Interactive Effects of CO_2 and Water Stress on Agricultural Crop Growth

SPPI
Science & Public Policy Institute
"science-based policy for a better world"

SPPI & CO2Science Original Paper ♦ July 23, 2013

INTERACTIVE EFFECTS OF CO_2 AND WATER STRESS ON AGRICULTURAL CROP GROWTH

Citation: Center for the Study of Carbon Dioxide and Global Change. "Interactive Effects of CO_2 and Water Stress on Agricultural Crop Growth." Last modified July 3, 2013. http://www.co2science.org/subject/g/summaries/growthwaterag.php.

As the air's CO_2 content continues to rise, nearly all of earth's plants will exhibit increases in photosynthesis and biomass production; but climate alarmists periodically claim that elevated concentrations of atmospheric CO_2 will lead to more droughty conditions in many parts of the world and thereby significantly reduce or totally negate these CO_2-induced benefits. Therefore, to help determine to what degree this claim has any validity, we here review and summarize the results of numerous CO_2-enrichment studies that were designed and conducted in such a way as to reveal the various means by which atmospheric CO_2 enrichment may actually *help* a number of important food crops to successfully cope with this potential problem of more frequent periods of less-than-optimal water availability.

One way in which atmospheric CO_2 enrichment helps plants in this regard is that it stimulates them to develop larger-than-usual and more robust root systems that enable them to probe greater volumes of soil for scarce and much-needed moisture. Wechsung *et al.* (1999)[1], for example, observed a 70% increase in lateral root dry weights of water-stressed wheat grown at 550 ppm CO_2, while De Luis *et al.* (1999)[2] reported a whopping 269% increase in root-to-shoot ratio of water-stressed alfalfa growing at 700 ppm CO_2. Thus, elevated CO_2 may often elicit stronger-than-usual positive root responses in agricultural species under conditions of water stress.

Elevated levels of atmospheric CO_2 also tend to reduce the openness of stomatal pores on leaves, thus decreasing plant stomatal conductance. This phenomenon, in turn, reduces the amount of water lost to the atmosphere by transpiration and, consequently, lowers overall plant water use. Serraj *et al.* (1999)[3], for example, report that water-stressed soybeans grown at 700 ppm CO_2 reduced their total seasonal water loss by 10% relative to that of water-stressed control plants grown at 360 ppm CO_2. And Conley *et al.* (2001)[4] found that a 200-ppm increase in the air's CO_2 concentration reduced cumulative evapotranspiration in water-stressed sorghum by approximately 4%.

Atmospheric CO_2 enrichment thus increases plant water *acquisition* by stimulating root growth, while it reduces plant water *loss* by constricting stomatal apertures. And these two phenomena typically enhance plant *water-use efficiency*, even under conditions of less-than-optimal soil water content. And they have other implications as well.

---

[1] http://www.co2science.org/articles/V2/N16/B4.php.
[2] http://www.co2science.org/articles/V3/N10/B5.php.
[3] http://www.co2science.org/articles/V2/N16/B2.php.
[4] http://www.co2science.org/articles/V4/N42/B2.php.

CO_2-induced increases in root development together with CO_2-induced reductions in stomatal conductance often contribute to the maintenance of a more favorable plant water status during times of drought. Sgherri *et al.* (1998)[5], for example, have reported that leaf water potential, which is a good indicator of overall plant water status, was 30% higher (less negative and therefore more favorable) in water-stressed alfalfa grown at an atmospheric CO_2 concentration of 600 ppm versus 340 ppm. In addition, Wall (2001)[6] found that leaf water potentials were similar in CO_2-enriched water-stressed plants and ambiently-grown well-watered control plants, which implies a complete CO_2-induced amelioration of water stress in the CO_2-enriched plants. And on top of this, Lin and Wang (2002)[7] demonstrated that elevated CO_2 caused a several-day delay in the onset of the water stress-induced production of the highly reactive oxygenated compound H_2O_2 in spring wheat. Also, they discovered that plants grown in elevated CO_2 maintained higher enzymatic activities of superoxide dismutase and catalase - two important *antioxidants* - relative to those observed in ambiently-grown plants, following the induction of water stress.

If atmospheric CO_2 enrichment allows plants to maintain a better water status during times of water stress, it is only logical to expect that they should exhibit greater rates of *photosynthesis* than plants growing in similarly-water-deficient soil in non-CO_2-enriched air.

So if atmospheric CO_2 enrichment allows plants to maintain a better water status during times of water stress, it is only logical to expect that they should exhibit greater rates of *photosynthesis* than plants growing in similarly-water-deficient soil in non-CO_2-enriched air. And so they typically do. With the onset of experimentally-induced water stress in India Mustard (*Brassica juncea*), for example, photosynthetic rates dropped by 40% in plants growing in ambient air, while plants growing in air containing 600 ppm CO_2 only experienced a 30% reduction in net photosynthesis, as was observed in the experiment conducted by Rabha and Uprety (1998)[8]. And in another manifestation of this phenomenon, Ferris *et al.* (1998)[9] reported that after imposing water-stress conditions on soybeans and allowing them to recover following complete rewetting of the soil, plants grown in air

[5] http://www.co2science.org/articles/V2/N5/B3.php.
[6] http://www.co2science.org/articles/V5/N1/B2.php.
[7] http://www.co2science.org/articles/V5/N41/B1.php.
[8] http://www.co2science.org/articles/V2/N5/B4.php.
[9] http://www.co2science.org/articles/V1/N7/B1.php.

containing 700 ppm CO_2 reached pre-stressed rates of photosynthesis after six days, while plants grown in ambient air *never* recovered to pre-stressed photosynthetic rates.

Reasoning analogously, it is also only to be expected that plant *biomass* production would be enhanced by elevated CO_2 concentrations under drought conditions. In exploring this idea, for example, Ferris *et al.* (1999)[10] reported that water-stressed soybeans grown at 700 ppm CO_2 attained seed yields that were 24% greater than those of similarly-water-stressed plants grown at ambient CO_2 concentrations, while Hudak *et al.* (1999)[11] reported that water-stress had *no* detrimental effect on yield in *CO_2-enriched* spring wheat. And there have been *many* such studies, where the CO_2-induced *percentage* biomass increase has actually been found to be *greater* for water-stressed plants than for well-watered plants, as demonstrated in the review of the subject produced by Idso and Idso (1994).

Subsequently, for example, Li *et al.* (2000)[12], reported that a 180-ppm increase in the air's CO_2 content increased final grain weights in the upper and lower sections of the main stems of the spring wheat they studied by 10 and 24%, respectively, under water-stressed conditions, but that under well-watered conditions elevated CO_2 increased final grain weights only in the lower sections of the main stems and by only 14%. Thus, elevated CO_2 had a greater positive impact on final grain weights of spring wheat under water-stressed field conditions compared to non-water-stressed field conditions, once again demonstrating that atmospheric CO_2 enrichment is often more important to stressed plants than it is to non-stressed plants.

Similarly, spring wheat grown in air containing an additional 280 ppm CO_2 exhibited 57 and 40% increases in grain yield under water-stressed and well-watered conditions, respectively (Schutz and Fangmeier, 2001[13]), while Ottman *et al.* (2001)[14] found that elevated CO_2 increased plant biomass in water-stressed sorghum by 15%, while no biomass increase occurred in well-watered sorghum. And so it was that in predicting maize and winter wheat yields in Bulgaria under future scenarios of increased air temperature and decreased precipitation, Alexandrov and Hoogenboom (2000)[15] noted that yield losses were likely to occur if the air's CO_2 content remained unchanged, but that if the atmospheric CO_2 concentration doubled, then maize and winter wheat yields would likely increase, even under the combined stresses of elevated temperature and reduced rainfall.

Continuing our plant science stroll through history, Widodo *et al.* (2003)[16] grew rice (*Oryza sativa* [L.] cv. IR-72) in eight outdoor, sunlit, controlled-environment chambers at daytime atmospheric CO_2 concentrations of 350 and 700 ppm for an entire season. In one pair of chambers the plants were continuously flooded, in a second pair drought stress was imposed during panicle initiation, in a third pair it was imposed during anthesis, and in a fourth pair it was imposed at both stages. This work revealed that in the elevated CO_2 treatment, midday

[10] http://www.co2science.org/articles/V2/N19/B4.php.
[11] http://www.co2science.org/articles/V4/N10/B2.php.
[12] http://www.co2science.org/articles/V4/N24/B3.php.
[13] http://www.co2science.org/articles/V4/N30/B1.php.
[14] http://www.co2science.org/articles/V4/N20/B1.php.
[15] http://www.co2science.org/articles/V3/N29/B2.php.
[16] http://www.co2science.org/articles/V6/N21/B2.php.

leaf photosynthetic *CO_2 exchange rates* (CER) and chlorophyll concentrations were higher at most sampling dates. In addition, the CO_2-enriched plants exhibited enhanced midday leaf sucrose and starch accumulation during early reproductive phases.

Near the end of the imposed drought periods, however, water deficits caused substantial decreases in midday leaf CER and chlorophyll concentrations, along with concomitant reductions in the primary products of photosynthesis. These drought-induced effects, according to Widodo *et al*., "were more severe for plants grown at ambient than at elevated CO_2." They report, for example, that "plants grown under elevated CO_2 were able to maintain midday leaf photosynthesis, and to some extent other photosynthetic-related parameters, longer into the drought period than plants grown at ambient CO_2," as has also been observed for a number of other plants (Rogers *et al*., 1984; Jones *et al*., 1985; Idso, 1988; Bhattacharya *et al*., 1990; Chaves and Pereira, 1992; Clifford *et al*., 1993; Baker *et al*., 1997; Vu *et al*., 1998).

Recovery from drought-induced water stress was also more rapid in the elevated CO_2 treatment. At panicle initiation, for example, Widodo *et al*. observed that "as water was added back following a drought induction, it took more than 24 days for the ambient CO_2-[water] stressed plants to recuperate in midday leaf CER, compared with only 6-8 days for the elevated CO_2-[water] stressed plants." Similarly, they report that "for the drought imposed during anthesis, midday leaf CER of the elevated CO_2-[water] stressed plants was fully recovered after 16 days of re-watering, whereas those of the ambient CO_2-[water] stressed plants were still 21% lagging behind their unstressed controls at that date." And what it all means, in the words of the five researchers, is that "rice grown under future rising atmospheric CO_2 should be better able to tolerate drought situations."

Triggs *et al*. (2004)[17] grew sorghum (*Sorghum bicolor* (L.) Moench, a C_4 grain crop) for two full seasons in control CO_2 plots (about 370 ppm) and FACE plots (Control + 200 ppm) under both well-watered (Wet) and water-stressed (Dry, less than half the total water received by the Wet treatment via rainfall and irrigation) conditions near Maricopa, Arizona, USA, while assessing evapotranspiration (ET) on a continuous basis by means of micrometeorological measurements designed to allow the calculation of all of the other elements (net radiation, sensible heat flux, and soil surface heat flux) of the energy balance of the crop-soil interface with the atmosphere. In addition, the final grain yields that were used to calculate sorghum water use efficiency (WUE) were obtained by Ottman *et al*. (2001).

In reporting what they learned from this experiment, Triggs *et al*. wrote that "in the Wet treatments, a reduction in ET of about 19%, combined with only a slight increase in total biomass (+4%), resulted in a 28% increase in WUE in elevated CO_2 conditions," while "in the Dry treatments, the relatively large increase in total biomass (+16% for both years) more than compensated for the approximate 5% increase in total ET, giving the FACE-Dry treatments an increase in WUE of 16% over both seasons." And based on these results, they concluded that "even if future climate change results in less water available for agriculture, higher atmospheric CO_2 concentrations will still benefit C_4 crops," but at the same time noting that "in regions with ample precipitation or irrigation, C_3 crops with higher growth responses may be preferable."

[17] http://www.co2science.org/articles/V7/N40/B2.php.

Kaddour and Fuller (2004)[18] grew three commercial cultivars of durum wheat (*Triticum durum* Desf.) registered in Syria (Cham 1, Cham 3 and Cham 5) from seed in 10-liter pots in different compartments of a phytotron, half of which compartments were maintained at an atmospheric CO_2 concentration of approximately 400 ppm and half of which were maintained at a concentration of approximately 1000 ppm. Half of each of these treatments were further subdivided into two soil water treatments: well-watered, where *available water content* (AWC) was replenished to 90% of full capacity when it had dropped to 60%, and water-stressed, where AWC was replenished to 70% of full capacity when it had dropped to 45%. Averaged over the three cultivars, the extra 600 ppm of CO_2 supplied to the CO_2-enriched compartments led to total plant biomass increases of 62% in the well-watered treatment and 60% in the water-stressed treatment. Also of interest was the fact that the extra CO_2 led to increases in the nitrogen concentrations of stems and ears. In the case of ears, nitrogen concentration was increased by 22% in the well-watered plants and by 16% in the water-stressed plants.

Where water availability is a prime limiting economic resource, it can be distributed more effectively under higher CO_2 conditions.

In commenting on these results, Kaddour and Fuller write that they "have important implications for the production of durum wheat in the future." They state, for example, that "yields can be expected to rise as atmospheric CO_2 levels rise," and that "this increase in yield can be expected under both water restricted and well irrigated conditions." Hence, as they continue, "where water availability is a prime limiting economic resource, it can be distributed more effectively under higher CO_2 conditions," and "for countries such as Syria where average national production is well below the physiological maximum due largely to drought stress, the predicted rise in atmospheric CO_2 could have a positive effect on production."

In introducing their study of the subject, Richter and Semenov (2005)[19] note that "with global warming, evapotranspiration is likely to increase and, with more variable rainfall, droughts could occur more often." Hence they decided to evaluate the impact of potential climate change on drought indicators and yields of winter wheat in England and Wales using a crop simulation model (*Sirius*) that also incorporates the effects of elevated atmospheric CO_2 concentration and temperature on crop growth and development, where the CO_2 scenario driving the model was one of medium to high anthropogenic emissions that raise the air's CO_2 concentration from 334 ppm (the 1961-1990 baseline) to 554 ppm in the 2050s. This effort suggested that probability distributions derived from multiple simulations using representative weather, soil types and sowing dates indicate that maximum soil moisture deficit "is likely to increase in the future, especially on shallow soils, and the probability of potential yield reductions exceeding 25% will increase by 10% until the 2050s." *However*, they found that, in

[18] http://www.co2science.org/articles/V8/N2/B3.php.
[19] http://www.co2science.org/articles/V8/N35/B1.php.

reality, "average wheat yields are likely to increase by 1.2 to 2 t/ha (15-23%) by the 2050s because of a CO_2-related increase in radiation use efficiency."

Moving ever forward in time, Bernacchi *et al*. (2006)[20] grew soybeans (*Glycine max* (L.) Merr.) for three years at the SoyFACE facility of the University of Illinois at Urbana-Champaign, Illinois (USA) at atmospheric CO_2 concentrations of either 375 or 550 ppm under natural field conditions with and without a 23% increase in ambient atmospheric ozone concentration, while a number of weather and plant physiological parameters were measured from pre-dawn to post-dusk on several days during the three growing seasons. In doing so, they determined that the mean daily integral of leaf-level net photosynthesis (A) was enhanced by nearly 25% in the CO_2-enriched air under ambient ozone concentrations, but by a slightly smaller 20% in the high-ozone air. In addition, they say "there was a strong positive correlation between daytime maximum temperatures and mean daily integrated A at elevated CO_2." And from their graphical representation of this relationship, it appears that at a daily maximum temperature of approximately 26.5°C, A was stimulated by about 14%, while at a daily maximum temperature of approximately 34.5°C, it was stimulated by about 35%. Also, the team of eleven researchers determined that "the effect of elevated CO_2 on photosynthesis tended to be greater under water stress conditions," rising from an approximate 17% enhancement of A at the most favorable soil moisture condition encountered to an enhancement close to 30% under the driest of the conditions experienced by the crop.

Average wheat yields are likely to increase by 1.2 to 2 t/ha (15-23%) by the 2050s because of a CO_2-related increase in radiation use efficiency.

Robredo *et al*. (2007)[21] grew well watered and fertilized barley (*Hordeum vulgare* L.) seedlings (seven per each 2.5-liter pot filled with perlite and vermiculite) in controlled-environment chambers maintained at atmospheric CO_2 concentrations of either 350 or 700 ppm, while at the conclusion of the 18th day after seedling emergence, the treatments were split, with one treatment continuing to be watered three times a week, but with the other treatment receiving no further water additions. Then, at that time and on several following dates, a number of soil and plant water parameters were measured, along with rates of leaf transpiration and net photosynthesis. This protocol revealed, as they describe it, that "during the period of drought, elevated CO_2 delayed by 3-4 days the depletion of soil water content," due to "the lower rates of transpiration in plants grown under CO_2 enrichment." As a result, they found that "under elevated CO_2, plant water stress developed more slowly," due to "a slower rate of soil water depletion," and as a result of this phenomenon, they report that "the stimulation of carbon assimilation by elevated CO_2 was even greater in droughted compared to well-watered plants," in spite of the fact that "elevated CO_2 caused stomata closure."

[20] http://www.co2science.org/articles/V10/N1/B1.php.
[21] http://www.co2science.org/articles/V10/N18/B2.php.

In summing up their findings and explaining their significance, the seven Spanish researchers say that "exposure to high carbon dioxide concentration resulted in an increase in photosynthesis and in a reduction in whole plant transpiration, contributing to an increase in water use efficiency that was more noticeable when plants were subjected to elevated CO_2 in conjunction with drought." Thus, they concluded that "growing plants under [an] elevated CO_2 environment mitigates or delays the effects of water stress in barley," which, obviously, is a very favorable phenomenon with positive real-world economic consequences.

Contemporaneously, Li *et al*. (2007)[22] described how they had employed open-top chambers to determine *net ecosystem CO_2 exchange* (NEE) before, during and after the severe Central Florida drought of 1998 in a scrub-oak ecosystem in ambient-CO_2 (AC) air and in elevated-CO_2 (EC) air that had been enriched with an extra 350 ppm of CO_2 since May 1996, focusing on the ecosystem's dominant species (*Quercus myrtifolia* Willd.), for which they measured net photosynthetic rate (PN) throughout the daylight hours of several days. This work revealed that that EC air generally increased PN while drought decreased it. Under droughty conditions, therefore, PN peaked at around 0830 each day, after which it declined in a fairly steady fashion until solar noon, after which it typically remained at a relatively low level throughout the remainder of the daylight hours. Consequently, they assessed the interactive impacts of elevated CO_2 and drought on tree PN by comparing the *percentage reduction in PN from 0830 to 1230* in the two CO_2 treatments. This approach demonstrated that in May of 1998, PN was reduced by 77% from 0830 to 1230 at AC but by only 48% at EC, while in July of 1998, when the drought had further intensified, PN was reduced by 82% at AC but by a lesser 69% at EC.

NEE responded in much the same way. In May and June of 1998, for example, its *midday depression* was 58% and 60% less at EC than at AC, while in July of 1999 it was 66% less. In addition, Li *et al*. report that "the mitigation of the effects of water stress by EC was reflected in the aboveground biomass growth," such that "the relative effect of EC on biomass accumulation of the dominant species *Q. myrtifolia* was higher during the drought year (210% for 1998) compared to the non-drought years (67% for 1997)."

Also publishing in the same year were Manderscheid and Weigel (2007)[23], who grew spring wheat (*Triticum aestivum* cv. Minaret) in open-top chambers on an experimental field of the Federal Agricultural Research Center in Braunschweig, Germany, in two different growing seasons at either current or future (current + 280 ppm) atmospheric CO_2 concentrations and under sufficient-water-supply (WET) or drought-stress (DRY) conditions, the latter of which was imposed just after the crop first-node stage was reached (approximately 35 days after emergence) by halving the subsequent water supplied to the plants. This work revealed, as they describe it, that "in both years, biomass and grain yield were decreased by drought and increased by CO_2 enrichment," with the positive CO_2 effect being greater under drought conditions. Averaged over both years, in fact, they indicate that "CO_2 enrichment increased biomass and grain yield under WET conditions by <=10% and under DRY conditions by >=44%." In addition, they likewise determined that the CO_2-induced increase in *crop water-use efficiency* was 20% in the sufficient-water-supply treatment and 43% in the drought-stress treatment.

[22] http://www.co2science.org/articles/V10/N31/B1.php.
[23] http://www.co2science.org/articles/V10/N41/B1.php.

Veisz *et al*. (2008)[24] grew seven cereal grain crops - winter barley (*Hordeum vulgare*, cv. Petra), winter wheat (*Triticum aestivum*, cvs. Libellula, Mv Regiment, Mv Mambo), winter durum wheat (*Triticum durum*, cv. Mv Makaroni), spring wheat (*Triticum aestivum*, cv Lona), and spring oats (*Avena sativa*, cv. Mv Pehely) - in a phytotron at the Agricultural Research Institute of the Hungarian Academy of Sciences at ambient and enriched atmospheric CO_2 concentrations (380 and 750 ppm, respectively) under both well-watered conditions and drought conditions, where water was withheld from the 10th day after heading, during which time soil volumetric water content dropped from approximately 25% to 6%, after which they measured a number of crop characteristics at harvest. And in doing so, they found, in their words, that the plants grown in the CO_2-enriched air "produced more organic matter, being taller, with more spikes and a higher grain number per plant than those grown at the present CO_2 level," and that "thanks to the more intensive incorporation of carbohydrate, there was an increase in the mean grain mass and in the grain yield per plant" in the CO_2-enriched air. However, there was a concomitant *decrease* in the protein *concentration* of the grains produced in the high CO_2 treatment.

Nevertheless, the net effect was still positive *because*, for the several cereal varieties averaged together, grain yield under the *well-watered* conditions rose by 12.37% (from 2.83 to 3.18 g/plant) in response to atmospheric CO_2 enrichment, while grain protein concentration dropped from 17.04% to only 16.23%, which resulted in a net *increase* of 7% in *total grain protein production*. Likewise, grain yield under the *water-stressed* conditions rose by 30.68% (from 1.76 to 2.30 g/plant) in response to atmospheric CO_2 enrichment, while the concentration of the grain protein dropped from 21.63% to 19.70%, which led to a net increase of 19% in *total grain protein production*.

Jumping ahead three additional years Chun *et al*. (2011)[25] grew corn plants from seed in naturally-sunlit *soil-plant-atmosphere-research* (SPAR) units in which temperature, humidity and CO_2 concentration were precisely controlled, the latter at either 400 ppm (ambient) or 800 ppm (elevated), beginning 21 *days after emergence* (DAE). These units were placed atop soil bins (2.0 m long by 0.5 m wide by 1.0 m deep) that were filled with a mixture of 75% coarse sand and 25% vermiculate, where soil water contents were monitored hourly by a *time domain reflectometry* (TDR) system that consisted of 15 TDR probes per chamber placed within three rows at depths of 0, 15, 30, 50 and 75 cm from the soil surface. And by means of this system of soil water content assessment, combined with nightly "fertigation," Chun *et al*. were able to provide the plants with the nitrogen they needed while maintaining four different soil water stress levels - control, mild, moderate and severe - which were also initiated 21 DAE. Thereafter, the height, number of leaves, leaf lengths and growth states of the corn plants were determined twice weekly, while samples of the plants were collected, dried and analyzed for biomass accumulation at 21 and 60 DAE (the beginning and the end of the different CO_2 and soil water content treatments).

Following these procedures, the five researchers determined that under both well-watered and water-stressed conditions, *higher* soil water contents were maintained in the *elevated* CO_2

[24] http://www.co2science.org/articles/V12/N24/B1.php.
[25] http://www.co2science.org/articles/V14/N14/B2.php.

treatment, *even though 20-49% **less** water was applied to the soil of the elevated CO_2 treatment*. Their study did *not*, however, provide any evidence that the elevated CO_2 treatment had a strong effect on plant height, leaf area or above-ground biomass. But *the water saving was amazing*; and as a result they concluded, that "under increased CO_2 concentrations as generally predicted in the future, less water will be required for corn plants than at present." And since water is already a scarce commodity in many parts of the world - and will only become more scarce, more expensive and more difficult to obtain in the days and years ahead - this finding is extremely welcome news.

Around this same time period, Robredo *et al*. (2011)[26] wrote in the introduction to their study of the subject that "barley, an economically important and extensively cultivated cereal worldwide, increases its yield in parallel with an increase in CO_2," but they also noted that barley "responds to drought stress through altered nitrogen metabolism and reduced productivity," which complexities they thus set out to explore by growing barley (*Hordeum vulgare* L. cv. Iranis) seedlings in 2.5-L pots containing a 3:1 mix of perlite:vermiclite in a controlled-environment growth chamber, first at *ambient* and then at *elevated* atmospheric CO_2 concentrations (350 and 700 ppm, respectively). Initially, the pots were watered twice a week with a complete Hoagland solution and with deionized water between each Hoagland solution application. Then, drought was initiated when the seedlings were 18 days old by withholding water for intervals of 9, 13 and 16 days, while the effects of these actions were analyzed at the end of each drought period and water recovery was analyzed three days after re-watering the 13-day droughted plants, with each complete experiment being replicated three times. And what did they learn?

Leaf water potential in [barley] plants subjected to drought but grown at elevated CO_2 was less negative than in their ambient CO_2 grown counterparts.

First of all, the six Spanish scientists say their barley plants showed a reduction in water use, even though under elevated CO_2 the plants had a larger leaf area, much as others have also found (Owensby *et al*., 1997; Niklaus *et al*., 1998). In addition, they report that "during the period of drought, the depletion of soil water content was delayed by 3-4 days in plants grown under elevated CO_2 conditions," and they state that in the CO_2-enriched plants "water stress also developed more slowly than at ambient CO_2 because of a slower rate of water depletion." And as a result, they report that "leaf water potential in plants subjected to drought but grown at elevated CO_2 was less negative than in their ambient CO_2 grown counterparts."

With respect to nitrogen issues, Robredo *et al*. determined that "absolute values for nitrogen uptake by barley plants were higher under elevated CO_2 compared to ambient CO_2." And they

[26] http://www.co2science.org/articles/V14/N17/B3.php.

say they "observed high nitrate reductase activity in plants grown at elevated CO_2, which should parallel an increase in photosynthesis (Robredo *et al*., 2007) and sugar content (Perez-Lopez *et al*., 2010)." In addition, they say that "under ambient CO_2 conditions, protein content decreased as the water stress progressed," but that "when plants grew under elevated CO_2 conditions, the rate of photosynthesis was higher [and] drought had less effect on the protein content." In fact, they report that the barley plants "showed a greater content of proteins under elevated CO_2," in harmony with the findings of Geiger *et al*. (1999), who they say "reported a similar outcome in tobacco with the same supra-optimal nitrogen concentration." And they remark that these findings also mesh with the results of studies reviewed by Idso and Idso (2001), who concluded that any negative effects of elevated CO_2 on crop protein content "could be ameliorated by increased use of nitrogen fertilizer." In the simplest of terms, therefore, Robredo *et al*. concluded that "elevated CO_2 mitigates many of the effects of drought on nitrogen metabolism and allows more rapid recovery following water stress."

Contemporaneously, Tohidimoghadam *et al*. (2011)[27] - while working out-of-doors at 35°59'N, 50°75'E - grew two varieties (Okapi and Talaye) of canola (*Brassica napus* L.) plants over the 2008 and 2009 growing seasons beneath rigid frames covered with polyethylene plastic film in air maintained at ambient and elevated atmospheric CO_2 concentrations of 400 and 900 ppm, at ambient and elevated levels of UV radiation, and under well-watered and deficit-watered conditions, during and after which periods they measured numerous plant properties. This experiment revealed, in their words, that "water stress significantly decreased yield and yield components, oil yield, protein percentage, height, specific leaf area and the number of branches," but that elevated CO_2 "increased the final yield, 1000-seed weight, oil percentage, oil yield, height, specific leaf area and number of branches."

Future increases in the atmosphere's CO_2 concentration will likely lead to increased crop growth and yield production, even in areas where reduced soil moisture availability produces significant plant water stress.

Like water stress, however, they found that elevated UV radiation also "decreased the yield, yield components, oil and protein percentages and growth parameters." But, again, they report that elevated CO_2 additionally ameliorated "the adverse effects of UV radiation in the final yield, seed weight, oil percentage, oil yield, plant height, specific leaf area and number of branches per plant." And thus they concluded that an increase in the atmosphere's CO_2 concentration could likewise improve the "yield, yield

[27] http://www.co2science.org/articles/V14/N36/B2.php.

components and growth parameters for plants subjected to elevated levels of UV radiation."

Rounding out the list studies dealing with the ability of atmospheric CO_2 enrichment to help ameliorate the negative effects of water stress on agricultural crops is the study of Varga *et al.* (2012)[28], who introduced their study of the subject by writing that "as well as damaging numerous physiological functions, abiotic stress [such as drought] also leads to higher concentrations of reactive oxygen species, which are present in nature in all plants, but which may damage cell components and disturb metabolic processes when present in larger quantities," citing Omran (1980), Larson (1988) and Dat *et al*. (2000). However, they indicate that "many authors have demonstrated that the [atmosphere's] CO_2 concentration has a substantial influence on the stress sensitivity of plants via changes in antioxidant enzyme activity," citing Fernandez-Trujillo *et al*. (2007), Ali *et al*. (2008) and Varga and Bencze (2009), with the consequence that increases in the atmosphere's CO_2 concentration tend to *increase* various *antioxidant enzyme activities* and thereby *reduce* the negative effects of abiotic stress.

In an experiment designed to further explore this subject, Varga *et al*. grew two varieties of winter wheat within phytotrons maintained at either 380 or 750 ppm CO_2, where the potted plants were watered daily and supplied with nutrient solution twice a week until the start of drought treatments, when drought was induced in three phases - at first node appearance, heading and grain filling - by completely withholding water for seven days, which ultimately dropped the volumetric soil water content in the pots from 20-25% to 3-5%. These actions, in the words of the four Hungarian researchers, led to "changes in enzyme activity" that "indicated that enhanced CO_2 concentration delayed the development of drought stress up to first node appearance, and stimulated antioxidant enzyme activity when drought occurred during ripening, thus reducing the unfavorable effects of [drought] stress." And they thus concluded that the increases in the antioxidant enzymes they analyzed "may help to neutralize the reactive oxygen species induced by stress during various parts of the vegetation period," which phenomenon may help mankind's crops to better cope with whatever extremes of moisture insufficiency might be lurking in our future.

To briefly summarize the findings of this review of the effects of water insufficiency on the productivity of the world's major agricultural crops, the earlier optimistic conclusions of Idso and Idso (1994) are found to be well supported by the recent peer-reviewed scientific literature, which indicates that the ongoing rise in the air's CO_2 content will likely lead to substantial increases in the photosynthetic rates and biomass production of the world's major agricultural crops, even in the face of the stressful conditions imposed by less-than-optimum soil moisture conditions. Therefore, future increases in the atmosphere's CO_2 concentration will likely lead to increased crop growth and yield production, even in areas where reduced soil moisture availability produces significant plant water stress.

REFERENCES

Alexandrov, V.A. and Hoogenboom, G. 2000. The impact of climate variability and change on crop yield in Bulgaria. *Agricultural and Forest Meteorology* **104**: 315-327.

[28] http://www.co2science.org/articles/V15/N38/B3.php.

Ali, M.B., Dewir, Y.H., Hahn, E. and Peak, K. 2008. Effect of carbon dioxide on antioxidant enzymes and ginsenoside production in root suspension cultures of *Panax ginseng*. *Environmental and Experimental Botany* **63**: 297-304.

Baker, J.T., Allen Jr., L.H., Boote, K.J. and Pickering, N.B. 1997. Rice responses to drought under carbon dioxide enrichment. 2. Photosynthesis and evapotranspiration. *Global Change Biology* **3**: 129-138.

Bernacchi, C.J., Leakey, A.D.B., Heady, L.E., Morgan, P.B., Dohleman, F.G., McGrath, J.M., Gillespie, K.M., Wittig, V.E., Rogers, A., Long, S.P. and Ort, D.R. 2006. Hourly and seasonal variation in photosynthesis and stomatal conductance of soybean grown at future CO_2 and ozone concentrations for 3 years under fully open-air field conditions. *Plant, Cell and Environment* 10.1111/j.1365-3040.2006.01581.x.

Bhattacharya, N.C., Hileman, D.R., Ghosh, P.P., Musser, R.L., Bhattacharya, S. and Biswas, P.K. 1990. Interaction of enriched CO_2 and water stress on the physiology of and biomass production in sweet potato grown in open-top chambers. *Plant, Cell and Environment* **13**: 933-940.

Chaves, M.M. and Pereira, J.S. 1992. Water stress, CO_2 and climate change. *Journal of Experimental Botany* **43**: 1131-1139.

Chun, J.A., Wang, Q., Timlin, D., Fleisher, D. and Reddy, V.R. 2011. Effect of elevated carbon dioxide and water stress on gas exchange and water use efficiency in corn. *Agricultural and Forest Meteorology* **151**: 378-384.

Clifford, S.C., Stronach, I.M., Mohamed, A.D., Azam-Ali, S.N. and Crout, N.M.J. 1993. The effects of elevated atmospheric carbon dioxide and water stress on light interception, dry matter production and yield in stands of groundnut (*Arachis hypogaea* L.). *Journal of Experimental Botany* **44**: 1763-1770.

Conley, M.M., Kimball, B.A., Brooks, T.J., Pinter Jr., P.J., Hunsaker, D.J., Wall, G.W., Adams, N.R., LaMorte, R.L., Matthias, A.D., Thompson, T.L., Leavitt, S.W., Ottman, M.J., Cousins, A.B. and Triggs, J.M. 2001. CO_2 enrichment increases water-use efficiency in sorghum. *New Phytologist* **151**: 407-412.

Dat, J., Vandenabeele, S., Vranova, A., Van Montagu, M., Inze, D., Van Breusegem, F. 2000. Dual action of the active oxygen species during plant stress responses. *Cellular and Molecular Life Sciences* **57**: 779-995.

De Luis, J., Irigoyen, J.J. and Sanchez-Diaz, M. 1999. Elevated CO_2 enhances plant growth in droughted N_2-fixing alfalfa without improving water stress. *Physiologia Plantarum* **107**: 84-89.

Ferris, R., Wheeler, T.R., Ellis, R.H. and Hadley, P. 1999. Seed yield after environmental stress in soybean grown under elevated CO_2. *Crop Science* **39**: 710-718.

Ferris, R., Wheeler, T.R., Hadley, P. and Ellis, R.H. 1998. Recovery of photosynthesis after environmental stress in soybean grown under elevated CO_2. *Crop Science* **38**: 948-955.

Frenandez-Trujillo, J.P., Nock, J.F. and Watkins, C.B. 2007. Antioxidant enzyme activities in strawberry fruit exposed to high carbon dioxide atmospheres during cold storage. *Food Chemistry* **104**: 1425-1429.

Geiger, M., Haake, V., Ludewig, F., Sonnewald, U. and Stitt, M. 1999. The nitrate and ammonium nitrate supply have a major influence on the response of photosynthesis, carbon metabolism, nitrogen metabolism, and growth to elevated carbon dioxide in tobacco. *Plant, Cell and Environment* **22**: 1177-1199.

Hudak, C., Bender, J., Weigel, H.-J. and Miller, J. 1999. Interactive effects of elevated CO_2, O_3, and soil water deficit on spring wheat (*Triticum aestivum* L. cv. Nandu). Agronomie 19: 677-687.

Idso, K.E. and Idso, S.B. 1994. Plant responses to atmospheric CO_2 enrichment in the face of environmental constraints: A review of the past 10 years' research. *Agricultural and Forest Meteorology* **69**: 153-203.

Idso, S.B. 1988. Three phases of plant response to atmospheric CO_2 enrichment. *Plant Physiology* **87**: 5-7.

Idso, S.B. and Idso, K.E. 2001. Effects of atmospheric CO_2 enrichment on plant constituents related to animal and human health. *Environmental and Experimental Botany* **45**: 179-199.

Jones, P., Jones, J.W. and Allen Jr., L.H. 1985. Seasonal carbon and water balances of soybeans grown under stress treatments in sunlit chambers. *Transactions of the American Society of Agricultural Engineers* **28**: 2021-2028.

Kaddour, A.A. and Fuller, M.P. 2004. The effect of elevated CO_2 and drought on the vegetative growth and development of durum wheat (*Triticum durum* Desf.) cultivars. *Cereal Research Communications* **32**: 225-232.

Larson, R.A. 1988. The antioxidants of higher plants. *Phytochemistry* **27**: 969-978.

Li, A.-G., Hou, Y.-S., Wall, G.W., Trent, A., Kimball, B.A. and Pinter Jr., P.J. 2000. Free-air CO_2 enrichment and drought stress effects on grain filling rate and duration in spring wheat. *Crop Science* **40**: 1263-1270.

Li, J.H., Johnson, D.P., Dijkstra, P., Hungate, B.A., Hinkle, C.R. and Drake, B.G. 2007. Elevated CO_2 mitigates the adverse effects of drought on daytime net ecosystem CO_2 exchange and photosynthesis in a Florida scrub-oak ecosystem. *Photosynthetica* **45**: 51-58.

Lin, J.-S and Wang, G.-X. 2002. Doubled CO_2 could improve the drought tolerance better in sensitive cultivars than in tolerant cultivars in spring wheat. *Plant Science* **163**: 627-637.

Manderscheid, R. and Weigel, H.-J. 2007. Drought stress effects on wheat are mitigated by atmospheric CO_2 enrichment. *Agronomy for Sustainable Development* **27**: 79-87.

Niklaus, P.A., Spinnler, D. and Korner, C. 1998. Soil moisture dynamics of calcareous grassland under elevated CO_2. *Oecologia* **117**: 201-208.

Omran, R.G. 1980. Peroxide levels and the activities of catalase, peroxidase and indoleacetic acid oxidase during and after chilling cucumber seedlings. *Plant Physiology* **65**: 407-408.

Ottman, M.J., Kimball, B.A., Pinter Jr., P.J., Wall, G.W., Vanderlip, R.L., Leavitt, S.W., LaMorte, R.L., Matthias, A.D. and Brooks, T.J. 2001. Elevated CO_2 increases sorghum biomass under drought conditions. *New Phytologist* **150**: 261-273.

Owensby, C.E., Ham, J.M., Knapp, A.K., Breemer, D. and Auen, L.M. 1997. Water vapor fluxes and their impact under elevated CO_2 in a C_4-tallgrass prairie. *Global Change Biology* **3**: 189-195.

Perez-Lopez, U., Robredo, A., Lacuesta, M., Munoz-Rueda, A. and Mena-Petite, A. 2010. Atmospheric CO_2 concentration influences the contributions of osmolyte accumulation and cell wall elasticity to salt tolerance in barley cultivars. *Journal of Plant Physiology* **167**: 15-22.

Rabha, B.K. and Uprety, D.C. 1998. Effects of elevated CO_2 and moisture stress on *Brassica juncea*. *Photosynthetica* **35**: 597-602.

Richter, G.M. and Semenov, M.A. 2005. Modeling impacts of climate change on wheat yields in England and Wales: assessing drought risks. *Agricultural Systems* **84**: 77-97.

Robredo, A., Perez-Lopez, U., Miranda-Apodaca, J., Lacuesta, M., Mena-Petite, A. and Munoz-Rueda, A. 2011. Elevated CO_2 reduces the drought effect on nitrogen metabolism in barley plants during drought and subsequent recovery. *Environmental and Experimental Botany* **71**: 399-408.

Robredo, A., Perez-Lopez, U., Sainz de le Maza, H., Gonzalez-Moro, B., Lacuesta, M., Mena-Petite, A. and Munoz-Rueda, A. 2007. Elevated CO_2 alleviates the impact of drought on barley improving water status by lowering stomatal conductance and delaying its effects on photosynthesis. *Environmental and Experimental Botany* **59**: 252-263.

Rogers, H.H., Sionit, N., Cure, J.D., Smith, H.M. and Bingham, G.E. 1984. Influence of elevated CO_2 on water relations of soybeans. *Plant Physiology* **74**: 233-238.

Schutz, M. and Fangmeier, A. 2001. Growth and yield responses of spring wheat (*Triticum aestivum* L. cv. Minaret) to elevated CO_2 and water limitation. *Environmental Pollution* **114**: 187-194.

Serraj, R., Allen Jr., L.H. and Sinclair, T.R. 1999. Soybean leaf growth and gas exchange response to drought under carbon dioxide enrichment. *Global Change Biology* **5**: 283-291.

Sgherri, C.L.M., Quartacci, M.F., Menconi, M., Raschi, A. and Navari-Izzo, F. 1998. Interactions between drought and elevated CO_2 on alfalfa plants. *Journal of Plant Physiology* **152**: 118-124.

Tohidimoghadam, H.R., Ghooshchi, F. and Zahedi, H. 2011. Effect of UV radiation and elevated CO_2 on morphological traits, yield and yield components of canola (*Brassica napus* L.) grown under water deficit. *Notulae Botanicae Horti Agrobotanici Cluj-Napoca* **39**: 213-219.

Triggs, J.M., Kimball, B.A., Pinter Jr., P.J., Wall, G.W., Conley, M.M., Brooks, T.J., LaMorte, R.L., Adam, N.R., Ottman, M.J., Matthaias, A.D., Leavitt, S.W. and Cerveny, R.S. 2004. Free-air CO_2 enrichment effects on the energy balance and evapotranspiration of sorghum. *Agricultural and Forest Meteorology* **124**: 63-79.

Varga, B. and Bencze, Sz. 2009. Comparative study of drought stress resistance in two winter wheat varieties raised at ambient and elevated CO_2 concentration. *Cereal Research Communications* **37**: 209-212.

Varga, B., Janda, T., Laszlo, E. and Veisz, O. 2012. Influence of abiotic stresses on the antioxidant enzyme activity of cereals. *Acta Physiologiae Plantarum* **34**: 849-858.

Veisz, O., Bencze, S., Balla, K., Vida, G. and Bedo, Z. 2008. Change in water stress resistance of cereals due to atmospheric CO_2 enrichment. *Cereal Research Communications* **36**: 10.1556/CRC.36.2008.Suppl.1.

Vu, J.C.V., Baker, J.T., Pennanen, A.H., Allen Jr., L.H., Bowes, G. and Boote, K.J. 1998. Elevated CO_2 and water deficit effects on photosynthesis, ribulose bisphosphate carboxylase-oxygenase, and carbohydrate metabolism in rice. *Physiologia Plantarum* **103**: 327-339.

Wall, G.W. 2001. Elevated atmospheric CO_2 alleviates drought stress in wheat. *Agriculture, Ecosystems and Environment* **87**: 261-271.

Wechsung, G., Wechsung, F., Wall, G.W., Adamsen, F.J., Kimball, B.A., Pinter Jr., P.J., LaMorte, R.L., Garcia, R.L. and Kartschall, Th. 1999. The effects of free-air CO_2 enrichment and soil water availability on spatial and seasonal patterns of wheat root growth. *Global Change Biology* **5**: 519-529.

Widodo, W., Vu, J.C.V., Boote, K.J., Baker, J.T. and Allen Jr., L.H. 2003. Elevated growth CO_2 delays drought stress and accelerates recovery of rice leaf photosynthesis. *Environmental and Experimental Botany* **49**: 259-272.

Cover photo of a ripening barley field in the Palouse region of the northwestern United States by Victor Szalvay as posted to wikimedia.org.

SPPI
Science & Public Policy Institute
"Science-based policy for a better world."
www.scienceandpublicpolicy.org

CO2 SCIENCE
www.co2science.org