive[20,21]
SD	unresponsive[20,21]
SS	unresponsive[20,21]
g_s	unresponsive[18−21,62]
g_m	unresponsive[18]
A	↑ 34−74%[18−21]
iWUE	↑ 56−112%[18,20]
C_c	↑ 50%[18]
R_d	unresponsive[20]
R_p/A_{gross}	↓ 20%[28]
A_{max}	unresponsive[20]
$V_{c,max}$	unresponsive[18]
J_{max}	unresponsive[18]
TSS	unresponsive[18]
NSC	unresponsive[20]
starch	↓ 25% − ↑ 69%[18−23]
RuBisCO	↑ 36−46%[20,21]
Ru5KP	↑ 35−63%[20,21]
chlorophyll	unresponsive[18,20]
carotenoid	unresponsive[20,21]
N	↓ 16−0%[18,19,23]
P	unresponsive[18,19,23]

[a] Stomatal index (SI), stomatal density (SD), stomatal size (SS), stomatal conductance (g_s), mesophyll conductance (g_m), net photosynthetic rate (A), intrinsic water use efficiency (iWUE), chloroplastic CO_2 concentration (C_c), dark respiration (R_d), photorespiration-to-gross photosynthesis ratio (R_p/A_{gross}), maximum net photosynthetic rate (A_{max}), maximum carboxylation capacity on a chloroplastic CO_2 concentration basis (V_{cmax}), maximum electron transport (J_{max}), total soluble sugar (TSS), non-structural carbohydrate (NSC), ribulse-1,5-bisphosphate carboxylase/oxygenase (RuBisCO), ribulose-1,5-bisphosphate kinase (Ru5KP), nitrogen (N), and phosphorus (P).

elevated C_a in coffee,[23,25,73] in sharp contrast to what has been observed elsewhere.[74] To the best of our knowledge, there is only one study (in coffee) reporting decreases in g_s at elevated C_a;[75] however, this response appears to be an experimental artifact associated with restricted root development[76] due to the extremely small containers (0.6 L) where the plants were grown.[75] Given that g_s does not respond to C_a, evaporative cooling is expected to be maintained, and ultimately changes in leaf temperature are not expected to occur in coffee, in contrast to what occurs in the majority of plant species (see Figure 1).

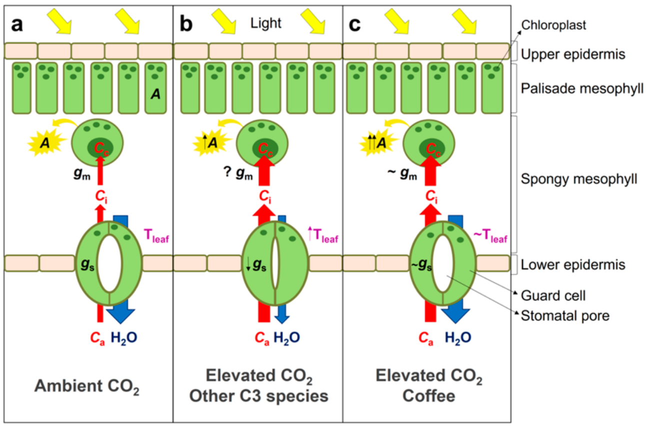

Figure 1. (a−c) Schematic diagram of CO_2 and H_2O diffusion pathways along the mesophyll of a leaf cross-section from a typical C3 plant. (a) CO_2 diffuses from the atmosphere (C_a) through the stomatal pore into the intercellular air space of the mesophyll (C_i), and then toward the site of RuBisCO carboxylation in chloroplasts (C_c), where CO_2 is used for photosynthesis in the presence of light. The main determinants of CO_2 diffusion are the leaf-to-air CO_2 concentration gradient and the resistance along the diffusional pathway, which are governed by conductance at the stomatal (g_s) and mesophyll (g_m) levels. Ultimately, high C_a, g_s, and g_m lead to higher photosynthetic rates (A). (b) Higher C_a induces stomatal closure in the majority of plant species, while its effect on g_m remains unclear. However, the elevated C_a compensates for the resistance offered by the reduced stomatal aperture and, as a consequence, A increases. Further, the low g_s leads to reduced evaporative cooling, thus resulting in higher leaf temperature (T_{leaf}). (c) Compared to other C3 plants, in coffee species both g_s and g_m remain mostly unchanged under elevated C_a (preventing increases in T_{leaf}), which together with the higher leaf-to-air CO_2 concentration gradient result in even higher A. This explains why coffee species may benefit from increases in C_a. Arrow thickness is proportional to relative diffusion rates.

The mesophyll conductance (g_m), i.e., the conductance of CO_2 from intercellular air spaces to the sites of carboxylation in chloroplasts, has also been shown to be invariant in response to C_a.[23]

Coffee plants grown at full sunlight and the current C_a display relatively low A (typically in the range of 4−11 μmol m^{-2} s^{-1}) when compared with many other tropical tree crops.[46] The reasons for such low A have been mostly attributed to high diffusive (low g_s and g_m) and hydraulic resistances, with minor biochemical limitation of photosynthesis.[23,53] In addition, a high stomatal sensitivity to VPD leads to a substantial stomatal closure from midday onward in tropical conditions. Given these enhanced diffusive limitations, it is not surprising that coffee's RuBisCO has been characterized as efficient and well-tuned for operating at a low chloroplastic CO_2 concentration, C_c (due to its high specificity factor, high affinity for CO_2 and a relatively high carboxylase turnover rate).[53,77] In contrast, these kinetic RuBisCO adaptations to low C_c reduce the revenue stream in response to elevated C_a, as the A of coffee leaves is expected to be limited by ribulose-1,5-bisphosphate (RuBP) regeneration (assuming it remains unchanged at high C_a) at relatively low C_c.[53]Therefore, we expect diminishing returns in A in coffee as C_a increases unless g_s and g_m are downregulated in response to high C_a; in such a scenario of high C_a and low g_s and g_m, coffee's RuBisCO would again become advantageous.

Elevated C_a has positive effects on A in coffee. In plants grown in large pots in growth chambers for one year, A was higher (34−49%) at elevated (700 ppm) than at normal (380 ppm) C_a.[25] Similarly, A was at least 40% higher under elevated (550 ppm) than under normal (390 ppm) C_a after two years of CO_2 "fertilization" in a free-air CO_2 enrichment (FACE) system.[24] These effects of CO_2 on A were associated not only with improved carboxylation rates coupled with a higher availability of CO_2 but also with a higher carboxylation activity of RuBisCO relative to oxygenation, leading to decreased photorespiration rates.[23] More recently, under these same FACE conditions described above, Rakocevic et al.[78] estimated A on a whole-tree basis and demonstrated a sustained increase in (>50%) A under elevated C_a after four years of CO_2 fertilization. This information suggests a lack of photosynthetic down-regulation (i.e., failure to sustain enhanced A through long-term CO_2 fertilization), in contrast with what has been observed in a range of plant species.[79] Other compelling evidence reinforces the observed lack of photosynthetic down-regulation in coffee under elevated C_a: (i) lack of significant differences in the A values of plants grown at ambient or elevated C_a when measurements were performed at ambient or elevated C_a;[24,25] (ii) A_{max} (assessed under saturating CO_2 in the absence of diffusion-mediated limitation of photosynthesis) was unresponsive to elevated C_a;[25] (iii) enhanced investment in key components of the photosynthetic machinery including thylakoid electron transport and RuBisCO activity, although these responses were genotype dependent;[25] (iv) sustained maximum carboxylation velocity of RuBisCO while the demand for photoassimilates is lowest (negligible growth and maximum starch levels), when down-regulation would be expected to be the greatest.[23] Furthermore, the lack of photosynthetic down-regulation under elevated C_a has been demonstrated to be independent of temperature in coffee.[26]

Martins et al.[28] reported that elevated C_a (700 ppm) promoted a moderate leaf "mineral dilution effect" in plants grown at 25/20 °C, ranging from 7 to 25% depending on the mineral and genotype. This was the case for N, Mg, Ca, Fe in *C. canephora*, or N, K and Fe in *C. arabica* cv. Icatu, whereas *C. arabica* cv. IPR 108 did not show any significant modification (except for Fe). Despite these dilution effects, plants grown at elevated C_a showed a significantly higher metabolic activity,[71] and therefore this dilution likely reflects qualitative physiological changes rather than nutrient deprivation.[80] In the above-mentioned FACE trial, leaf N was decreased by 5.2% at elevated C_a (550 ppm) in one of two cultivars,[24] but no decrease in N was subsequently observed in these same cultivars.[23] Taken together, this information suggests that a decrease in leaf N under enhanced C_a may be genotype-dependent in coffee or it may occur only at even higher C_a, such as 700 ppm.[23,25]

The maintenance of A during long-term C_a elevation, coupled with the unresponsiveness of both g_s and g_m (Table 1) and the maintenance of adequate mineral balance, seem to be key factors explaining the stimulation of crop yields (28% on average, based on three harvests) under FACE conditions (unpublished results). This increase (rainfed conditions) is above the mean stimulation of 17% in FACE experiments with a range of species.[81] These findings highlight the suitability of the coffee crop to grow at elevated C_a.

Elevated C_a Mitigates Heat Impacts on Coffee Physiological Performance. At supra-optimal temperatures (42/34 °C), the clear impairments of the photosynthetic apparatus that have been found in both *C. arabica* and *C. canephora* genotypes (especially in their levels of Calvin-Benson cycle enzymes) can be attenuated by enhanced C_a.[26,27] Indeed, plants grown under elevated C_a were able to maintain a significantly higher photosynthetic activity[26] and a lower photoinhibition status.[27] For example, despite the significant decreases in A at 42/34 °C (relative to 25/20 °C), the A values were 2−5-fold higher at elevated C_a than at the ambient level. Most of these impacts on A at 42/34 °C were linked to impairments in RuBisCO and ribulose 5-phosphate kinase. In contrast, photosystem performance was quite heat tolerant irrespective of C_a, as evidenced by the maintenance of functionality in both physical (energy capture) and photochemical (electron transport) processes.[26] Moreover, at 42/34 °C, the improved photosynthetic performance of plants grown at elevated C_a relative to those grown at ambient C_a was accompanied by a greater reinforcement of protective and antioxidant mechanisms in both *C. arabica* and *C. canephora* genotypes.[27]

Taking into account both the strong plant resilience to warming (up to 37 °C under normal C_a and further enhanced to 42 °C by elevated C_a) and the relevance of elevated C_a in enhancing plant physiological function and vigor, a new look at the predicted future of the coffee crop in the context of climate change and global warming is fully justified. Very recently, the first modeling approach describing a potential beneficial effect of CO_2 on the coffee crop noted that yields might not be threatened by global warming. In fact, coffee production might even slightly increase in countries such as Brazil, as long as adequate irrigation is provided.[82] This study therefore establishes new discussion terms regarding future perspectives on the sustainability of the coffee crop in current and new cropping areas, as their outcomes clearly suggest less of a catastrophe than previously predicted.[15,17] Nevertheless, while C_a enhancement could mitigate the negative effects of elevated temperatures on coffee productivity, the predicted increases in extreme rainfall events, drought, and overall climate variability bring large uncertainties as to how these environmental factors will ultimately impact coffee yields and beverage quality.

Agronomical and Physiological Strategies for Mitigating the Impacts of Climate Change on the Coffee Crop. Adaptation and mitigation strategies should be implemented as a means to improve crop sustainability in the context of climate change. Plant screening and breeding are fundamental adaptation strategies to produce new cultivars with improved tolerance to (a)biotic stresses with acceptable yields. For example, small coffee plants with denser canopies are prone to have lower transpiration rates,[29,51] whereas plants with larger and deeper root systems could explore increased soil volumes, reaching water resources that other plants with shallower root systems cannot.[29] Nonetheless, the implementation of these strategies to develop elite cultivars requires several years; hence, ready-to-use strategies should be implemented, namely, those that effectively mitigate the negative environmental impacts on currently cropped cultivars. 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 with coffee.

Overall, abiotic stresses are manifested in coffee plants as a range of disorders, including leaf chlorosis, extensive defoliation, and branch die-back, which are exacerbated by drought, supra-optimal temperatures, and mineral deficiencies.[52,83,84] Biotic stresses, including the most important coffee disease, leaf rust (*Hemileia vastatrix*), and important plagues (e.g., coffee leaf miner; *Leucoptera coffeella*) also affect the crop, resulting in severe defoliation in affected plants. Therefore, proper control of pathogens and insect attacks, coupled with adequate fertilization and irrigation (and related agronomic practices, such as the incorporation of organic matter into the soil and mulching terraces in high-slope areas), should markedly decrease the negative impacts of these (a)biotic constraints on the agronomic performance of coffee plantations. Several specific strategies for mitigating the impacts of climate change are described below.

Hardening of Seedlings. Coffee seedlings are often grown under shade before being transplanted to the field. At the seedling phase, coffee plants are thus extremely sensitive to sharp exposure to high irradiance and to drought. Production of seedlings directly in full sunlight is now considered a viable option due to the superior performance (e.g., less photo-oxidative damage) of these seedlings compared to their counterparts grown in the shade.[85] In addition, hardening of seedlings to their water supply before transplanting them to the field can improve their survivorship and early growth.[86] Indeed, coffee plants can develop a differential acclimation (suggesting the existence of a "drought memory") when subjected to repeated drought episodes, potentiating their defense mechanisms and allowing them to be kept in an "alert state" to successfully cope with further drought events.[87] Together, acclimation of seedlings to both irradiance and water supply would ultimately result in a relatively low mortality rate and improved growth after transplanting, which would therefore decrease the costs of establishing a coffee plantation.

Water-Use Efficiency (WUE) and Irrigation Management. Overall, coffee plants display high WUE, which is, to a large extent, associated with low transpiration rates. Positive correlations of long-term WUE with the relative growth rate[88] as well as with bean yields[89] have been found in *C. arabica*, suggesting that selection for high WUE might increase growth and overall productivity. More recently, Tesfaye et al.[35] achieved increases in WUE by managing irrigation. They found that plants subjected to partial root zone drying demonstrated significant improvements in WUE compared with plants in well-watered conditions or a normal irrigation deficit. This was achieved while saving as much as 50% of the water required to irrigate well-watered plants, without a significant decrease in crop yield. Therefore, the partial root zone drying technique is a promising irrigation strategy for coffee in situations of water scarcity. Additional information on this technique has been reviewed elsewhere.[90]

Shading. Overall, shading (e.g., in agroforestry systems) has been recommended for marginal areas in which adverse climatic conditions may limit the successful exploitation of the coffee crop. Furthermore, intercropping systems with fast-growing trees have been implemented to increase ground cover and maximize the efficiency of nutrient and water utilization, particularly during the juvenile phase of the coffee crop.[11]

A relative yield advantage of coffee plantations at full light exposure over their shaded counterparts is often observed in optimal or near-optimal soil and climatic conditions. In marginal areas, and due to anticipated future temperature increases coupled with other global climate changes, shading is likely to become an increasingly important management option and a key strategy to mitigate the negative impacts of climate change. The ameliorative effects of shading have been ascribed to the lower radiation input at the level of the coffee canopy along with reduced wind speeds and temperature fluctuations (by as much as 4−5 °C), higher relative humidity, and changes in the aerodynamic roughness of cropped areas.[11,47−49] Adequate shade management can also improve the water status of both the soil and coffee plants after prolonged drought.[29] These ameliorative effects may reduce the extent of oxidative stress and the associated photo-oxidative damage, ultimately improving coffee growth and production, especially in hot, dry regions.[46] In addition, the reduced air temperature in shaded plantations can decrease maintenance respiration by as much as 40%, as found in *C. arabica* plants in Costa Rica,[50] reinforcing the key ameliorative role of shading under elevated temperatures.

Other beneficial features of shaded plantations include reduced damage to berries caused by sun scorch, greater conservation of natural resources, increased biodiversity, and smaller fluctuations in biennial production. Shade trees can also guarantee supplementary income from fruit and/or timber to coffee farmers. In addition, the use of shelter trees can be a sustainable and financially viable coping strategy for smallholders who have little access to technological improvements for mitigating the harmful consequences of global climate change.[91−93] Even when considering only the income from coffee production, the premiums paid both for the quality and the other ecological attributes of shade-grown coffee can economically compensate for the lower yields frequently obtained under shade.[94] In each of these cases, the level of shade should be neither so high that productivity is markedly reduced nor too low to effectively protect coffee plants from adverse environmental conditions.[95] Shade management in coffee plantations has been reviewed elsewhere,[96,97] as has the physiology and production of coffee trees grown under shade conditions.[14,46]

As an alternative to the use of shelter trees, Steiman et al.[98] studied the application of kaolin (a particle that forms a reflective film over leaf surfaces) in Hawaii as a strategy to protect the coffee canopy from excessive temperature and solar radiation. They found a significant 10% decrease in leaf temperature, which was accompanied by increases in both A and crop yield. This improved yield may be due to the elevated reflectance of light from the kaolin film to more highly shaded inner canopy nodes, thus increasing floral initiation. Although these results are interesting and present clear potential benefits, the authors investigated a low-yield shade-loving cultivar, so research using modern high-yield cultivars is necessary to ascertain the full potential of this kaolin particle film technology. Presently, this technology has been applied to *C. canephora* in southeastern Brazil; empirical evidence shows that the use of kaolin technology is promising, given that it can improve the survivorship of seedlings transplanted to the field, but there is currently no precise information on the improvement of crop yields.

Gene Transfer and Grafting. Given that *C. canephora* performs much better at elevated temperatures[9] in addition to being generally better able to cope with drought stress (despite a wide intraspecific variability in drought tolerance[30,34]) than *C. arabica*,[10] transferring genes from *C. canephora* to *C. arabica* may provide an opportunity to obtain new elite cultivars with improved tolerance to drought and heat stress. Indeed, with the recent completion of the coffee genome map, new opportunities will likely arise in the field of molecular physiology to identify genes and transcription factors to reach those goals.[14] In this context, some of the molecular mechanisms by which coffee trees respond to drought[99−102] and heat stress[27,103] have been revealed.

In addition to gene transfer, grafting of *C. arabica* scions onto selected vigorous *C. canephora* rootstocks may be a good, rapid alternative to the relatively slow breeding process for increasing tolerance to environmental stresses such as drought.[104] Grafting of *C. arabica* onto *C. canephora* has been previously used in countries like Indonesia as a means of overcoming attacks to roots by various fungi and nematodes.[105] It was later shown that the use of nematode-tolerant *C. canephora* rootstocks markedly increased *C. arabica* yields even in the absence of nematodes in Brazil.[106] Under drought conditions, the better scion performance was associated with increased gas-exchange rates (higher A and g_s).[104] It has also been demonstrated in *C. canephora* that drought symptoms were postponed when a drought-sensitive genotype was grafted onto a drought-tolerant counterpart.[107] Compared with control plants, this response was accompanied by improved photosynthetic performance, higher leaf abscisic acid levels, and reduced symptoms of oxidative stress.[107] Nonetheless, other studies (e.g., refs 108 and 109) have found no significant effects of grafting *C. arabica* scions onto *C. canephora*, although this may be due to a degree of incompatibility between scions and rootstocks, e.g., the appearance of plugged vascular connections.[110] In summary, grafting is a promising tool to enhance scion (*C. arabica*) performance, when properly grafted onto *C. canephora* rootstocks, under growth conditions in which plants (roots) have to address limited water availability. It remains to be ascertained if *C. canephora* rootstocks also improve heat tolerance in *C. arabica* scions.

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ABBREVIATIONS USED

A, net photosynthetic rate; C_a, atmospheric CO_2 concentration; C_c, chloroplastic CO_2 concentration; C_i, intercellular CO_2 concentration; FACE, free-air CO_2 enrichment; g_m, mesophyll conductance; g_s, stomatal conductance; ROS, reactive oxygen species; RuBP, ribulose-1,5-bisphosphate; RuBisCO, RuBP carboxylase/oxygenase; VPD, vapor pressure deficit; WUE, water-use efficiency; Ψ_w, water potential

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