BENEFITS OF ATMOSPHERIC CO₂ ENRICHMENT ON TOMATO

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Nearly all crops respond to increases in the air's CO₂ content by displaying enhanced rates of photosynthesis and biomass production; and in this brief review of some recent pertinent papers, we find that tomato is no exception to the rule, even when grown under stressful conditions of fungal infection and high soil salinity.

Ziska et al. (2001)¹ grew tomato plants at a nocturnal atmospheric CO₂ concentration of 500 ppm, obtaining total plant biomass values that were 10% greater than those exhibited by control plants growing in air containing 370 ppm CO₂. This result was likely the consequence of the elevated CO₂ reducing the rate of nocturnal respiration in the plants, which would have allowed them to utilize the retained carbon to produce more biomass.

Writing as background for their study, Wang et al. (2013)² state "it has been reported that tomato plants grown under elevated CO₂ have greater total root length, root surface area, root diameter, root volume and number of lateral roots than those under ambient CO₂, leading to a greater root system," citing Wang et al. (2009). And they indicate that "as a result, elevated CO₂ significantly increased the uptake of N, P, K, Ca, Mg and micronutrients (Cu, Fe, Mn and Zn)," which in turn was found to have promoted "plant growth and development (Prior et al., 1998)."

In a study designed to further explore this phenomenon, Wang et al. (2013) assessed the lateral root production of 19-day-old tomato (Solanum lycopersicum) seedlings grown in basal nutrient solution for an additional four days under hydroponic conditions in the laboratory at atmospheric CO₂ concentrations of either 350 or 800 ppm. Consistent with the findings of Wang et al. (2009), the seven scientists found that the number of lateral roots increased by 75% under elevated CO₂ compared to ambient CO₂ and that the length of the roots increased as well. And with more and longer lateral roots in a future CO₂-enriched atmosphere, tomato plants (and likely other plants as well) should be better equipped to take up both major and micro nutrients from the soils in which they grow, making them both bigger and better and more apt to produce larger and more nutritious fruit ... and more of it.

¹ http://www.co2science.org/articles/V5/N4/B1.php
² http://www.co2science.org/articles/V16/N24/B2.php
This CO₂-induced benefit, as well as a host of other positive effects of atmospheric CO₂ enrichment, are also manifest under unfavorable growing conditions. Jwa and Walling (2001), for example, grew tomato plants hydroponically for eight weeks in controlled environment chambers receiving atmospheric CO₂ concentrations of 350 and 700 ppm. At week five of the study, half of all plants growing in each CO₂ concentration were infected with the fungal pathogen *Phytophthora parasitica*, which attacks plant roots and induces water stress that ultimately decreases plant growth and yield. In consequence of pathogenic infection, total plant biomass was reduced by nearly 30% at both atmospheric CO₂ concentrations. However, elevated CO₂ increased the total biomass of healthy and infected plants by approximately the same degree (+30%). In other words, infected tomato plants grown at 700 ppm CO₂ had biomass values that were similar to those of healthy tomato plants grown at 350 ppm CO₂. Thus, atmospheric CO₂ enrichment completely counterbalanced the negative effects of pathogenic infection on overall plant productivity. Therefore, increased harvests in a future CO₂-enriched world due to reductions in yield loss caused by this pathogenic fungal organism may well occur in the future.

Introducing their work, Huang et al. (2012) write that the tomato yellow leaf curl virus (TYLCV) "causes severe damage to tomato crops in many tropical and subtropical regions worldwide (Czosnek and Laterrot, 1997; Zhou et al., 2009)," and they say that "in China, TYLCV is the most important viral pathogen of tomato in the major tomato-producing areas," citing Zhu et al. (2008).

In an attempt to determine the impact of this virus at different CO₂ concentrations, Huang et al. grew tomatoes (*Lycopersicon esculentum*) from seed in pots filled with sterilized loamy field soil that were enclosed within ventilated insect-proof cages placed inside open-top chambers located in Xiaotangshan County, Beijing, China, where half of the cages were infected with TYLCV and the plants in both sets of cages were allowed to grow for approximately two months in both 2009 and 2010 in ambient or CO₂-enriched air of either 363 or 758 ppm in 2009 and either 372 or 746 ppm in 2010. Results indicated that "elevated CO₂ decreased TYLCV disease incidence (by 14.6% in 2009 and 11.8% in 2010) and decreased disease severity (by 20.0% in 2009 and 10.4% in 2010)." In addition, they found that "elevated CO₂ increased tomato plant height by 40.8% and 36.5%, and increased the aboveground biomass by 23.3% and 14.3%, in uninfected plants and TYLCV-infected plants in 2009, respectively," while "elevated CO₂ increased plant height by 36.9% and 26.0% and increased the aboveground biomass by 53.9% and 28.7%, in uninfected plants and

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4 http://www.co2science.org/articles/V16/N16/B2.php
TYLCV-infected plants in 2010, respectively." Such findings suggest that, in addition to the fact that atmospheric CO₂ enrichment significantly enhances the productivity of uninfected tomato plants, Huang et al. say they imply that the predicted increases in tomato productivity under normal conditions may be further enhanced "by reduced susceptibility to plant viruses under projected rising CO₂ conditions."

Examining the topic of pathogen infection from a slightly different angle, Li et al. (2015)⁵ note that elevated atmospheric CO₂ concentrations in agricultural and natural ecosystems are known to reduce plant stomatal openings; but they say it is unclear how this CO₂-induced stomatal alteration may or may not alter foliar pathogen infections. And, therefore, in an attempt to answer this important question, they grew tomato plants, some of which they inoculated with Pseudomonas syringae tomato strain DC3000 -- which they say is virulent to tomatoes -- under ambient (380 ppm) and elevated (800 ppm) atmospheric CO₂ concentrations.

In discussing their findings, the twelve Chinese researchers report that "elevated CO₂ enhanced tomato defense against P. syringae," based on scanning electron microscopy that revealed that the stomatal apertures of elevated CO₂ plants were considerably smaller than those of their ambient counterparts; and this state of affairs negatively affected the behavior of P. syringae bacteria on the upper surfaces of epidermal peels. In addition, the elevated-CO₂-induced decrease in stomatal conductance was accompanied by a simultaneous increase of endogenous NO content that further mediated stomatal closure, thereby implying, in the words of Li et al., that "factors other than the stomata also play a role in elevated-CO₂-induced P. syringae resistance." And in light of these findings, Li et al. declare, in the concluding sentence of their paper, that "this information is important for making proper predictions with regard to disease pressure and for designing strategies to improve plant pathogen resistance."

In another stressful situation, Maggio et al. (2002)⁶ grew tomato (Lycopersicon esculentum Mill.) in environmental chambers receiving atmospheric CO₂ concentrations of 400 and 900 ppm in combination with varying degrees of soil salinity for one month to determine the effects of elevated CO₂ on salt tolerance in this important agricultural crop. They found that plants grown in elevated CO₂ tolerated an average root-zone salinity threshold value that was about 60% greater than that exhibited by ambiently-grown plants (51 vs. 32 mmol dm⁻³ Cl⁻). In addition, the water-use of CO₂-enriched plants was about half that exhibited by ambiently-grown plants. Moreover, the amount of chloride in the leaves of CO₂-enriched plants was significantly lower than that in the leaves of ambiently-grown plants, supporting the supposition that water and salt uptake are linked. Such findings collectively suggest that as the air's CO₂ concentration increases, tomato plants will likely fare better than they presently do on older agricultural soils that may have inherently high soil salinities, due to CO₂-induced increases in root-zone salt tolerance and reductions in salt uptake. Thus, there should less yield reductions in this valuable agricultural crop resulting from salinity-induced stresses in the future.

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⁵ http://www.co2science.org/articles/V18/jul/a11.php
Scientists have also explored the response of tomato plants growing in stressful saline soils under both ambient and elevated CO\textsubscript{2} concentrations. Takagi et al. (2008)\footnote{http://www.co2science.org/articles/V12/N24/B3.php}, for example, grew well watered and fertilized tomato \([\textit{Solanum lycopersicum} \text{ (formerly \textit{Lycopersicon esculentum}) \text{ L. cv. Momotarou}}]\) seedlings for two weeks at two different levels of irrigation-water salinity (0 or 100 mM NaCl) in 3-L pots inside the greenhouse of Hiroshima University, Japan, at atmospheric CO\textsubscript{2} concentrations of either 370 or 1000 ppm, while measuring various plant properties and physiological responses. In so doing, Takagi et al. report that the "salt-stress treatment severely decreased whole-plant biomass," as well as "leaf photosynthesis and transport of carbon assimilates," but that "the impact of stress on these activities was alleviated under elevated CO\textsubscript{2} concentration." This alleviation, as they describe it, "was promoted when sink activity relative to source activity was higher," which they say was "probably owing to improvement of oxidative stress," due "at least partially to the higher constitutive antioxidant enzymes' activities," as well as improved water status "through stomatal closure at high CO\textsubscript{2} concentration." The seven scientists conclude that their study "corroborates earlier reports that the interaction between salinity stress and CO\textsubscript{2} concentration result[s] in the alleviative effect of elevated CO\textsubscript{2} on the negative effects of salinity on plant growth," which conclusion has also been reached by Sánchez-Gonzále\textsc{z} et al. (2015).\footnote{http://www.co2science.org/articles/V18/oct/a20.php}

Writing as background for their work, Sánchez-Gonzále\textsc{z} et al.\footnote{http://www.co2science.org/articles/V18/oct/a20.php} note that "the South-Eastern region of Spain is an important area for both production and exportation of very high quality tomatoes for fresh consumption." This is primarily due to favorable growing conditions such as a mild climate, good soils and saline waters that promote "exceptional fruit quality of some varieties," including the Raf tomato hybrid. However, Sánchez-Gonzále\textsc{z} et al. additionally note that, "despite the high value of Raf tomatoes in the Spanish national market, their productivity is relatively low and the consumer does not always get an acceptable quality, often because the fruit growth conditions, mainly thermal and osmotic, were not adequate." Against this backdrop, the team of six researchers set out to determine if they could improve the production value of this high value commercial crop by manipulating the environmental conditions in which the tomatoes are grown. To accomplish this objective, they grew hybrid Raf tomato plants \(\textit{Lycopersicon esculentum} \text{ Mill. cv. Delizia}\) in controlled environment greenhouses at two salinity levels (low and high) under ambient (350 ppm) and elevated (800 ppm) CO\textsubscript{2} concentrations. Then over the course of the growing season, and at harvest, they measured several parameters related to the growth and quality of the hybrid tomatoes. And what did their analysis of those measurements reveal?
According to the researchers, the high salinity treatment "increased firmness, total soluble solids content, titratable acidity and the percentage of dry matter of the fruit," leading them to conclude that the high salinity growth medium "is necessary to obtain high quality tomato fruits." However, this benefit did not come without a price, as higher salinity decreased marketable yield (47% less), fruit numbers (9.5% less), and average weight of the fruits (19% less) when compared to tomatoes grown under low salinity conditions. With respect to CO$_2$, elevated levels increased tomato yield, fruit numbers and average weight of the fruits in the low salinity treatment, and they reduced the deleterious effects of salinity on these measures in the high salinity treatment. Additionally, elevated CO$_2$ shortened the time required for fruit development by two days and it had little to no effect on fruit quality. Consequently, the authors conclude by stating "the results of this work suggest that the utilization of a [high salinity] nutrient solution ... is necessary to obtain high quality tomato fruits and CO$_2$ application increases its production," while adding "CO$_2$ enrichment allows increase in the production of a high value commercial crop grown under saline conditions by reducing the time needed for complete fruit development without compromising organoleptic quality." And in the future, therefore, the Spanish national market of hybrid Raf tomatoes will benefit thanks to the ever-increasing CO$_2$ concentration of the atmosphere.

Finally, we come to the study of Zhang et al. (2014)$^9$, who write that "in China, tomatoes are often grown in greenhouses, in order to provide early-ripening fruit that meet the demands of consumers." But they say that "the quality of greenhouse tomato, as indicated by characteristics such as color and flavor, as well as content of ascorbic acid and carotenoids, is usually found to be poor." And because of those facts, they report that "many complaints about poor quality of tomato fruit have been made in the past few years (Baldwin et al., 2000), and consumers demand products with better flavor (Causse et al., 2003)."

In response to these widespread consumer complaints, Zhang et al. conducted a two-greenhouse study, where one was subject to prior standard operating procedures and the other differed by merely having a composting unit of the type described by Jin et al. (2009) placed in its center. And this single alteration led to greenhouse CO$_2$ concentrations in the range of 800-900 ppm, as compared to the 100-250 ppm daytime concentrations characteristic of the control greenhouses due to their "hermetic conditions, which impair plant growth," as described by Klaring et al. (2007).

In the words of the five Chinese researchers who analyzed the consequences of this one simple addition to prior standard greenhouse culture conditions, "the contents of health-promoting compounds, including lycopene, β-carotene, and ascorbic acid, as well as the flavor, indicated by sugars, titratable acidity, and sugar/acid ratio, were markedly increased in CO$_2$ enrichment fruits." And they additionally state that "CO$_2$ enrichment significantly enhanced other organoleptic characteristics, including color, firmness, aroma, and sensory attributes in tomato fruits."

Bolstering their observations, Zhang et al. add that "the finding of increased content of ascorbic acid by CO$_2$ enrichment is consistent with the effect of CO$_2$ enrichment on orange (Idso et al., 2002), and leaf lettuce (Jin et al., 2009)," while noting that the positive effects of elevated CO$_2$ on flavor "have also been found in grape," citing Bindi et al. (2001). And they end their paper by

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$^9$ http://www.co2science.org/articles/V17/N22/B1.php
adding that their conclusion that high concentrations of carotenoids and ascorbic acid "highlight the nutrient value of tomato," is additionally supported by the findings of Crozier et al. (1997), who also found the same to be true for tomato, as well as for onions, lettuce and celery. Thus, the tomato fruit plucked from the plants growing in the greenhouse with the composting unit in the midst of it looked better, felt better, smelled better, tasted better and were better for one's health. What more could one possibly ask? ... especially of what the Obama Administration and many other world government leaders wrong-headedly call an air pollutant?

Clearly, the evidence reveals that as the CO\textsubscript{2} content of the air increases, tomato plants will likely display greater rates of photosynthesis and biomass lead to greater fruit yields, even under stressful conditions of fungal infection and high soil salinity.

For more information on tomato growth responses to atmospheric CO\textsubscript{2} enrichment see Plant Growth Data: Tomato (dry weight\textsuperscript{10}, photosynthesis\textsuperscript{11}).

REFERENCES


\textsuperscript{10} http://www.co2science.org/data/plant_growth/dry/l/lycopersicone.php

\textsuperscript{11} http://www.co2science.org/data/plant_growth/photo/l/lycopersicone.php

Huang, L., Ren, Q., Sun, Y., Ye, L., Cao, H. and Ge, F. 2012. Lower incidence and severity of tomato virus in elevated CO$_2$ is accompanied by modulated plant induced defense in tomato. *Plant Biology* **14**: 905-913.


