EFFECTS OF ELEVATED CO_2 ON THE STOMATAL CONDUCTANCE OF AGRICULTURAL CROPS

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CO2SCIENCE & SPPI ORIGINAL PAPER ♦ July 30, 2014

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Citation: Center for the Study of Carbon Dioxide and Global Change. "Effects of Elevated CO_2 on the Stomatal Conductance of Agricultural Crops." Last modified July 30, 2014. http://www.co2science.org/subject/s/summaries/stomatalag.php.

As the air's CO_2 content continues to rise, nearly all plants will respond by reducing their leaf stomatal apertures, through which water vapor exiting the leaf and carbon dioxide entering the leaf diffuse during transpiration and photosynthesis, respectively. This phenomenon typically leads to an increase in water use efficiency at elevated CO_2 concentrations, because with more CO_2 in the air, plants don't need to open their stomates as wide as they do at lower atmospheric CO_2 concentrations to allow for sufficient inward diffusion of CO_2 for use in photosynthesis. And as a consequence of this phenomenon, plants typically exhibit reductions in transpirational water loss, smaller yield losses attributable to the uptake of aerial pollutants, and increases in water-use efficiency. This summary document thus reviews some of the scientific literature pertaining to this important effect of elevated CO_2 on the stomatal conductances of agricultural crops.

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With more CO_2 in the air, plants don't need to open their stomates as wide as they do at lower atmospheric CO_2 concentrations to allow for sufficient inward diffusion of CO_2 for use in photosynthesis. And as a consequence of this phenomenon, plants typically exhibit reductions in transpirational water loss, smaller yield losses attributable to the uptake of aerial pollutants, and increases in water-use efficiency.

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With respect to stomatal conductance itself, in the Free-Air-CO_2-Enrichment (FACE) study of Garcia *et al*. (1998)[1] a 190-ppm increase in the atmosphere's CO_2 concentration reduced the average mid-day stomatal conductance in spring wheat by 28% over the entire growing season. Similarly, Hakala *et al*. (1999)[2] reported that average stomatal conductances in spring wheat grown at twice-ambient levels of atmospheric CO_2 were about 25% lower than those observed in ambiently-grown control plants, regardless of a concomitant exposure to an elevated air temperature treatment (3°C greater than ambient air temperature). Likewise, twice-ambient levels of CO_2 generally decreased stomatal conductances in wheat, regardless of whether the elevated CO_2 exposure was maintained on a 12- or 24-hour basis (Heagle *et al*., 1999[3]). In addition, a 400-ppm increase

1 http://www.co2science.org/articles/V2/N12/B2.php.
2 http://www.co2science.org/articles/V4/N13/B2.php.
3 http://www.co2science.org/articles/V2/N11/B2.php.

in the air's CO_2 concentration reduced stomatal conductances in hydroponically-grown peanuts by 44% ([Stancielet *al*., 2000](http://www.co2science.org/articles/V3/N17/B1.php)[4]), while a 750-ppm CO_2 increase reduced the stomatal conductances of a C4 maize crop by 71% ([Maroco *et al*., 1999](http://www.co2science.org/articles/V3/N11/B2.php)[5]).

With respect to the *consequences* of CO_2-induced reductions in stomatal conductance, Smart *et al*. (1998)[6] reported reduced rates of transpirational water loss for wheat grown at 1000 ppm CO_2 for 23 days in controlled environment chambers. McKee *et al*. (2000)[7] additionally found that a 310-ppm increase in the air's CO_2 concentration, which reduced stomatal conductances in spring wheat by about 50%, also completely alleviated high-O_3-induced reductions in leaf rubisco content and activity. And in a somewhat similar study of soybeans, Heagle *et al*. (1998)[8] observed that O_3-induced foliar injuries decreased with increasing atmospheric CO_2 concentration as a consequence of CO_2-induced reductions in stomatal conductance. Likewise, Malmstrom and Field (1997)[9] noted that twice-ambient levels of atmospheric CO_2 caused greater reductions in stomatal conductances in oats infected with a pathogenic virus than in control plants that were unaffected (50% vs. 34%). And as a result, infected oats displayed the greatest CO_2-induced percentage increases in both biomass production and water-use efficiency.

Moving on to the 21st century, enough work in this area had already been conducted for Kimball *et al*. (2002)[10] to produce a review article on the subject based on Free-Air-CO_2-Enrichment studies conducted in agricultural fields, where a 300 ppm increase in the air's CO_2 concentration was employed. And in their review, they said that, on average, wheat experienced a 51% decrease in stomatal conductance at ample water and nitrogen, plus a 66% decrease at low nitrogen. Likewise, they found that sorghum experienced a 56% stomatal conductance decrease at ample water and nitrogen; while cotton and grapes each experienced decreases of 22% at ample water and nitrogen.

In further discussing these and several other observations, Kimball *et al*. noted that "growth stimulations were as large or larger under water-stress compared to well-watered conditions." They also reported that "roots were generally stimulated more than shoots," and that although growth stimulations of non-legumes were reduced at low-soil nitrogen, "elevated CO_2strongly stimulated the growth of the clover legume both at ample and under low nitrogen conditions."

Contemporaneously, Lawson *et al*. (2002)[11] grew potatoes (*Solanum tuberosum* L.) in open-top chambers maintained at atmospheric CO_2 concentrations of 380, 550 and 680 ppm. In addition, the chambers were fumigated with air containing ambient and elevated levels of ozone (O_3). And what did they find? Overall, elevated CO_2 had a greater effect on gas exchange than did elevated ozone. Plants grown at 680 ppm CO_2, for example, exhibited stomatal conductances

4 http://www.co2science.org/articles/V3/N17/B1.php.
5 http://www.co2science.org/articles/V3/N11/B2.php.
6 http://www.co2science.org/articles/V2/N16/B3.php.
7 http://www.co2science.org/articles/V3/N37/B2.php.
8 http://www.co2science.org/articles/V2/N13/B3.php.
9 http://www.co2science.org/articles/V2/N16/B1.php.
10 http://www.co2science.org/articles/V5/N31/EDIT.php.
11 http://www.co2science.org/articles/V5/N18/B1.php.

that were 62 and 47% lower than those displayed by plants growing at 380 ppm CO_2 while exposed to ambient and elevated concentrations of ozone, respectively. Neither did elevated CO_2 nor ozone impact rates of carbon fixation to any significant degree, except for plants growing at 550 ppm CO_2 and ambient ozone, where there was an 80% increase in net photosynthesis due to atmospheric CO_2 enrichment. Nevertheless, elevated CO_2 progressively increased instantaneous water use efficiency, regardless of ozone exposure. Thus, as the air's CO_2 content continues to rise, it is highly likely that potatoes will be able to better deal with water stress, enabling them to be grown in more arid regions of the globe.

Also experimenting concurrently - and with potatoes - Olivo *et al.* (2002)[12] grew *two* species (*Solanum curtilobum* cv. Ugro Shiri, from high altitude, and *S. tuberosum* cv. Baronesa, from low altitude) in pots placed within open-top chambers maintained at atmospheric CO_2 concentrations of 350 and 700 ppm for 30 days following the onset of reproductive growth in order to study the effects of elevated CO_2 on gas exchange and biomass production in these two potato species adapted to different altitudes. This work revealed that doubling the atmosphere's CO_2 content increased rates of net photosynthesis by 56 and 53% in the high- and low-altitude potato species, respectively, while reducing their stomatal conductances by 55 and 59% and increasing their instantaneous water-use efficiencies by 90 and 80%, respectively. In addition, it increased tuber dry mass production by 85 and 40% in the high- and low-altitude potato species, respectively.

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One year later, Agrawal and Deepak (2003)[13] grew two cultivars of wheat (*Triticum aestivum* L. cv. Malviya 234 and HP1209) in open-top chambers maintained at atmospheric CO_2 concentrations of 350 and 600 ppm alone and in combination with 60 ppb SO_2 to study the interactive effects of elevated CO_2 and this major air pollutant on the growth and yield of this important crop. And in doing so, they determined that exposure to elevated CO_2 significantly increased photosynthetic rates by 58 and 48% in M234 and HP1209, respectively. In contrast, fumigation with elevated SO_2 did not significantly impact rates of photosynthesis in either cultivar. However, plants grown in the combined treatment of elevated CO_2 and elevated SO_2 displayed photosynthetic rates that were 42 and 38% greater than those measured in control plants for M234 and HP1209, respectively.

The wheat plants grown in elevated CO_2 also displayed an approximate 20% reduction in stomatal conductance, while those grown in elevated SO_2 exhibited an average

[12] http://www.co2science.org/articles/V6/N1/B1.php.
[13] http://www.co2science.org/articles/V6/N4/B1.php.

conductance *increase* of 15%. When exposed simultaneously to *both* gases, however, the wheat plants displayed an average 11% reduction in stomatal conductance. Consequently, this phenomenon contributed to an approximate 32% increase in water-use efficiency for plants simultaneously exposed to both gases, whereas those exposed to elevated SO_2 alone displayed an average *decrease* in water-use efficiency of 16%.

Contemporaneously, Kyei-Boahen *et al*. (2003)[14] grew well watered and fertilized plants of four carrot (*Daucus carota* var. sativus L.) cultivars (Cascade, Caro Choice, Oranza and Red Core Chantenay) from seed in 15-cm-diameter plastic pots in a controlled environment facility for 30 days past emergence, whereupon leaf stomatal conductance (Gs) was measured at 100-ppm intervals of short-term (5-minute) atmospheric CO_2 enrichment yielding absolute CO_2 concentrations (Ca) stretching from 50 to 1050 ppm; and in doing so, they found that "increasing Ca from 50 to 350 ppm increased Gs to a maximum and thereafter Gs declined by 17% when Ca was increased to 650 ppm," while "a three-fold increase in Ca from 350 to 1050 ppm decreased Gs by 53%."

Moving ahead another year, Cardoso-Vilhena *et al*. (2004)[15] grew individual spring wheat (*Triticum aestivum* L. cv. Hanno) plants in 3-dm^3 pots in controlled environment chambers for 77 days at atmospheric CO_2 concentrations of either 350 or 700 ppm and at ozone (O_3) concentrations of either less than 5 or 75 ppb, while gas exchange measurements of leaves number 4 and 7 on the plants' main shoots were made at regular intervals throughout the study, after which the plants were harvested and their total dry weights determined, while in parallel with these measurements Rubisco activity and chlorophyll fluorescence were also assessed throughout the experiment.

This work revealed that in air of less than 5 ppb O_3, the doubling of the air's CO_2 concentration increased total plant dry weight by 66%; while in air of 75 ppb O_3, it increased total plant dry weight by 189%. Over the lifespans of leaves 4 and 7, elevated CO_2 also reduced cumulative O_3 uptake by 10 and 35%, respectively, due to the decrease it caused in leaf stomatal conductance, while it protected against the decline in apparent quantum yield of CO_2 assimilation caused by high O_3 in the ambient CO_2 treatment. In addition, elevated CO_2 protected against the reduction in the maximum *in vivo* rate of Rubisco carboxylation induced by high O_3 in both leaves 4 and 7.

In light of these findings, the five scientists said their data revealed that "rising atmospheric CO_2 concentrations are likely to afford protection against the adverse effects of O_3 on plant growth and photosynthesis, with the effect due, at least in part, to the decline in stomatal conductance triggered by increases in atmospheric CO_2." In addition, they wrote that their study suggested that "rising atmospheric CO_2 concentrations may also enhance the tolerance of leaf tissue to O_3-induced oxidative stress," remarking that "this finding is consistent with reported shifts in the antioxidant status of leaves under the combined influence of elevated CO_2+O_3 (Rao *et al*., 1995)." And when considering the bottom line of total plant dry weight

[14] http://www.co2science.org/articles/V9/N4/B2.php.
[15] http://www.co2science.org/articles/V7/N25/B2.php.

production, it can once again be seen that atmospheric CO_2 enrichment *more* than ameliorated the deleterious effects of ozone pollution.

In a concomitant study of rice, Yoshimoto *et al.* (2005)[16] grew *Oryza sativa* L. cv. Akita-Komachi from hand-transplanting to harvest (May to September) under normal paddy culture near Shizukuishi, Iwate, Japan, within FACE rings maintained at either ambient or ambient + 200 ppm CO_2 for 24 hours per day, over which period they measured a number of micrometeorological parameters and plant characteristics. This work revealed, as they described it, that "elevated CO_2reduced stomatal conductance by 13% in upper leaves and by 40% in lower leaves at the panicle initiation stage," but that the reduction declined thereafter. In addition, they observed that "stomata closed more in the elevated CO_2 plot as vapor pressure deficit increased," i.e., during drier conditions. And so it was that averaged over the entire growing season, the Japanese researchers determined that the total water used by the crop was 268.7 mm in the ambient CO_2 treatment and 246.7 mm in the elevated CO_2 treatment, thanks to the CO_2-induced increase in plant stomatal conductance.

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Advancing two more years, Bernacchi *et al.* (2007)[17] wrote as background for their study that "with very few exceptions, deceased stomatal conductance (gs) is one of the most consistent and conserved responses of leaves to growth at elevated CO_2," but they went on to note that less well understood was the extent to which *leaf-level* responses translate to changes in *ecosystem* evapotranspiration (ET); and, therefore, they said that it "is not certain that a decrease in gs will decrease ET in rain-fed crops."

To try to provide some certainty in this regard was thus the primary purpose of their study; and to do so, the five researchers grew soybean (*Glycine max*) under field conditions in Free-Air CO_2 Enrichment (FACE) plots maintained at ambient (~375 ppm) and elevated (~550 ppm) atmospheric CO_2 concentrations for four complete growing seasons at the SoyFACE facility in central Illinois (USA), making season-long measurements of both leaf gs and canopy ET once complete canopy closure had been achieved, after which they conducted a number of analyses of the data thereby obtained.

[16] http://www.co2science.org/articles/V9/N19/B3.php.
[17] http://www.co2science.org/articles/V10/N15/B3.php.

Based on their real-world field observations, Bernacchi *et al*. were able to report that "elevated CO_2 caused ET to decrease between 9% and 16% depending on year and despite large increases in photosynthesis and seed yield," and that "ecosystem ET was linked with gs of the upper canopy leaves when averaged across the growing seasons, such that a 10% decrease in gs results in a 8.6% decrease in ET."

In discussing the implications of their meticulous and voluminous field observations, the researchers confirmed that their findings "are consistent with model and historical analyses that suggest that ... decreased gs of upper canopy leaves at elevated CO_2 results in decreased transfer of water vapor to the atmosphere." They also noted that their findings were "consistent with the recent mechanistic modeling and statistical fingerprinting analysis of global trends in increasing river discharge across the 20th century," which suggested, last of all, that "suppression of plant transpiration due to the effect of rising CO_2 on stomatal closure is the most consistent factor in explaining observed [river discharge] changes (Gedney *et al*., 2006)." And *this* conclusion, in turn, finally confirmed what was suggested to be the case *well over two decades earlier* by Idso and Brazel (1984) in a paper entitled "Rising atmospheric carbon dioxide concentrations may increase streamflow."

Moving on three more years, Shimono *et al*. (2010)[18] wrote as background for their study that "by 2050, the world's population will have increased by about 37%, from the current level of 6.7 billion to an estimated 9.2 billion (UN, 2009), with a corresponding increase in global food demand." They also stated that "about 0.6 billion Mg of rice is produced annually from an area of 1.5 million km^2, making rice one of the most important crops for supporting human life," *especially*, as noted by Pritchard and Amthor (2005), since it supplies the planet's human population with an estimated 20% of their energy needs (on a caloric basis) and 14% of their protein requirements (on a weight basis).

Within this context, the six scientists further noted that "rice production depends heavily on water availability," stating that "irrigated lowlands account for 55% of the total area of harvested rice and typically produce two to three times the crop yield of rice grown under non-irrigated conditions (IRRI, 2002)." And because the demand for ever greater quantities of water will continue to rise, due to our need to adequately feed humanity's growing numbers, they concluded that "efficient use of water will thus be essential for future rice production."

As a result, and in an attempt to determine how the agricultural enterprise may be impacted in this regard by the ongoing rise in the air's CO_2 content, the Japanese researchers conducted a two-year *free-air CO_2 enrichment* or FACE study in fields at Shizukuishi, Iwate (Japan) to learn how elevated CO_2 may reduce crop water use via its impact on the leaf stomatal conductance (g_s) of three varieties of rice (*Oryza sativa* L.): early-maturing Kirara397, intermediate-maturing Akitakomachi, and latest-maturing Hitomebore.

In response to the 53% increase in daytime atmospheric CO_2 concentration employed in their experiments, Shimono *et al*. determined that "the reduction in g_s due to elevated CO_2 was similar across measurements, averaging around 20% in the morning, 24% around noon and 23%

[18] http://www.co2science.org/articles/V13/N20/B2.php.

in the afternoon across all growth stages." And they added that "there was no significant CO_2 x cultivar interaction." Therefore, with the concomitant increase in grain yield that also results from atmospheric CO_2 enrichment, it should be apparent to all that a continuation of the historical and still-ongoing rise in the air's CO_2 content will play a major role in enabling humanity to meet its food needs at the mid-point of the current century, without having to lay claim to all of the planet's remaining fresh water resources and much of its undeveloped land and thereby driving many of the species - with which we share the terrestrial biosphere - to *extinction* for lack of land and water to meet *their* needs.

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Rounding out this review of CO_2 effects on plant stomatal conductance is the paper of Burkart *et al.* (2011)[19]. Working in a 20-hectare field near the German city of Braunschweig in southeastern Lower Saxony, they began a *free-air CO_2 enrichment* (FACE) experiment in 1999 by enriching the air above portions of the field to a CO_2 concentration of 550 ppm. This study included two rotation cycles (six years in total) of a typical local crop rotation that went from winter barley (*Hordeum vulgare*) to a cover crop of Italian ryegrass (*Lolium multiflorum*) to sugar beet (*Beta vulgaris*) to winter wheat (*Triticum aestivum*), during which time they measured a number of soil, plant and atmospheric properties, while managing the crops in accordance with current local farming practices in which "field irrigation was applied in order to avoid drought stress during the main growing season, keeping soil water content above 50% of maximum plant available soil water content."

Averaged across the two rotation cycles, Burkart *et al*. determined that the approximate 47% increase in the air's CO_2 content they supplied to portions of the field reduced canopy *stomatal conductance* by 9%, 17% and 12% in barley, sugar beet and wheat, respectively, and that it likewise reduced canopy *transpiration* by 9%, 18% and 12% in the same three crops. And as a consequence of the lower canopy transpirational water loss, they found that the CO_2 increase "increased plant water available soil water content in the course of the season by *ca*. 15 mm ... for all crops and years."

In discussing the implications of their findings, the five German scientists thus said that the cumulative increase of soil moisture due to CO_2 enrichment found in their study suggests that

[19] http://www.co2science.org/articles/V14/N17/B1.php.

in a future atmosphere, "CO_2-related water savings may improve crop water status and reduce the need for irrigation in Central Europe," which could prove to be a huge boon to the inhabitants of that continent.

In succinctly stating the main message of the experimental findings described in this summary document, it would appear that atmospheric CO_2 enrichment reduces the stomatal conductances of nearly all agricultural plants under many different growing conditions, including unfavorable ones characterized by elevated air temperatures, elevated ozone concentrations, and the presence of pathogenic viruses. Thus, as the air's CO_2 content continues to rise, agricultural crops should exhibit ever-increasing *reductions* in transpirational water losses and yield losses that result from various diseases and aerial pollutants, while simultaneously experiencing significant increases in crop water-use efficiency.

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Cover photo of US long grain rice by Keith Weller, as posted to ars.usda.gov.