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Benefit from Biomass Boiler Emissions to Increase Greenhouse CO_2 Levels for Optimal Growth and Yield in Tomato, Cucumber, and Strawberry

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Rising greenhouse gas emissions, especially CO_2, has become a major environmental issue by contributing to the aggravation of the effects of climate change. Despite this, elevated CO_2 has been demonstrated to positively affect plants by stimulating their growth, development, and water-use efficiency through the stimulation of photosynthesis. Therefore, this study aims to evaluate the potential use of elevated CO_2 from industrial heating emissions as a biostimulant for tomato (*Solanum lycopersicum* L.), cucumber (*Cucumis sativus* L.), and strawberry (*Fragaria vesca* L.) plants grown in a semiclosed greenhouse. For this, the effect of 1000 ppm of CO_2 on plant gas exchange, nutrient uptake, and metabolism is determined. Additionally, a biofilter system is designed to retain particles and toxic substances generated during combustion. Air quality analyses demonstrate the efficiency of the biofilter in capturing these substances, preventing their emissions in the greenhouse. On the plants, elevated CO_2 levels significantly improve photosynthesis, growth, and fruit yield in all the species. Moreover, the increase in mineral nutrient requirements and changes in the dynamics of the metabolites indicate a physiological adaptation of the plants. These changes highlight the potential use of CO_2-rich pollutant gases in optimizing agricultural practices, thus reducing their emissions into the atmosphere.

1. Introduction

Climate change has become one of the foremost global concerns in the last few decades due to the potential adverse effects it may have on various sectors in the coming years.[1] One of the primary causes is the gradual increase in the concentration of greenhouse gases (GHGs) in the atmosphere as a result of uncontrolled pollutant emissions from human activity over the past few decades.[2] CO_2 is one of the main gases that constitutes the greenhouse effect,[3] whose concentration has been increasing steadily in the atmosphere over the last century. According to the Intergovernmental Panel on Climate Change,[4] atmospheric CO_2 levels have risen from about 270 ppm in preindustrial times to 400 ppm nowadays and are estimated to reach 800 ppm by 2050 with modeled mitigation pathways that limit warming to 1.5 °C (>50%) with no or limited overshoot or to 2 °C (>67%), assuming immediate action, which implies deep, rapid, and sustained global GHG emission reductions this decade. This prominent increase in CO_2 levels will likely result in changes in the climatic conditions of many areas around the world.[5]

Thermal energy constitutes 50% of worldwide final energy consumption, making it the predominant end-use energy form and responsible for 40% of global carbon dioxide (CO_2) emissions.[6] Approximately half of the total thermal energy generated was utilized in industrial processes. Another 46% was employed in the residential and commercial sectors for space heating, water heating, and, to a lesser degree, cooking. The remaining fraction is applied in agricultural activities, primarily for the heating of greenhouses.[7] This phenomenon is especially prominent in vulnerable regions, where the resources available to deal with these conditions are highly scarce. Therefore, reducing GHG emissions is imperative to mitigate these impacts and ensure agricultural resilience. Strategies such as transitioning to low-emission technologies and the implementation of a circular economy are critical for reducing the carbon footprint caused by human activity in the face of a changing climate.[8]

Despite these adverse effects, in recent years, various studies have shown that elevated levels of atmospheric CO_2 are associated with increased plant growth and development by enhancing their photosynthetic rate and, therefore, carbon fixation.[9] Additionally, it has been observed that elevated CO_2 leads to more efficient water use by reducing stomatal conductance during the exposure time, thereby decreasing water loss through gaseous exchange.[10] Furthermore, the nutrient absorption

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pattern is significantly altered under elevated CO_2, according to several studies, as there is a greater requirement for nutrients due to the increased metabolism of the plant.[11] In short, all these effects confer elevated CO_2 a biostimulant effect on plant physiology.

Although the impact of elevated CO_2 on the primary plant metabolism has been widely studied in recent years,[12] its influence on the secondary metabolism remains under investigation. Among the secondary metabolites, flavonoids are a diverse group of phenolic compounds that are abundant in several plants and play a critical role in many biological processes since higher concentrations have been related to tolerance to abiotic stress and UV protection, being also important for human nutrition, owing to their antioxidant effects.[13] Some studies carried out in growth chambers have demonstrated the effect of high CO_2 on altering the biosynthesis pathway of phenolic compounds and especially flavonoids in tomato and strawberry plants, which would have decisive implications on the nutritional quality of the fruits and plant defense.[14] That is why it is of interest to investigate their influence on the biosynthesis of flavonoids in other crop plants and under greenhouse conditions.

As a result, in the last few years, several studies have been carried out on the effect of elevated CO_2 in large-scale greenhouse crops to evaluate the potential effects of elevated CO_2 as a plant biostimulant under different growth conditions, most of them using pure CO_2 cylinders as a source to enhance its concentration in the greenhouse.[15] Although it is a reliable technique for supplying CO_2 in experimental assays, it would not be feasible for large-scale production in commercial greenhouses due to its high cost.[16] In contrast, using CO_2 from the combustion of biomass produced from human activities would not only be a more cost-effective alternative in the long term but would also help to reduce the emission of large quantities of GHGs into the atmosphere while increasing crop yields.[17] However, previous studies have warned that incomplete biomass combustion could generate, in addition to CO_2, other harmful volatile substances for both plants and humans, such as CO, nitrogen oxides, and particulate matter (PM).[18] This might have been influenced by the fact that, so far, there are no studies that seriously consider the potential use of CO_2 from human activity-related emission sources for plant growth biostimulation in a greenhouse.

Despite this, in the last few years, ongoing advancements in sustainable technologies have demonstrated, in an innovative approach, to prevent the emission of harmful substances into the environment. Biofiltration is an alternative technique, as it offers numerous environmental benefits. This system consists of a biological process and requires low maintenance costs, being more effective than other techniques, as it generates lower amounts of harmful byproducts and has a wide range of applications.[19] Moreover, biofiltration can treat numerous pollutants at the same time.[20] When designing an appropriate biofilter, some vital parameters that impact biofilter performance and microbial growth must be considered. These include moisture content, types and concentrations of the contaminants, nutrients concentration, loading rate, pH level, temperature, oxygen concentration, residence time, and degree of contact between pollutants and biofilters.[21] For this study, a specific prototype biofilter has been designed and constructed by CARTIF (Valladolid, Spain), SingularGreen S.L. (Alicante, Spain), and PROJAR Group (Valencia, Spain) to capture the pollutants from the exhaust emissions of a biomass boiler that can be harmful to both humans and plants, within the greenhouse.

The main objective of the present study was to evaluate the potential use of pollutant emissions containing CO_2 from the combustion of wood pellets in a pilot boiler in a semiclosed greenhouse, analyzing its effect on plant physiology and metabolism in three crops: tomato (*Solanum lycopersicum* L.), cucumber (*Cucumis sativus* L.), and strawberry (*Fragaria vesca* L.). These are highly important crops due to their economic value in the Mediterranean area.[22] For this study, the effect of elevated atmospheric CO_2 concentration (1000 ppm) on plant physiology, nutrient uptake, and metabolism was investigated. To reach 1000 ppm CO_2 concentration, a multilayer biofilter system was designed to capture harmful substances from combustion, thereby preventing their absorption by plants or the greenhouse surface, and was assembled between the biomass heating boiler and the greenhouse. The emission of polluting gases inside the greenhouse, combined with the use of a biofilter, was studied as a potential technique for stimulating plant growth, production, and metabolism while preventing the release of harmful gases into the environment and minimizing the exposure of the plants to harmful substances from combustion. Therefore, plant biomass, fruit production, leaf gas exchange, C fixation, mineral nutrient absorption, and the concentration of primary metabolites (organic acids, amino acids, and carbohydrates) and secondary metabolites (flavonoids) were determined.

2. Results

2.1. Filtration of Polluting Gases

Figure 1 shows the differences between the gas concentration before and after installing the biofilter when CO_2 reached 1000 ppm and with no gas emission (400 ppm CO_2) (Figure 1G). The concentration of formaldehyde (Figure 1A) was significantly reduced after the installation of the biofilter, dropping to levels between 1 and 2 $\mu g\,m^{-3}$, close to the control levels, while in the condition with no biofilter, despite the fluctuations, remained slightly elevated (18–20 $\mu g\,m^{-3}$).

The total volatile organic compound (TVOC) levels showed a considerable decrease with the biofilter compared to the measurement without the biofilter. Values started from $\approx$13 000 $\mu g\,m^{-3}$, dropping to below 450 $\mu g\,m^{-3}$, which is similar to the control conditions with no-emission conditions (350–400 $\mu g\,m^{-3}$) (Figure 1B). Large-sized PM (PM $\leq$ 2.5) (Figure 1C), as well as formaldehyde, was completely retained by the biofilter, dropping from levels over 100 to close to 0 $\mu g\,m^{-3}$.

The biofilter system managed to capture all the CO generated during combustion, reducing levels to 0 ppm (Figure 1D). Nitrogen oxides showed a variable response (Figure 1E,F). With the biofilter, NO and total NO_x concentrations were significantly lower at certain times, decreasing from levels around 210–300 and 290–320 ppb, respectively, to 150–175 and 190–220 ppb, respectively. However, despite the biofilter effect, the concentration of both nitrogen oxides remained considerably high compared to the no-emission levels (0–20 ppb).

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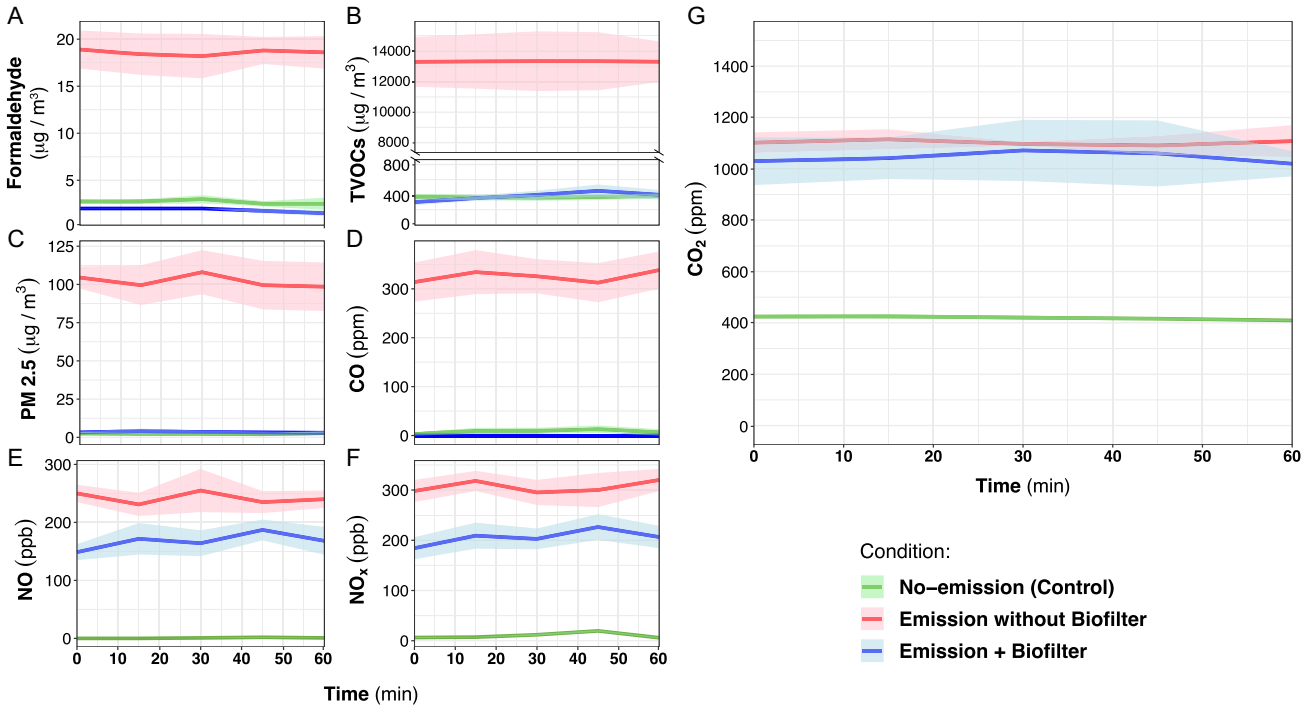


Figure 1. Analysis of the retention capacity of the biofilter by measuring air quality indicator gases over 60 min, by comparing a nonemission period (control; green line), emission with no biofilter (CO_2 1000 ppm; red line), and emission after the installation of the biofilter (CO_2 1000 ppm + biofilter; blue line). Air quality indicator gases include: A) formaldehyde, B) total volatile organic compounds (TVOCs), C) particulate matter up to 2.5 µm (PM 2.5), D) carbon monoxide (CO), E) nitrogen monoxide (NO), and F) total nitrogen oxides (NOx). G) shows the CO_2 concentration for each condition during the analyzed period. The values represent the mean of 3 consecutive days measured every 10 min ($n = 3$) ± SE (shaded area).

2.2. Aerial Part Relative Growth Rate and Fruit Dry Weight

The results of the aerial vegetative part relative growth rate (RGR) and fruit dry weight (DW) are shown in **Figure 2**. For the tomato plants, elevated CO_2 conditions did not significantly alter the RGR in the aerial part compared to the control plants. However, fruit DW did significantly increase in treated plants compared to the control ones (7.03 versus 10.83 g). Moreover, in cucumber plants, CO_2 treatment considerably promoted an increase in plant growth as shown by the improved RGR in the aerial part (1.06 versus 2.77%) and DW in the fruit (14.60 versus 28.87 g). In the case of strawberry plants, as in cucumber,

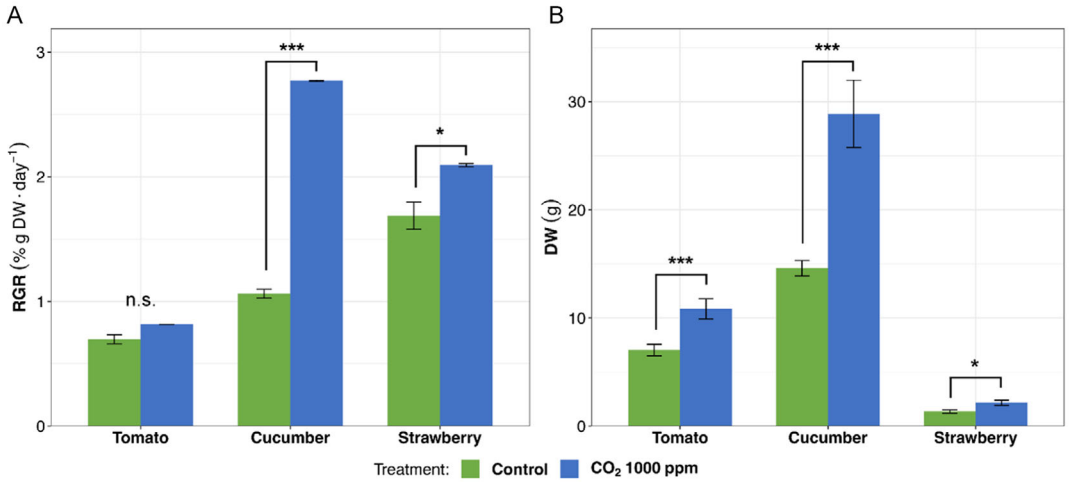


Figure 2. A) RGR of the whole aerial part and B) fruit DW (g) of tomato, cucumber, and strawberry plants produced in 10 days under control conditions and elevated CO_2 (1000 ppm). Each bar represents the mean of nine plants ($n = 9$) ± SE. Significant differences between both treatments for each species were measured according to Student's *t*-test: n.s. for "no significant," * for $p < 0.05$, and *** for $p < 0.001$.

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RGR showed an increase in the aerial part (1.68 versus 2.09%) together with the DW in the fruit (1.34 versus 2.15 g) under elevated CO_2 in comparison with the control plants.

On the other hand, the fruit production during 10 days, in terms of the number of fruits per plant, was significantly increased in all plants under high CO_2. However, the increase was higher in cucumber.

2.3. Gas Exchange

Figure 3 shows the results of gas exchange parameters. In all the species, plants grown under conditions of elevated CO_2 experienced a considerable drop in the transpiration rate (E) compared to the control plants (Figure 3A).

Stomatal conductance (G_s) (Figure 3B) considerably decreased both in cucumber (218.17 versus 144.00) and strawberry plants grown with high CO_2 levels, reaching the greatest difference in the second one (550.14 versus 158.07). However, the stomatal conductance remained unchanged in tomato plants.

The photosynthesis rate (A) (Figure 3C) was higher in the plants of all species subjected to elevated CO_2 levels compared to the control ones. This increase was especially prominent in tomato plants (6.75 versus 38.95), this value being approximately four times higher than in the control treatment.

As expected, the substomatal concentration of CO_2 (C_i) significantly increased in the plants of all species subjected to elevated CO_2 levels, reaching ≈1000 ppm of CO_2, close to the atmospheric concentration at the time of measurement (Figure 3D).

2.4. C/N Concentration

The results of the C concentration reveal a different pattern between the leaf and fruit (**Figure 4**). The greatest increase in C was observed in the fruits, where the concentration was significantly higher in all species compared to the control. In the case of leaves, only the tomato plants increased the levels of C under conditions of elevated CO_2 compared to the control (36714.96 versus 37325.28 mmol kg^{-1}). Conversely, the concentration of C decreased in cucumber plants subjected to high atmospheric CO_2 levels compared to the control (37947.82 versus 37361.09 mmol kg^{-1}). In the case of strawberry plants, the levels of C between both growth conditions did not significantly vary.

The concentration of N was significantly lower in the plants of all the species grown under conditions of elevated CO_2 compared to the control ones, both in the leaves and in the fruits. However, it was in the leaves where the greatest differences were observed.

2.5. Concentration of Mineral Elements

The results of the analysis of mineral elements are shown in **Figure 5**. Tomato and cucumber plants subjected to elevated CO_2 levels showed a generalized decrease in the concentration of the main macro- and micronutrients, both in the leaves and in the fruits, compared to the control.

CO_2 provoked a decrease of all the main macronutrients analyzed in the leaves of tomato plants, especially Ca, whose concentration was nearly 50% lower compared to the control plants

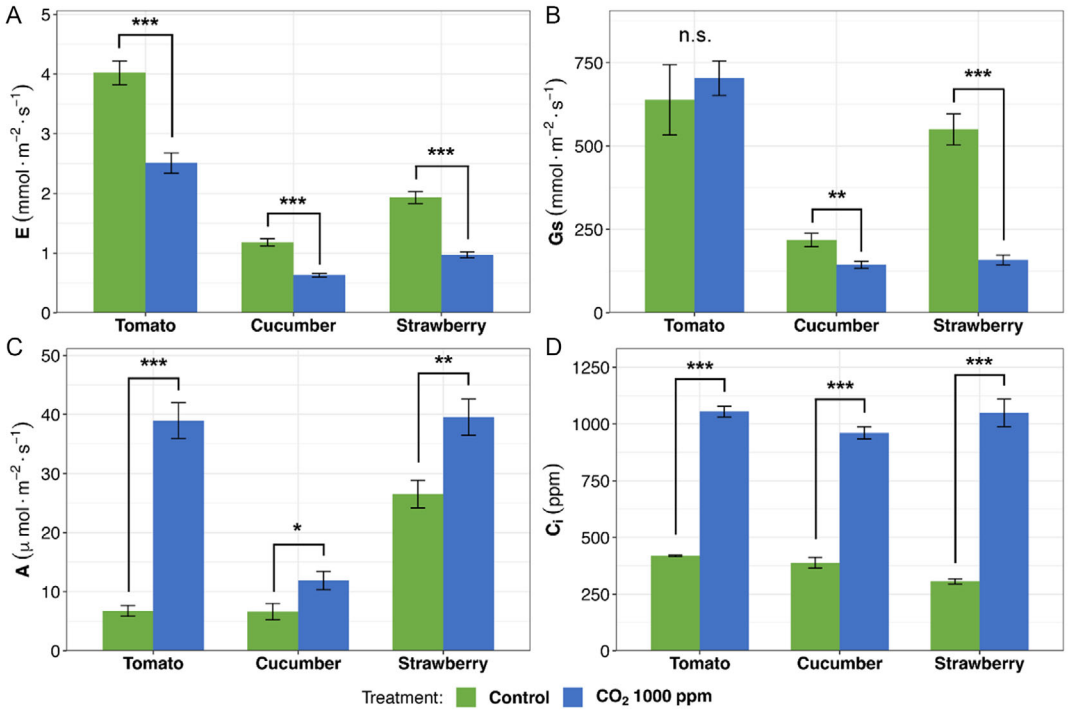


Figure 3. Leaf gas exchange parameters in tomato, cucumber, and strawberry plants: A) transpiration rate, E; B) stomatal conductance, G_s; C) net photosynthesis rate, A; and D) substomatal CO_2 concentration, C_i. Each bar represents the mean of the measurement of three leaves per plant of six plants in each growth period ($n = 18$) ± SE. Significant differences between both treatments for each species were measured according to Student's t-test: n.s. for "no significant," * for $p < 0.05$, ** for $p < 0.01$, and *** for $p < 0.001$.

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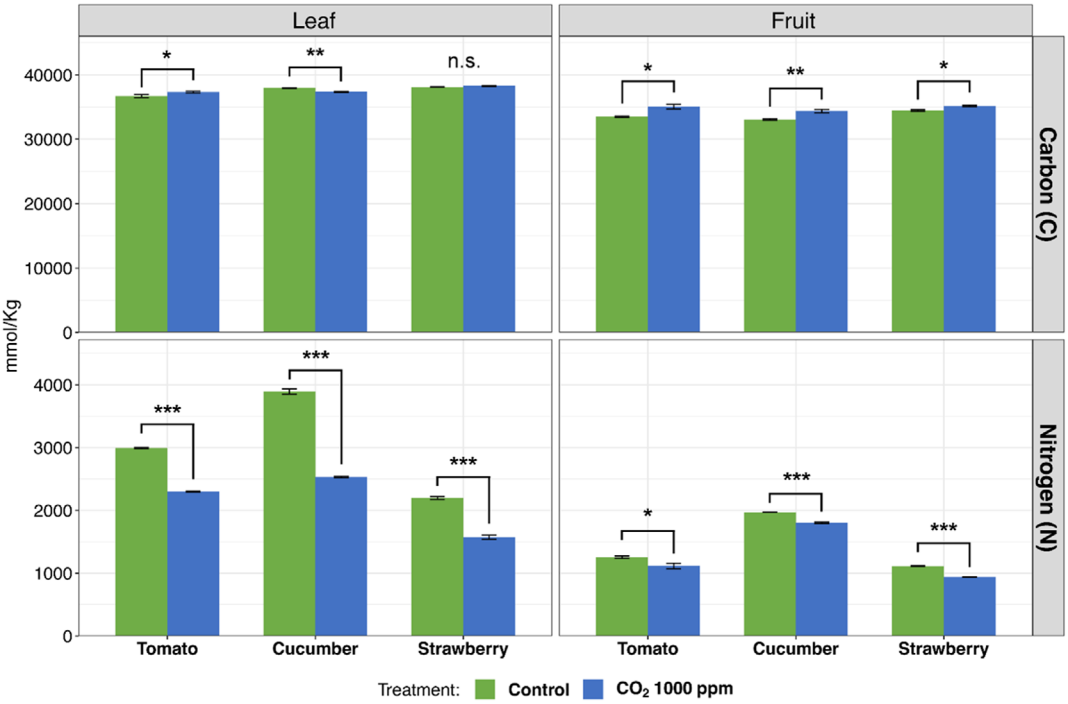


Figure 4. Carbon and nitrogen concentration (mmol kg^{-1}) in the leaves and fruits of tomato, cucumber, and strawberry plants under control conditions and elevated CO_2 (1000 ppm). Each bar represents the mean of three biological replicates ($n = 3$) ± SE. Significant differences between both treatments for each species were measured according to Student's *t*-test: n.s. for "no significant," * for $p < 0.05$, ** for $p < 0.01$, and *** for $p < 0.001$.

(489.05 versus 251.96 mmol kg^{-1}). Regarding micronutrients, a decrease in B, Fe, Cu, Mn, and Si concentrations was observed. A similar pattern was observed in the fruits, where a significant decrease in Ca, K, Mg, and S was observed, in comparison with the control plants. Only Na experienced a slight increase in its concentration (13.88 versus 17.36) compared to the control. Fruit micronutrients were not as affected as those in the leaves, where only Fe and Cu experienced a significant decrease, compared to the control plants. Only Mn was considerably increased in the tomato fruits compared to the control.

Cucumber plants, like tomato plants, experienced a generalized decrease in the main macro- and micronutrients under high CO_2 levels; however, a different pattern was observed. In the case of macronutrients, Ca, Mg, P, and S significantly decreased in CO_2-treated plants compared to the control, whereas, in the case of micronutrients, the concentration of all of them considerably dropped compared to the control plants, except for B and Fe, whose concentration remained unchanged. Nevertheless, unlike tomato plants, most of the differences were observed in the fruits. Except for P, all the macronutrients experienced a significant decrease in the fruits of plants subjected to elevated CO_2 levels. In the case of micronutrients, a decrease in the concentration of B, Fe, Cu, and Si was observed; meanwhile, as in tomato fruits, Mn was significantly increased in comparison with the control.

Unlike the previous species, strawberry plants showed unchanged concentrations of most of the mineral elements under high CO_2 levels. In the case of the leaves, only K was altered among all macronutrients, whose concentration was lower in CO_2-treated plants compared to control plants. Among micronutrients, Mn was the only element whose concentration experienced a significant decrease compared to the control. In strawberry fruits subjected to elevated CO_2 levels, only the concentration of some micronutrients was significantly altered compared to the control: Zn and Mn, whose concentration decreased compared to the control, and an increase in the levels of Cu and Si.

2.6. Concentration of Flavonoids

The total concentration of flavonoids (**Figure 6**) experienced a significant decrease in the plants of tomato (310.82 versus 282.44 µM) and cucumber (46.99 versus 27.40 µM) under elevated CO_2 levels compared to those grown in control conditions. In contrast, strawberry leaves showed a significant increase in the levels of flavonoids when the plants were subjected to elevated CO_2 (110.17 versus 134.25 µM).

2.7. Primary Metabolites

The analysis of primary metabolites showed several differences among the species (**Figure 7**). Among organic acids, tomato plants subjected to high levels of CO_2 showed a significant increase in formate (Figure 7B) and malate (Figure 7C). Regarding amino acids (Figure 7D–I), only an increase in glutamate levels was observed, while γ-aminobutyric acid (GABA) polyvinylidene fluoride significantly decreased compared to the

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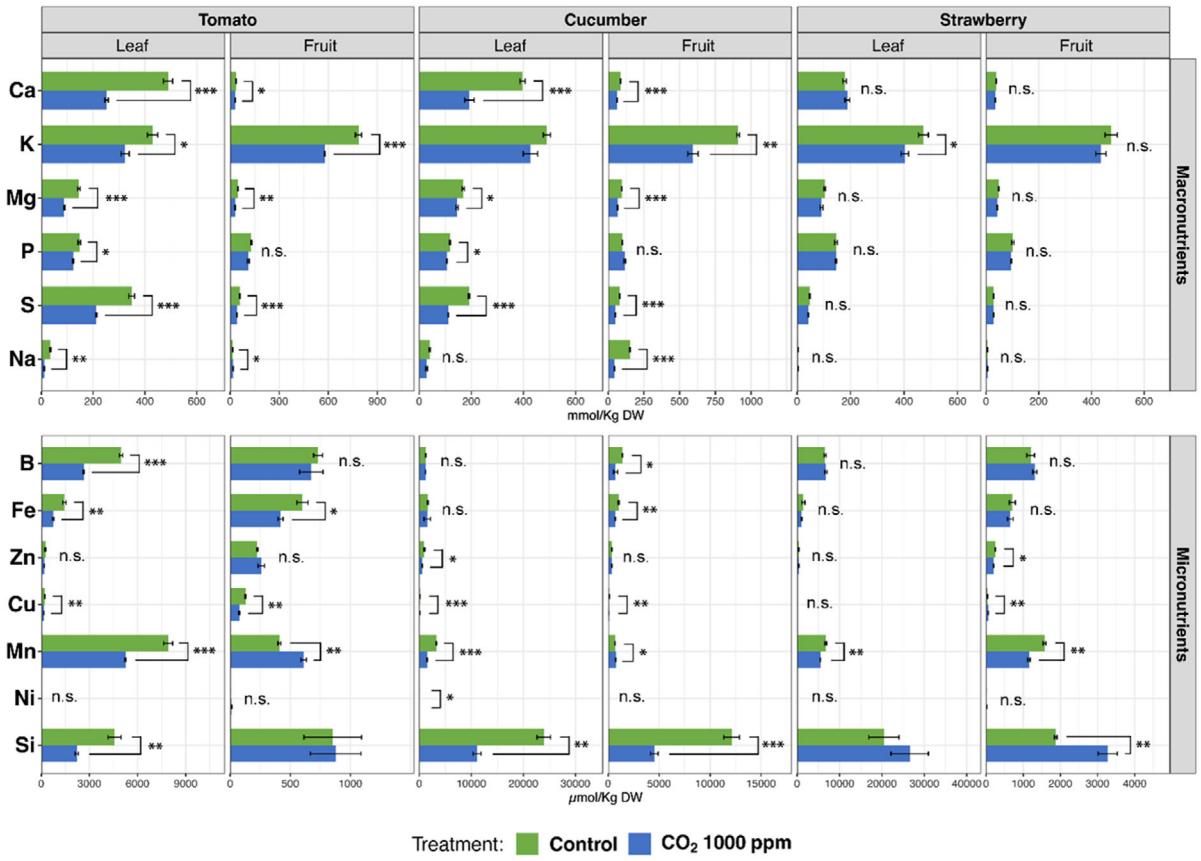


Figure 5. The concentration of macronutrients (mmol kg^{-1} DW) and micronutrients (μmol kg^{-1} DW) in the leaves and fruits of tomato, cucumber, and strawberry plants under control conditions and elevated CO_2 (1000 ppm). Each bar represents the mean of three biological replicates ($n = 3$) ± SE. Significant differences between both treatments for each species were measured according to Student's *t*-test: n.s. for "no significant," * for $p < 0.05$, ** for $p < 0.01$, and *** for $p < 0.001$.

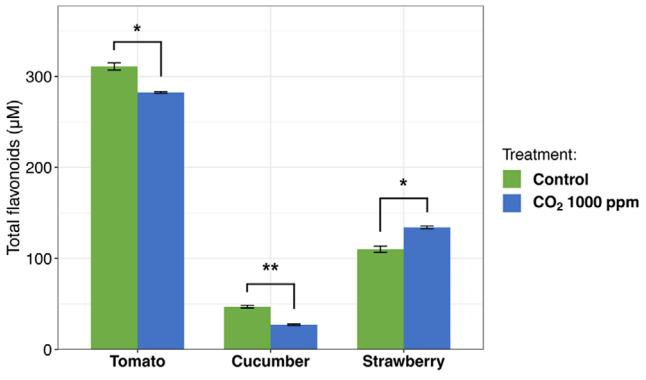


Figure 6. The concentration of total flavonoids (μM) in tomato, cucumber, and strawberry leaves under control conditions and elevated CO_2 (1000 ppm). Each bar represents the mean of three biological replicates ($n = 3$) ± SE. Significant differences between both treatments for each species were measured according to Student's *t*-test: n.s. for "no significant," * for $p < 0.05$, and ** for $p < 0.01$.

control leaves. All the carbohydrates, except myo-inositol, increased in the leaves of all plants treated with high CO_2 compared to the control (Figure 7J–M).

Cucumber leaves, unlike those of tomato plants, showed a significant decrease in citrate levels (Figure 7A), among organic acids, in comparison with the control plants. More differences were found in the case of amino acids (Figure 7D–I), where an increase in glutamate and valine and a decrease in GABA and glutamine were observed, compared to the control plants. However, carbohydrates variations showed a similar pattern as in tomato plants (Figure 7J–M): fructose, glucose, and sucrose were considerably increased for the control plants. Only myo-inositol levels decreased in the leaves of CO_2-treated plants.

Strawberry leaves grown under elevated CO_2 concentration showed no significant change in any of the analyzed organic acids (Figure 7A–C). In the case of amino acids, as in cucumber and tomato plants, GABA (Figure 7D) significantly decreased their concentration regarding the control plants. In addition, a significant increase in the levels of glutamine (Figure 7H) and valine (Figure 7I) was observed, the latter as in tomato and cucumber leaves. Regarding carbohydrates (Figure 7J–M), the same variations were observed as in tomato leaves, significantly increasing the concentration of fructose, glucose, and sucrose under high CO_2 levels compared to the control plants.

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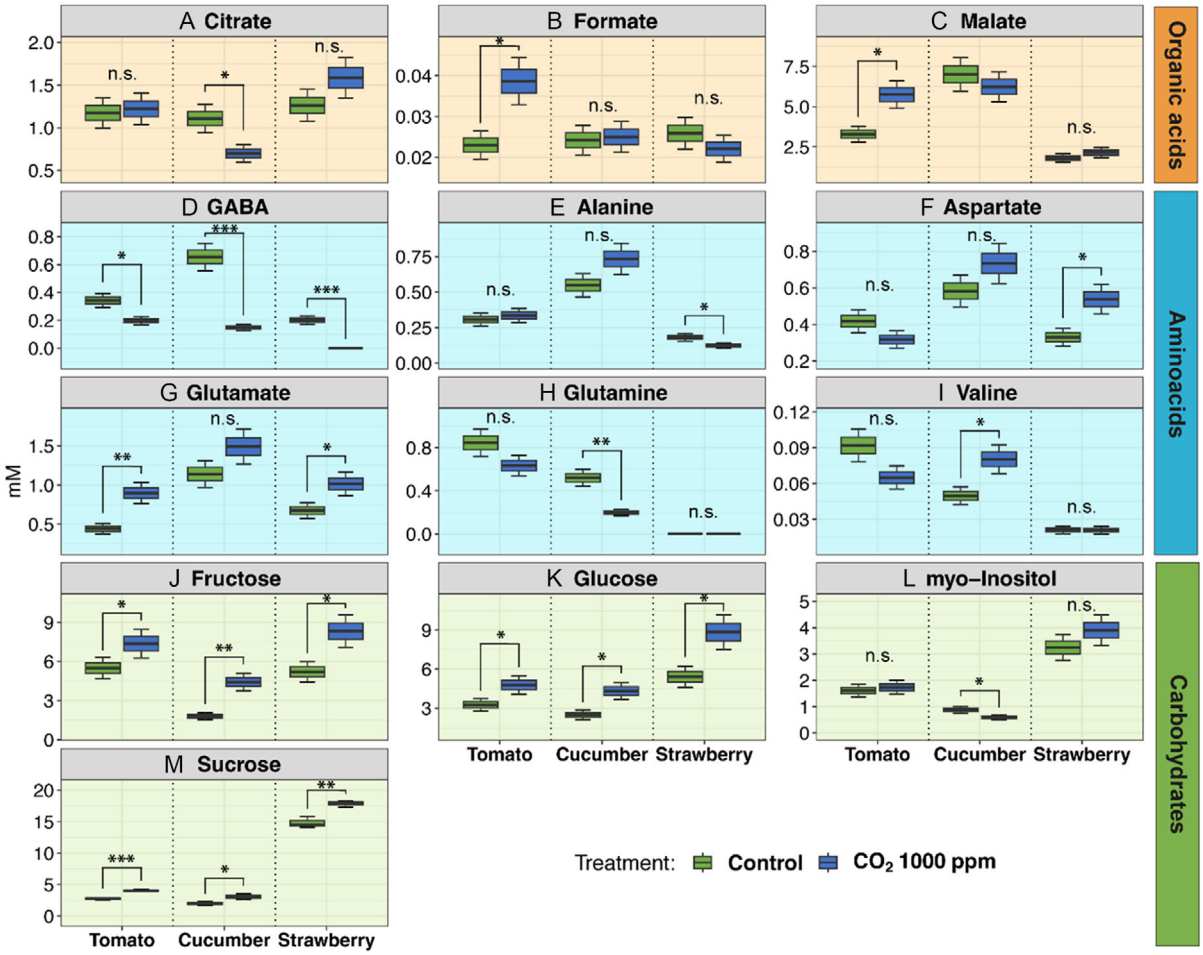


Figure 7. The concentration of primary metabolites (organic acids, amino acids, and carbohydrates) (mM) in tomato, cucumber, and strawberry leaves under control conditions and elevated CO_2 (1000 ppm). Primary metabolites include: organic acids A) citrate, B) formate and C) malate, aminoacids, D) GABA, E) alanine, F) aspartate, G) glutamate, H) glutamine and I) valine and carbohydrates, J) fructose, K) glucose, L) myo-inositol and M) sucrose. Each bar represents the mean of three biological replicates ($n = 3$) ± SE. Significant differences between both treatments for each species were measured according to Student's *t*-test: n.s. for "no significant," * for $p < 0.05$, ** for $p < 0.01$, and *** for $p < 0.001$.

3. Discussion

3.1. Biofilter Efficiency in Capturing Pollutant Gases

The increase in atmospheric levels of CO_2 has proven to be a very effective technique for the biostimulation of growth and development in plants by several studies carried out both in growth chambers and greenhouses.[15a,15c,15d,23] However, to date, none have evaluated the potential use of CO_2 generated by combustion from human activities in a realistic trial that translates to a reduction of GHG emissions into the atmosphere. Therefore, the integration of a biofilter system to retain toxic and polluting substances from the gases generated during combustion was necessary. Previous studies have demonstrated the potential of biochars, carbon-based materials produced by biomass pyrolysis,[24] as a cheap and efficient system for retaining gaseous pollutants produced by the combustion of materials.[25] In the system designed for our trial, we went further by integrating other materials such as fiberglass and substrate to allow the absorption of other toxic substances, such as PM and volatile compounds.[26] The results of the gas composition inside the greenhouse showed that the installation of the biofilter significantly reduced the air concentration of formaldehyde and TVOCs, which are potentially carcinogenic substances,[27] and PM ($PM \leq 2.5\,\mu m$), responsible for respiratory diseases.[28] Furthermore, the biofilter reduced CO concentrations to undetectable levels. This gas, produced by incomplete combustion, is not only a pollutant but also highly lethal; the levels before the biofilter installation would have prevented personnel from being inside the greenhouse, even for a limited time.[29] Finally, the significant reduction in nitrogen oxides (NO and NO_x) concentrations with the presence of the biofilter demonstrated improved air quality inside the greenhouse. However, for both nitrogen oxides and TVOCs, the biofilter was unable to completely eliminate the presence of these substances during the gas emission period, remaining significantly elevated compared to the no-emission period. Nevertheless, these TVOC levels would not exert an important risk to human health or the

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physiology of the plants.[30] On the contrary, the measured levels of NO and NO_x resulting from the application of the biofilter (150–175 and 190–220 ppb, respectively) have been reported to cause harmful effects on human health under prolonged exposure.[31] In this regard, it is recommended that greenhouse personnel limit their exposure to these substances for a short period.

3.2. Growth and Fruit Production

Regarding biomass, under elevated CO_2, tomato plants maintained the RGR in the aerial part; however, the fruits increased their DW. This phenomenon is consistent with the results of previous studies results conducted in greenhouses,[15a,15b] indicating that, under conditions of high CO_2, most of the carbon fixed by these plants is accumulated in the fruits.[32] In contrast, cucumber and strawberry plants did increase the growth under elevated CO_2, both the RGR in the aerial part and the DW in the fruits. This result demonstrates that increased CO_2 levels enhanced growth and biomass in both species, caused by an increase in carbon fixation due to a higher photosynthesis rate. Previous studies conducted in growth chambers agree with these results, where in all cases, an increase in biomass as a consequence of elevated CO_2 was observed in these two species.[11b,23b,33]

The significant increase in fruit production across all species underlines the CO_2 fertilization effect. The pronounced increase in tomato plants could be attributed to their potentially higher responsiveness to CO_2 in terms of photosynthesis rate and carbon assimilation, leading to enhanced growth and fruit yield.[34] The increase in fruit biomass without a corresponding increase in fruit number in cucumber and strawberry plants indicates that elevated CO_2 may have a more pronounced effect on fruit growth rather than on reproductive development in these species. This is consistent with the results shown in previous studies where, despite increasing the fruit biomass, the yield in terms of number of fruits did not significantly vary.[11b,15c,35] In the case of strawberry plants,[23b] supports that the inhibition of flowering induction caused by elevated CO_2 may have decisively influenced the lack of increase in the fruit yield.

3.3. Gas Exchange

Gas exchange parameters clearly reflected the physiological species-specific adaptations to elevated CO_2. As expected, C_i considerably increased across all species under elevated CO_2, being a direct consequence of the increased atmospheric CO_2 levels. This increase in C_i is expected to enhance the carboxylation rate of Rubisco, responsible for fixing CO_2 during photosynthesis, thereby potentially increasing the rate of photosynthesis.[36]

E considerably dropped in the plants of all the species, which aligns with previous studies showing that elevated CO_2 often leads to reduced stomatal opening, thereby decreasing water loss through transpiration.[23c,37] This response can be attributed to the ability of the plants to maintain an adequate CO_2 uptake for photosynthesis while minimizing water loss.

G_s decreased in all the species when they were subjected to elevated CO_2. Stomatal closure under high CO_2 is a typical response in most plants, which allows them to reduce water loss via transpiration.[10,23c,37,38] This is why stomata are critical organs in the response of the plant to CO_2. The stomatal pore is formed by two guard cells, which regulate the aperture and closure through turgor pressure changes.[39] The entire pathway by which the guard cells regulate stomatal closure under increased CO_2 is continuously under study; however, previous research has highlighted that some isoforms of aquaporins , mostly plasma membrane intrinsic proteins (PIPs) are essential in the diffusion of CO_2 through the membrane, which, by interacting with carbonic anhydrases, facilitate the conversion of CO_2 into bicarbonate (HCO_3^-),[40] triggering the signaling process in response to high CO_2.[23a,41]

The increase in A under elevated CO_2 conditions across all species is consistent with the enhanced photosynthetic capacity due to increased C_i. It is well demonstrated that high CO_2 levels enhance the carboxylation rate of Rubisco, responsible for fixing it during photosynthesis, thereby potentially increasing the rate of photosynthesis.[39] The particularly high increase in tomato and cucumber plants suggests that these species might be more responsive to elevated CO_2 levels, possibly due to a higher CO_2 assimilation capacity or more efficient photosynthetic machinery. This increase in photosynthesis is crucial for supporting greater biomass production,[9] consistent with the enhanced RGR in the aerial part of cucumber and strawberry plants, but not in tomato plants.

3.4. C and N Concentration

The higher photosynthetic activity as a result of the elevated CO_2 levels led to an increase in carbon concentration in the fruits of all species and in the leaves of tomato plants. Higher CO_2 levels increase the availability of the primary substrate for photosynthesis, leading to increased C fixation and accumulation in plant tissues.[34] This phenomenon is known as the CO_2 fertilization effect and is commonly observed in C3 plants.[38a] The decrease in carbon concentration in cucumber leaves under elevated CO_2, in contrast to the increase in fruits, suggests a differential allocation of carbon between different plant tissues. This might be a result of species-specific physiological adaptations to elevated CO_2, where plants might prioritize carbon allocation to fruits over leaves.[41] The unchanged C levels in strawberry plants under elevated CO_2 could be indicative of either a saturation point in carbon assimilation. This could also reflect an inherent limitation in photosynthetic capacity or other growth-related factors in strawberries that might not be significantly enhanced by elevated CO_2.[9]

On the contrary, nitrogen concentration significantly decreased both in the leaves and in the fruits of all species subjected to elevated CO_2 compared to control plants. It is well known that increased CO_2 levels lead to imbalances in C/N ratios, mainly as a consequence of the faster growth and the increase in biomass production.[42] The greater differences in nitrogen concentration observed in the leaves compared to the fruits might be related to the more direct involvement of leaves in photosynthesis and their role as primary sites of carbon assimilation. In addition, the lower transpiration rate in all the species grown under high levels of CO_2 may have influenced the reduction of N concentration in the leaves, by reducing the xylem

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flux.[43] On the other hand, several studies have pointed out that this reduction of N concentration can impact protein synthesis and affect plant growth and nutrient uptake.[15a,44]

3.5. Concentration of Mineral Elements

Elevated CO_2 levels also produced a general decrease in most macronutrients, especially in tomato and cucumber plants. This phenomenon is especially linked to increased growth and a higher biomass accumulation, which leads to a relative decrease in nutrient concentrations. It is well documented in previous studies, that most of the nutrients reduced their concentration in the plants when they were exposed to elevated CO_2 levels over a prolonged period of time. However, some studies have highlighted that, despite this decrease in the concentration of nutrients in the tissues, nutrient uptake increased under elevated CO_2 due to a higher nutrient demand.[11a] Our results showed that tomato and cucumber plants significantly reduced the Ca concentration both in the leaves and fruits, which could be related to changes in the transpiration rate under elevated CO_2. Calcium is primarily mobilized through the plant via the transpiration stream, and reduced transpiration can lead to lower calcium transport to plant tissues.[45] The decrease in other micronutrients such as B, Fe, Cu, Mn, and Si could be related to altered root uptake mechanisms or changes in internal nutrient allocation in response to elevated CO_2.[46] In contrast, the concentration of mineral elements was relatively stable in strawberry plants under high CO_2, except for specific changes like the decreased K in leaves and changes in Zn, Mn, Cu, and Si in fruits, which suggests species-specific responses to elevated CO_2. This could be due to inherent differences in nutrient uptake, transport mechanisms, or a more balanced growth rate that does not lead to significant nutrient dilution.[34]

The widespread reduction in mineral nutrient concentrations, particularly in tomato and cucumber plants, could significantly affect the nutritional quality of their fruits for human consumption.[11b] Several solutions have been proposed to address this issue, including selecting cultivars that are better adapted to elevated CO_2 levels, creating favorable cultivation conditions under elevated CO_2, inducing moderate abiotic stress, or harvesting the fruits earlier.[47]

On the other hand, the observed increase in carbohydrate concentrations (glucose, fructose, sucrose, and myo-inositol) in the three analyzed species could greatly enhance their taste and flavor and human nutritional concentration. This phenomenon, along with the rise in fruit DW, is consistent with the results observed in previous studies, where they could help compensate for the decline in the nutritional quality of the fruit along with achieving higher sustainability.[43b,47,48]

3.6. Effect on the Plant Metabolism

The effect of high CO_2 provoked changes in several pathways of the secondary metabolism of the plants as evidenced by the variations in the concentration of total flavonoids, which play a crucial role in plant defense against pathogens and herbivores, UV protection, and oxidative stress mitigation.[39] Previous research has shown that elevated CO_2 could modulate genes involved in the plant stress response and activation of the secondary metabolism, mainly involving flavonoids.[49] Our results showed a significant decrease in the levels of total flavonoids in tomato and cucumber plants subjected to elevated atmospheric CO_2. This phenomenon is in contrast to the results of most studies carried out, where the concentration of most flavonoids is stimulated by the stress caused by the increase in CO_2.[50] In this sense, some studies attribute a decrease in total flavonoids concentration under elevated CO_2 to the enhancement of the photosynthetic carbon assimilation, which leads to an increased allocation of carbon to primary metabolic pathways and growth-related processes, while reducing the synthesis and allocation pathways of secondary metabolites.[51] However, in agreement with our results,[14b] and[52] observed a significant decrease in the flavonoids content in plants grown under elevated CO_2 in tomato leaves and cucumber roots, respectively. These studies attribute this response to the lower stress experienced by these plants grown with high CO_2 compared to the control. Conversely, total flavonoids were significantly increased in strawberry leaves under elevated levels of CO_2, which is consistent with the results reported in the literature.[14a] This result could indicate that the plant has a greater response capacity toward stress due to the increase in CO_2 or that this increase does not represent stress for the plant. In any case, as evidenced by our results, the response of the metabolic pathway of the plant for the synthesis of flavonoids under CO_2 stress is species-specific.[53]

The observed changes in primary metabolites also reflect species-specific metabolic adjustments to elevated CO_2. Elevated CO_2 levels increased formate and malate concentrations in tomato plants, which is indicative of the stimulation of the tricarboxylic acid (TCA) cycle and related pathways. These changes are associated with increased photosynthetic carbon assimilation, leading to a surplus of carbon that is channeled into various metabolic pathways.[12c] The decrease in citrate levels in cucumber plants under high CO_2 is also linked to changes in the TCA cycle. These alterations might reflect a shift in energy and carbon metabolism, potentially influencing growth and stress responses.[12b]

Glutamate was notably increased in tomato and strawberry plants when they were subjected to elevated CO_2. Glutamate is a key amino acid in plant nitrogen metabolism and serves as a precursor for the synthesis of other amino acids.[54] According to previous studies, the increase in glutamate concentration is closely correlated with the increase in tissue levels of N.[55] However, elevated levels of CO_2 led to a generalized decrease in N concentration in the analyzed species. On the one hand, this phenomenon can be explained by the stimulation of the TCA cycle under conditions of high CO_2, leading to the increase in the biosynthesis of α-ketoglutarate, a glutamate precursor.[54] On the other hand, previous research highlighted that elevated CO_2 stimulates glutamate synthesis via glutamate dehydrogenase, to avoid NH_4^+ toxicity, because of the inhibition of the glutamine synthetase–glutamate synthase (GS/GOGAT) pathway, the main route for glutamate synthesis.[56] The maintenance of the glutamine levels and even the decrease in its concentration in cucumber leaves, together with the accumulation of glutamate in tomato and strawberry plants, evinced the inhibition of the GS/GOGAT pathway as a consequence of the high atmospheric CO_2 levels.[54,57] However, as shown in our results,

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the alteration in these metabolic pathways varies among each species. Stimulation of the TCA cycle and inhibition of the GS/GOGAT pathway under elevated CO_2 levels could also have influenced the significant decrease in GABA concentration in the leaves of all the analyzed species since previous studies have related the accumulation of GABA with partial inhibition of the TCA cycle and the increased activity of the GS/GOGAT pathway.[12a,58]

The considerable increase in carbohydrates such as fructose, glucose, and sucrose across all species under elevated CO_2 is consistent with enhanced photosynthetic activity and carbon fixation efficiency, evidenced by the increase of both parameters in tomato leaves and the fruits of all the analyzed species. These carbohydrates serve as primary energy sources and building blocks for growth and development.[34] However, the decrease in myo-inositol concentration in cucumber plants, a component involved in cell signaling and stress responses, might suggest adjustments in metabolic pathways related to plant signaling and adaptation.[59] These results are consistent with previous studies carried out in growth chambers, in which the concentration of the main carbohydrates notably increased under elevated CO_2.[11b,23b,60]

4. Conclusions

The biofilter designed to retain polluting and toxic gases generated by the combustion during the CO_2 treatment has proven to be an efficient system in capturing these substances, thus preventing their absorption by the plants. Furthermore, the elevated CO_2 sourced from the pollutant emissions of the industrial boiler significantly enhances photosynthesis, biomass growth, and fruit yield in a general way across the different plant species, suggesting a potent biostimulation strategy for crops grown in greenhouses. These physiological adaptations, including a decrease in stomatal conductance and shifts in metabolite dynamics, highlight the potential for optimizing agricultural practices by taking advantage of CO_2-rich pollutant gases. Importantly, the scalability of this approach is facilitated by the fact that the experiment was conducted at a prepilot scale, demonstrating its practical application in larger agricultural systems. Future studies should delve into the long-term effects of CO_2 enrichment on crop systems, particularly focusing on the balance between growth enhancement and nutrient content to build climate-resilient crops. These goals could lead to targeted genetic and agronomic strategies to maximize the positive impacts of elevated CO_2 on crop productivity, turning polluting gas emissions into a valuable resource for sustainable agricultural practices and the mitigation of global warming.

5. Experimental Section

Plant Material and Growth Conditions: The experiments were carried out with plants of tomato (*S. lycopersicum* L. cv. Marmande), cucumber (*C. sativus* L. cv. Dogo F1), and strawberry (*F. vesca* L. cv. M-11). The tomato and cucumber seeds were prehydrated with distilled water and continuously aerated for 24 h. Subsequently, they were germinated in vermiculite under dark conditions in a 28 °C chamber for 48 h. After that, germinated plants were transferred to a growth chamber under controlled conditions: 16 h light and 8 h dark cycle with temperatures of 25 and 20 °C, and relative humidity of 80 and 60% day/night, respectively. Photosynthetically active radiation (PAR) was 400 µmol m^{-2} s^{-1}, provided by LED (Pacific LED, WT 470 C, LED8OS/840 PSD WB L1600 lights, Philips, Jena, Germany). The plants continued growing under the conditions described above for 2 weeks until the true leaves appeared. In contrast, strawberry plants were supplied by Viveros Sor Valentina as bare root plants after growing in commercial greenhouse conditions for 8 weeks.

The growth stage of the experiment was carried out in an automated plastic greenhouse located at the CEBAS-CSIC Experimental Field in Santomera (Murcia, Spain), under conditions of sunlight (PAR between 700 and 800 µmol m^{-2} s^{-1} at midday), temperature controlled at 25 °C during day and 18 °C during night. The humidity was 65 and 85% day/night, respectively.

The plants were transferred to a hydroponic system on coconut fiber substrates. The experimental design comprised three cultivation lines, one for each species, with 27 plants in each, distributed across nine substrates. Within each substrate, three plants were cultivated. The substrates were irrigated through continuous dripping at regular 7 min intervals, 4 times a day, with the drippers having a dosing capacity of 3 L h^{-1}. The irrigation solution consisted of the Standard Hoagland Solution, containing 6 mM KNO_3, 4 mM $Ca(NO_3)_2$, 1 mM KH_2PO_4, and 1 mM $MgSO_4$, along with 25 µM H_3BO_3, 2 µM $MnSO_4$, 2 µM $ZnSO_4$, 0.5 µM $CuSO_4$, 0.5 µM $(NH_4)_6Mo_7O_{24}$, and 20 µM Fe-EDDHA.

The plants grew under these conditions for 2 months, until the plants reached the stage of fruit production. After that period, the plants continued to grow for 2 months (60 days), categorized into two periods based on the growth conditions: 1) Control (first 30 days): the plants continued growing in standard greenhouse conditions described above. 2) Elevated CO_2 (last 30 days): emissions from an experimental biomass boiler began to be released into the greenhouse, gradually reaching a concentration of 1000 ppm of CO_2. To capture the toxic gases resulting from combustion, the gases were filtered through a biofilter consisting of activated charcoal, fiberglass, and coconut fiber substrate. The gas emission period lasted for 8 h each day, throughout the daylight hours (from 8:00 to 20:00), continuously.

Two days before the conclusion of each period, nine alternate plants from the central area of each cultivation line were harvested, and samples were collected for subsequent analysis. All the measurements were carried out during the central 15 days of each treatment, taking into account that the plants were at the fruit production stage.

CO_2 Supply and Capture of Polluting Gases: The CO_2 used for the experimental assay was generated from the combustion of pine wood pellets in an experimental industrial boiler designed and constructed by Sugimat S.L. (Valencia, Spain). The boiler mainly consisted of a pellet feeding system via a storage tank and an extractor screw, an automatic combustion furnace equipped with air supply fans and an automatic burner, a hot gas conduction system, an air cooler, and a gas extraction system directed toward the greenhouse or to a chimney to release gases into the atmosphere, regulated by a rotary valve.

For the combustion process, the furnace was automatically fed with wood pellets for 10 min, followed by manual ignition of the boiler through the automatic burner and activation of the ventilation system. Once the internal furnace temperature reached 900 °C, the gases were emitted into the greenhouse until the CO_2 concentration stabilized at 1000 ppm. The maintenance of the CO_2 concentration was automatically regulated by the boiler control system.

To capture the pollutants and harmful substances resulting from combustion, a biofilter was designed for industrial heating emissions. This biofilter system was designed with three specific layers: a compact fibrous material to capture small-sized particles, an activated carbon layer (3–4 cm) to retain less oxidized gases such as CO and NO, and a final layer with a specialized substrate to capture NO_2. The operational lifespan of the activated carbon layer is estimated at 5 years under standard operating conditions, while the compact fibrous material and substrate layers are projected to last 3 years. Semiannual maintenance inspections are recommended to evaluate the structural integrity and filtration efficiency of the layers. Replacement costs are estimated at 0.87 €/m^2/year for the activated carbon layer and 2.97 €/m^2 for the specialized substrate layer. These

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estimations ensure the biofilter system is economically viable and scalable for larger agricultural applications.

Figure 8 represents the boiler-biofilter system coupled with the experimental greenhouse.

The effect of the biofilter was evaluated by measuring the concentration of pollutant gases inside the greenhouse before and after its installation during an emission period (emission without biofilter and emission + biofilter, respectively) and with no emission (control). Control measurements were taken 2 weeks before starting the emission period for the gas measurements, over 1 h for 3 consecutive days, at the same time every day. For the emission period measurements, the gases were emitted into the greenhouse without the biofilter for 1 h for 3 consecutive days and, after the installation of the biofilter, the gases were emitted again for 1 h for another 3 consecutive days, at the same time every day. All the measurements for each condition were taken between 8:30 and 9:30 a.m.

Formaldehyde, TVOCs, large-sized atmospheric suspended particles up to 2.5 µm (PM $\leq$ 2.5), carbon monoxide (CO), and nitrogen oxides (NO and NO_x) were measured using two air quality meters: MICA (inBiot Monitoring S.L., Navarre, Spain) and Kunak AIR Pro (Kunak Technologies, Navarre, Spain).

Growth Analysis and Fruit Biomass: DW was measured from the aerial part (stem + leaves) at two different time points (day 10 and day 20) and fruits of nine plants of each species during the last 10 days of the month of the treatment. For DW, each sample was placed in a 60 °C oven for 7 days. For the aerial part, growth was estimated by calculating the RGR as % g DW day^{-1} (g 100 g^{-1} DW day^{-1}). Fruit biomass was expressed as the average DW (g) of single fruits during 10 days of production for each treatment. The root weights were not determined due to the difficulties in separating them from the compacted substrate.

Leaf Gas Exchange: The gas exchange parameters including transpiration, stomatal conductance, net photosynthesis rate, and substomatal CO_2 concentration were measured in fully developed leaves, using a TPS-2 Portable Photosynthesis System gas exchange meter (PP Systems, Inc., Amesbury, USA) in a total of three leaves per plant of six plants in each growth period. Leaves were measured using the PLC4 (B) leaf cuvette of the equipment, under the environmental greenhouse CO_2 concentration (400–450 ppm in control and 1000–1100 ppm in elevated CO_2 samples), airflow rate of 300 cm^3 min^{-1}, vapor pressure deficit from 2.2 to 2.4 KPa, air temperature between 23 and 25 °C, and PAR of 1100 µmol m^{-2} s^{-1} using an attached LED light unit. Measurements were done 3 h after the beginning of the photoperiod.

Analysis of the Concentration of C, N, and Mineral Elements: Macro- and microminerals contents were determined according to the ISO 11 885:1996 by Inductively Coupled Plasma-Optical Emission Spectrometry (ICP-OES) using a Thermo ICAP 6500 Duo equipment (Thermo Fisher Scientific, Waltham, MA, USA). Lyophilized samples of leaf, root, and fruit from nine selected plants of each cultivation were ground into a fine powder using a grinder (Taurus Aromatic, Lleida, Spain). For each ground sample, 200 mg was added to a microwave digestion equipment in a 25 mL tube with a mixture of 4 mL of HNO_3 (68% purity) and 1 mL of H_2O_2 (33% purity) for their subsequent digestion. 300 mL high-purity deionized water, 30 mL H_2O_2 (33% purity), and 2 mL H_2SO_4 (98% purity) were also added to the Teflon reactor. The microwave heating digestion program consisted of three steps: starting at 20 °C and 40 bar; increasing 10 bar min^{-1} for 30 min up to 220 °C; and keeping at 220 °C for 20 min. After cooling, the mineralized samples were transferred to double graduated tubes of 10 mL (microminerals) and 25 mL (macrominerals), and the volume was filled with high-purity

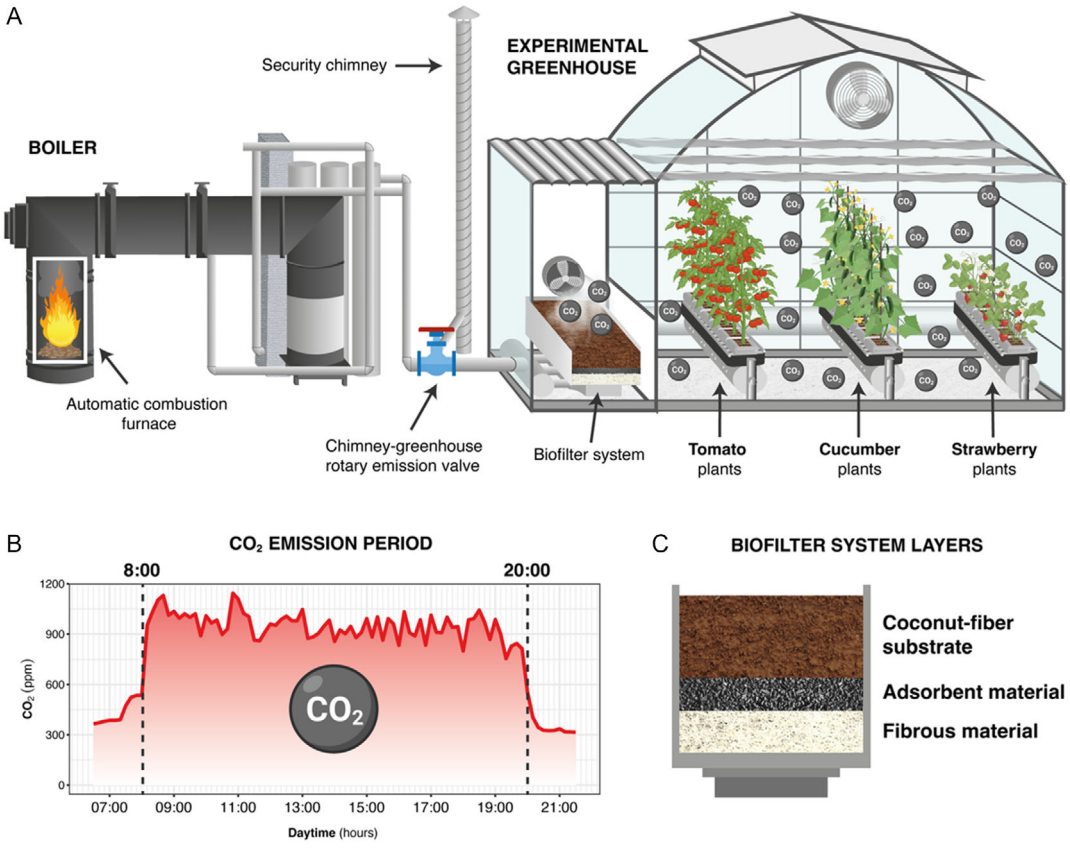


Figure 8. A) Schematic image of the boiler-biofilter system connected to the experimental greenhouse where the experiments with elevated CO_2 were conducted. B) CO_2 emission period throughout the day during the elevated CO_2 treatment phase. C) A detailed view of the layers within the biofilter system installed in the greenhouse.

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deionized water. A multimineral standard solution containing 31 minerals supplied by SCP Science (Quebec, Canada) was used to prepare calibration standards in high-purity deionized water. For ICP-OES analyses, two control samples containing high-purity deionized water and a multimineral standard were used. Each mineral determination was performed at specific wavelengths ranging from 167.1 to 670.8 nm. The concentration of macronutrients is displayed as mmol $\cdot$ kg^{-1} DW and micronutrients as µmol kg^{-1} DW.

Carbon and nitrogen contents in organic samples were determined using an elemental analyzer TruSpec CN628 (LECO Co., St. Joseph, MI, USA). 0.15 g of ground lyophilized samples used for the ICP-OES analysis was weighed, encapsulated, and placed in the autosampler, which was transferred to the purge chamber to eliminate atmospheric gases. The sample is then introduced into a combustion furnace with pure oxygen, where it rapidly oxidizes to carbon dioxide (CO_2), water (H_2O), and nitrogen oxides (NO_x). Minerals and metals form oxides that remain in the crucible. The gases pass through a secondary furnace and a series of reagents to enhance oxidation and remove impurities. Subsequently, the gases are cooled and condensed, removing the water vapor and resulting particles. The gas mixture is homogenized in a ballast container, and a gas aliquot is analyzed using infrared cells to detect CO_2 and a thermal conductivity cell to detect N_2. The results are displayed as mmol kg^{-1} DW.

Flavonoids Extraction and Analysis: Freeze-dried powder from leaves (0.1 g) was extracted with 1.5 mL of a mixture of methanol:water:formic acid (25:24:1) and sonicated for 1 h, followed by an overnight maceration at 4 °C. Samples were centrifuged for 15 min at 15 000 × g and supernatants were collected and filtered through a 0.22 µm pore diameter polyvinylidene fluoride (PVDF) membrane. The chromatographic analyses were performed in an Agilent HPLC 100 series (Agilent Technologies, Waldbronn, Germany), with a Phenomenex reverse-phase column (250 × 4.6 mm, Luna 3 µm C18(2), 100 Å). Gradient conditions and the phases used were followed as described in ref. [61].

Primary Metabolites Analysis: The concentration of organic acids, amino acids, carbohydrates, and other metabolites in the leaves was determined using 50 mg of lyophilized sample in 2 mL Eppendorf tubes. To this tube, 1200 µL of a methanol and water mixture (MeOH:H_2O; 1:1) was added and vigorously shaken. Subsequently, the samples were sonicated three times and incubated for 30 min at 4 °C. Later, the samples were centrifuged at 11 000 × g for 20 min at 4 °C. The supernatant was transferred to a new 1.5 mL Eppendorf tube and dried under rapid vacuum overnight at a maximum temperature of 30 °C to thoroughly dry the samples. The dried samples were resuspended in 800 µL of 100 mM potassium phosphate buffer (KH_2PO_4) at pH = 6.0 (diluted in 100% H_2O) + 0.58 mM TSP-d4 (internal standard). Subsequently, the samples were filtered using 0.45 µm pore diameter nylon filters. Finally, 600 µL of the filtered samples were placed in a 5 mm NMR tube for quantification using proton nuclear magnetic resonance spectroscopy (1H-NMR).

Statistical Analysis: Data analyses were performed using RStudio software (RStudio 16 PBC, Boston, Massachusetts, USA) with R version 4.1.0. All the parameters were analyzed with a Student's *t*-test, with a previous Levene's test, considering in all cases values $p < 0.05$ as significant: * means $p < 0.05$, ** means $p < 0.01$, *** means $p < 0.001$, and n.s. means no significant differences. Outliers were identified and excluded using Rosner's test ($p \leq 0.05$).

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Conflict of Interest

The authors declare no conflict of interest.

Author Contributions

Alberto Martinez-Alonso: conceptualization (supporting); formal analysis (lead); investigation (supporting); methodology (supporting); software (supporting); visualization (supporting); writing—original draft (lead). **Jose Fermoso**: data curation (supporting); investigation (lead). **Francisco Verdugo**: data curation (equal); investigation (supporting); writing—original draft (equal); writing—review and editing (supporting). **Micaela Carvajal**: conceptualization (lead); funding acquisition (lead); resources (lead); validation (lead); writing—review and editing (lead).

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Keywords

biofilters, elevated carbon dioxide, emissions, greenhouse, metabolism, photosynthesis

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