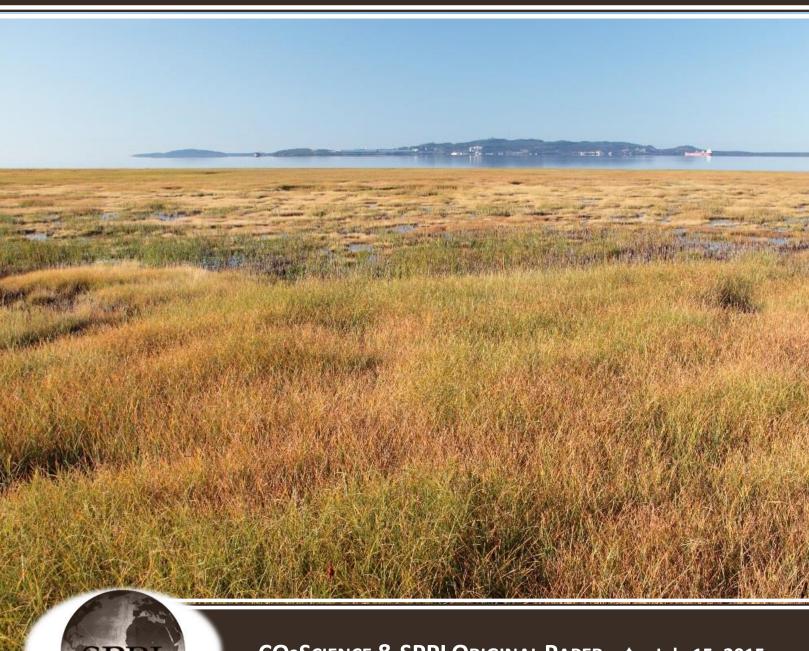
INTERACTIVE EFFECTS OF CO2 AND SALINITY STRESS ON PLANT GROWTH



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Interactive Effects of CO₂ and Salinity Stress on Plant Growth

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In agricultural enterprises the buildup of soil salinity from repeated irrigations can sometimes reduce crop yields. Similarly, in unmanaged ecosystems where exposure to brackish or salty water is commonplace, saline soils can induce growth stresses in plants that are not naturally adapted to coping with this problem. Consequently, it is important to understand how rising atmospheric CO₂ concentrations may interact with soil salinity to affect plant growth; and in the paragraphs that follow, we summarize the results of a number of experiments that were designed to obtain knowledge pertinent to this endeavor.

We begin with the paper of <u>Ball et al.</u> (1997)¹, who grew two Australian mangrove species -- Rhizophora stylosa and Rhizophora apiculata, the former of which has a slower relative growth

rate than *R. apiculata* but also a greater salt tolerance -- for 14 weeks in glasshouses with different combinations of atmospheric CO₂ (340 and 700 ppm), relative humidity (43 and 86%), and salinity (25 and 75% of seawater) with the purpose of determining the effects of these variables on their development and growth; and averaged across the entire experiment, the elevated CO₂ treatment significantly increased the rates of net photosynthesis in both species, but only when they were grown at the lower salinity level.

Working with an agricultural crop, Mavrogianopoulos et al. (1999)² grew parnon melons (Cucumis melo) in greenhouses subjected to atmospheric CO₂ concentrations of 400, 800, and 1200 ppm for the first five hours of each day, irrigating them with nutrient solutions containing 0, 25, and 50 mM NaCl to determine the interactive effects of elevated CO₂ and salinity on

CO₂ enrichment

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and leaf chlorophyll

content.

plant growth and yield. This work revealed that exposure to CO₂ concentrations of 800 and 1200 ppm increased net photosynthetic rates by averages of 75 and 120%, respectively -- regardless of salinity -- relative to rates measured at 400 ppm CO₂. In addition, the CO₂ enrichment partially reversed the negative effects of salinity on shoot growth, leaf growth, and leaf chlorophyll content; and although melon yields were significantly increased with atmospheric CO₂

¹ http://www.co2science.org/articles/V2/N17/B2.php

² http://www.co2science.org/articles/V2/N22/B3.php

enrichment at all salinity levels, the greatest CO₂-induced enhancement was observed at the lowest salinity level.

Tomato plants grown in the elevated CO_2 treatment tolerated an average root-zone salinity threshold value that was about 60% greater than that exhibited by plants grown in the low CO_2 treatment.

Also working in the agricultural sector, Maggio et al. $(2002)^3$ grew tomato (Lycopersicon esculentum Mill.) controlledplants chambers environment maintained atmospheric CO2 concentrations of either 400 or 900 ppm in combination with varying degrees of soil salinity for a period of one month, finding that plants grown in the elevated CO₂ treatment tolerated an average root-zone salinity threshold value that was about 60% greater than that exhibited by plants grown in the low CO2 treatment, while the water-use of the CO2enriched plants was about half that of the low-CO₂ plants. In addition, the amount of chloride in the leaves of the CO2-enriched plants was significantly lower than that in the leaves of the low- CO₂ plants.

Very similar findings were reported in a review paper produced during the same time period by Poorter and Perez-Soba (2001)⁴, who found there were few changes in the effects of elevated CO₂ on the growth responses of most plants over a wide range of soil salinities, in harmony with the still earlier findings of Idso and Idso (1994) in their review of the literature. Hence, there is abundant evidence that suggests

that plants should respond positively to future increases in the air's CO₂ content, even in situations where mild to moderate stresses may be present due to high soil salinity levels. Nevertheless, new research on the topic continues to be conducted, as scientists strive to "dig deeper" and learn ever more about what we can expect in this regard as the air's CO₂ content continues its upward trend.

Syvertsen and Levy (2005)⁵, for example, reviewed what is known about salinity stress in citrus trees and how it may be modified by atmospheric CO₂ enrichment, beginning by noting that rapidly growing plants almost always use more water than slower growing plants, and that, "in citrus, many vigorous rootstocks that produce fast-growing trees also tend to have poor salt tolerance (Castle *et al.*, 1993)," possibly because they accumulate more salt in their tissues because of their greater uptake of water. When growing plants in CO₂-enriched air, however, plant stomatal conductance and water use are often decreased at the same time that net

³ http://www.co2science.org/articles/V5/N21/B2.php

⁴ http://www.co2science.org/articles/V4/N42/B1.php

⁵ http://www.co2science.org/articles/V8/N14/B2.php

photosynthesis and growth are increased, so that, in the words of the two scientists, "elevated CO₂ almost always leads to higher water use efficiency as it disconnects rapid tree growth from high water use." Consequently, as they explain, "if salt uptake is coupled with water uptake, then leaves grown at elevated CO₂ should have lower salt concentrations than leaves grown at ambient CO₂ (Ball and Munns, 1992)." So, do things really work that way?

"As expected," Syvertsen and Levy continue, "all citrus rootstock species studied increased growth and water use efficiency in response to elevated CO₂ that was twice ambient," and they say that *generally*, but not always, "the salinity-induced accumulation of sodium (Na+) in leaves was less when seedlings were grown at elevated CO₂ than at ambient CO₂." One specific exception -- where Na+ accumulation was not affected by elevated CO₂ -- was Rangpur lime (*Citrus reticulata*); but they report that this citrus variety is already relatively salt-tolerant, and that another variety of the same species (Cleopatra mandarin) had lower leaf chloride concentrations in CO₂-enriched air than in ambient air.

Contemporaneously, Rasse et al. (2005)⁶ reported on the long-term effects of atmospheric CO₂ enrichment on the net CO₂ exchange, shoot density and shoot biomass of the wetland sedge, Scirpus olneyi, as well as how those effects were influenced by salinity (which is one of the main environmental stressors of the wetlands), in one of the longest (17 years) in situ atmospheric CO₂ enrichment experiments ever conducted -- in this particular case, in a natural wetland located at the Smithsonian Environmental Research Center on the Chesapeake Bay (USA). In every year of that period, the net CO₂ exchange rate and shoot biomass and density of the plants growing in the CO₂-enriched (ambient +340 ppm) air were all greater than they were among the plants growing in ambient air.

In the case of the net CO₂ exchange rate, for example, the extra CO₂ boosted this primary process by 80% in the first year of the study; but the enhancement declined to about 35% by the end of the third year and remained relatively constant at that value over the following 15 years. Shoot biomass and density also increased; but whereas the CO₂-induced stimulation of the net CO₂ exchange rate remained essentially constant over the last 15 years of the study, the CO₂-induced stimulations of shoot biomass and density *increased* over time. After 5 years of a nearly constant stimulation of 16%, for example, shoot density increased in near linear fashion to a value 128% above the ambient-air value at the end of year 17.

The response of shoot biomass to CO₂ enrichment was also nearly linear, reaching a value approximately 70% above ambient at year 17. What is more, the trends in shoot density and biomass do not appear to be leveling off, leading one to wonder just how high the CO₂-induced stimulations will ultimately rise.

Net CO₂ exchange, shoot density and shoot biomass were also closely correlated with salinity, such that the higher the salinity, the more detrimental were its effects on these variables. But even at the highest levels of salinity reported, atmospheric CO₂ enrichment was able to produce a positive, albeit reduced, stimulatory effect on net CO₂ exchange. For shoot biomass and density, the responses were better still. Not only did atmospheric CO₂ enrichment essentially *eradicate*

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⁶ http://www.co2science.org/articles/V8/N28/B1.php

the detrimental effects of salinity, there was, in the words of Rasse *et al.*, "evidence suggesting that salinity stress increased the stimulation of shoot density by elevated atmospheric CO₂ concentration."

Several important things were demonstrated by this experiment. First, as the researchers state, their results "leave no doubt as to the sustained response of the salt march sedge to elevated atmospheric CO₂ concentration." Second, given the fact that the initial responses of the three growth variables declined or remained low during the first few years of the study, but leveled out or increased thereafter, it is clear that much more *long-term research* needs to be carried out if we are to ascertain the full and correct impacts of atmospheric CO₂ enrichment on plants. In the case of the wetland sedge of this study, for example, it took about ten growing seasons before an increasing trend in the shoot density could clearly be recognized. Last of all, there is what the researchers call their "most important finding," i.e., the fact that "a species response to elevated atmospheric CO₂ concentration can continually increase when [it] is under stress and declining in its natural environment."

One year later, <u>Garcia-Sanchez and Syvertsen (2006)</u>⁷ grew well-watered and fertilized three-month-old rootstock seedlings of Cleopatra mandarin (*Citrus reticulata* Blanco) and Carrizo citrange (*Citrus sinensis* (L.) Osb. x *Poncirus trifoliata* L.), with and without salt stress (an additional 50 mM NaCl), for eight additional weeks, one plant each in 1.5-liter containers located in controlled-environment greenhouses maintained at either 360 or 700 ppm CO₂, during which time, and at the end of the experiment, they measured a number of plant properties and physiological processes that allowed them to test the hypothesis that "salinity tolerance of citrus rootstock seedlings would be increased when grown in elevated CO₂."

At the end of their study, the two researchers had indeed found that "elevated CO₂ increased plant growth, shoot/root ratio, leaf dry weight per area, net assimilation of CO₂, chlorophyll, and water-use efficiency." And they report that the increase in the last of these parameters was caused by a decrease in transpiration and an increase in plant biomass, the latter of which plant properties received a 27% CO₂-induced boost in the salt-stress treatment and a 40% boost in the non-salt-stress treatment for Cleopatra mandarin, while it was enhanced by 49% in the salt-stress treatment and by 43% in the non-salt-stress treatment for Carrizo citrange. In addition, they report that "elevated CO₂ increased salinity tolerance in the relatively salt-sensitive Carrizo more than in the salt-tolerant Cleopatra."

Focusing once again on tomato plants, <u>Takagi et al.</u> (2008)⁸ grew well-watered and fertilized *Solanum lycopersicum* (formerly *Lycopersicon esculentum*) seedlings for two weeks at two different levels of irrigation-water salinity (0 or 100 mM NaCl) in 3-L pots inside a greenhouse of Hiroshima University (Japan), at atmospheric CO₂ concentrations of either 370 or 1000 ppm, while measuring various plant properties and physiological responses. In doing so, they found that the "salt-stress treatment severely decreased whole-plant biomass," as well as "leaf

⁷ http://www.co2science.org/articles/V9/N18/B2.php

⁸ http://www.co2science.org/articles/V12/N24/B3.php

photosynthesis and transport of carbon assimilates," but that "the impact of stress on these activities was alleviated under elevated CO₂ 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 CO₂ concentration." Hence, they concluded that their study "corroborates earlier reports that the interaction between salinity stress and CO₂ concentration results in the alleviative effect of elevated CO₂ on the negative effects of salinity on plant growth."

Shifting gears slightly, <u>Geissler et al.</u> (2009a)⁹ write that "desertification is often accompanied by soil salinization ... leading to growth conditions inacceptable for most conventional crops." However, they note that what they call "a promising solution" to the problem is "the desalinization and reclamation of degraded land by making sustainable use of naturally salt-tolerant

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halophytes under seawater irrigation (including drainage mechanisms which avoid salt accumulation in the soil)."

In a study germane to this function, the three researchers grew well-fertilized two-month-old *Aster tripolium* plants in a hydroponic system maintained at *seawater salinity* (sws) levels of 0, 50 and 100% within open-top chambers that were maintained at atmospheric CO₂ concentrations of either 380 ppm (ambient) or 520 ppm (elevated), during which time they measured several plant properties and processes. This work revealed that growing the plants with water of 100% sws (as opposed to 0% sws) resulted in "a significant decrease in photosynthesis and water use efficiency and to an increase in oxidative stress." But when the air's CO₂ concentration was raised by 37% (from 380 to 520 ppm), there was a subsequent increase of 84% in photosynthesis and 60% in water use efficiency. In addition, they determined that "the improved water and energy supply was used to increase the investment in mechanisms reducing water loss and oxidative stress." Hence, they concluded that because "elevated CO₂ concentration enhances the energy and water supply of *Aster tripolium*, ameliorates oxidative

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⁹ http://www.co2science.org/articles/V12/N19/B2.php

stress, and thus enhances the survival of this plant in saline habitats," it "can help in desalinizing and reclaiming degraded land and sequestering CO₂, thus counteracting the greenhouse effect."

In a second paper that focused on a different aspect of the same experiment, <u>Geissler et al.</u> (2009b)¹⁰ wrote that *halophytes* are "naturally salt tolerant plants which are able to complete their life cycle on a substrate rich in NaCl," and that *cash-crop halophytes* "can be used for various economical and ecological purposes, e.g. for food, fodder, for obtaining timber, fibers, reeds or chemicals, as ornamental plants, for coastal protection, land reclamation or greenification of deserts," noting that *Aster tripolium*, in particular, "can be used for food (the leaves have a high nutritional value and can be eaten as salad or vegetable), for fodder and as an ornamental plant."

In this paper, the three scientists report that the 40% increase in the air's CO₂ content increased the light-saturated rate of *net photosynthesis* by 56%, 82% and 71%, respectively, in the plants irrigated with water of 0, 50 and 100% sws, while it increased their *water use efficiencies* by 14, 26 and 61% at the same respective sws percentages. Other positive impacts of the CO₂-enriched air were "an enhanced synthesis of proline, carbohydrates and proteins," and they say that "these mechanisms led to a higher survival rate under saline conditions, i.e. to an improved salt tolerance." Hence, they concluded that "A. tripolium is a promising cash crop halophyte which will probably benefit from rising atmospheric CO₂ concentrations in the future," and that "its sustainable use can help feeding the growing world population."

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Working with a more common crop, Perez-Lopez et al. (2009a)¹¹ grew two barley (Hordeum vulgare L.) cultivars, Alpha and Iranis. within controlled-environment chambers at ambient (350 ppm) or elevated (700 ppm) atmospheric CO₂ concentrations in a 3:1 perlite:vermiculite mixture that was watered with Hoagland's solution every two days (until the first leaf was completely expanded at 14 days), after which a salinity treatment was administered by adding 0, 80, 160 or 240 mM NaCl to the Hoagland's solution every two days for 14 more days. Then, after a total of 28 days, the primary leaf of each barley plant was harvested and assessed for a number of biochemical properties.

In following these procedures, the seven scientists found that in the various ambient-air salinity treatments, the deleterious effects of reactive oxygen species on barley leaves were

¹⁰ http://www.co2science.org/articles/V12/N11/B2.php

¹¹ http://www.co2science.org/articles/V12/N9/B3.php

made apparent through ion leakage and increases in thiobarbituric acid reactive substances (TBARS), which rose ever higher as salt concentrations rose ever higher. "On the other hand," as they continue, "when [the] salinity treatment was imposed under elevated CO₂ conditions, lower solute leakage and TBARS levels were observed, suggesting that the oxidative stress caused by salinity was lower." Hence, they concluded that "elevated CO₂ protects barley cultivars from oxidative stress," noting that "the relief of oxidative stress damage observed in our barley leaves grown under a CO₂ enriched atmosphere has also been observed in alfalfa (Sgherri *et al.*, 1998), pine (Vu *et al.*, 1999) and oak (Schwanz and Polle, 2001)."

Working with the same plants in the same experiment, but focusing on different phenomena, Perez-Lopez et al. (2009b)¹² measured relative water content, water potential and its components, transpiration rate, hydraulic conductance, and water use efficiency, computed as plant dry weight produced per unit of water transpired. And as a result, it was determined, in their words, that "elevated CO₂ improves barley water relations under saline conditions because elevated CO₂ permits a greater osmotic adjustment, most likely due to a greater carbon supply from increased photosynthesis, and a lower passive dehydration due to reductions in stomatal conductance and hydraulic conductance."

More specifically, they found that by the end of their study, the water use efficiency of salt-stressed plants grown in the elevated CO₂ treatment was 61% greater in Alpha and 43% greater in Iranis compared to the water use efficiency of plants grown in the ambient CO₂ treatment. Thus, the five researchers concluded that "elevated CO₂ will mitigate the negative impact of salinity on barley growth and will enable plants to remain turgid and functional for a longer period and for a higher salt concentration," noting that "these facts open the possibility of a future successful development of this species in saline areas in which nowadays growth is not possible." And this finding has *enormous* implications, in light of the fact that Frommer *et al.* (1999) have estimated that approximately one-third of the world's irrigated land is currently unsuitable for crop production because of its high salinity.

In yet a third paper devoted to still other characteristics of barley plants grown in the same experiment, Perez-Lopez et al. (2010)¹³ report the results of their measurements of midday leaf water potential, osmotic potential, osmotic potential at full turgor, dehydration and osmotic adjustment, and their subsequent harvesting of the primary leaf of each plant and their assessments of its concentrations of various minerals and organic compounds. This work revealed, as they describe it, that "elevated CO₂ permitted plant metabolism to be maintained at a better status under salt stress than did ambient CO₂," and that "growth was reduced more at ambient than at elevated CO₂." They also found that "elevated CO₂ widens the range of salt concentrations at which osmotic adjustment continues to be efficient by providing a greater supply of carbon and Adenosine-5'-triphosphate," which is a multi-functional nucleotide that transports chemical energy within cells for metabolism and is, in their words, "needed to perform the energetically expensive salt tolerance mechanisms." Thus, they concluded -- much as they

¹² http://www.co2science.org/articles/V12/N37/B2.php

¹³ http://www.co2science.org/articles/V13/N14/B3.php

had in their earlier papers -- that "under future environmental conditions, barley species will be able to succeed in salinized areas in which growth is not currently possible."

Writing in the *Pakistan Journal of Botany* a few years earlier, <u>Azam et al. (2005)</u> ¹⁴ had stated that "in agro-ecosystems, green manuring legumes occupy a key position in maintaining/improving soil fertility and productivity," noting that the important role of these plants as a source of nitrogen had increased further due to economic and pollution concerns associated with nitrogen supplied by *chemical* fertilizers. And they wrote, in this regard, that "species of sesbania have generally been considered as most important for green manuring, especially in wheat-rice rotation systems."

In many situations, however, the growth of sesbania is *negatively* impacted by varying degrees of water stress and *salinity*; but the five Pakistani scientists remind us that "elevated CO₂ favors different physiological processes of plants, thereby leading to increased biomass production and ecosystem functioning," citing the studies of Drake and Leadley (1991), Idso and Idso (1994) and Azam and Farooq (2001). They also report that this effect is more pronounced for plants facing stresses imposed through the soil or atmosphere, citing the collection of papers compiled and edited by Koch and Mooney (1996). And, therefore, they went on to explore the possibility that rising atmospheric CO₂ concentrations might *mitigate* salinity stress in sesbania, enabling the rotation cover-crop to more effectively "fix" atmospheric nitrogen and deposit the plant-usable form of it in the soil, where it can help promote the growth of such important agricultural staples as wheat and rice.

Conducting greenhouse experiments designed to assess the effects of elevated atmospheric CO₂ concentrations on growth and nitrogen fixation in *Sesbania aculeata* exposed to different salinity and water regimes, Azam *et al.* thus determined that "elevated CO₂ favored N₂ fixation leading to a greater contribution of fixed N to the total plant N." In addition, they report that "biological nitrogen fixation decreased with salinity," but they say that "elevated CO₂ arrested the decrease to a significant extent."

These findings, in their words, "are in conformity with those of Yu et al. (2002), who showed stimulation of symbiotic N₂ fixation at higher levels of CO₂," as well as those of Zanetti et al. (1997), who reported that "the total N yield increased consistently and the percentage of plant N derived from symbiotic N₂ fixation increased significantly in *Trifolium repens* under elevated CO₂." And they add that in studies of several different kinds of plants, Luscher et al. (1998) "found legumes to be the most responsive to elevated CO₂."

In concluding, the five researchers say "it is possible, therefore, to enhance the biomass yield of this green manuring crop [sesbania] by elevating the level of CO₂ in the plant canopy." And one low-tech way of doing so is suggested by their statement that "plant residues decomposing on the soil surface following mulching may help elevate the level of CO₂ and thus the plant growth," while a longer-term strategy would be for the nations of the earth to not overtly strive to reduce

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¹⁴ http://www.co2science.org/articles/V14/N36/EDIT.php

anthropogenic CO₂ emissions associated with the burning of fossil fuels; for CO₂ is "the elixir of life."

In a subsequent study, Perez-Lopez et al. (2012)¹⁵ wrote that "salt stress has a threefold effect on plant health," in that it (1) reduces water availability, (2) causes ion imbalance, and (3) causes toxicity, all of which phenomena, as they describe the situation, "curtail growth, photosynthesis, protein synthesis, energy storage, and lipid metabolism," as described in detail by Munns (2005) and Parida and Das (2005). Therefore, in a study designed to explore these negative consequences of potentially greater salt stress in a CO₂-enriched world of the future, they grew barley (Hordeum vulgare) plants in pots containing a 3:1 mix of perlite:vermiculite within controlled-environment chambers maintained at either ambient or elevated atmospheric CO₂ concentrations (350 or 700 ppm) for the last 14 days of a 28-day post-planting period, where they also instituted four different salt-stress treatments on the 15th day by supplying the plants then and thereafter with water possessing one of four different degrees of saltiness (0, 80, 160 or 240 mM NaCl), while at the end of the full 28-day period they measured a number of plant physiological properties and processes related to the maximal rate of net photosynthesis (A_{max}) exhibited by the first fully-expanded attached leaf of each plant. And what did they thereby learn?

In the words of the five Spanish scientists, "in the zero-saline treatment, elevated CO_2 increased the A_{max} by 49% compared with the A_{max} measured at ambient CO_2 ," while "under ambient CO_2 conditions, saline treatments (80-, 160- and 240-mM NaCl) reduced the A_{max} by 18, 32 and 39%, respectively." But they add that "these reductions were lower at elevated CO_2 : 8, 22 and 28% for 80-, 160- and 240-mM NaCl." And based on the graphical representations of their results, the CO_2 -induced enhancements of A_{max} in the four saline treatments (0-, 80-, 160- and 240-mM NaCl) were approximately 49%, 68%, 71% and 76%, respectively. In a nutshell, therefore, the greater the salinity-induced percentage reduction in barley A_{max} becomes, the greater the CO_2 -induced percentage in barley A_{max} becomes.

One year later, Perez-Lopez et al. (2013)¹⁶ analyzed "the effect of salinity on nitrogen acquisition, distribution and assimilation, the consequences of these effects on growth in barley (Hordeum vulgare L., cv. Iranis), and the possible effects on these processes provoked by elevated CO₂ levels." This they did in controlled environment chambers maintained at either ambient (350 ppm) or elevated (700 ppm) CO₂ concentrations, where -- from the time of sowing six barley seeds in each of several 2.5-liter pots containing a 3:1 mix of perlite/vermiculite -- they watered the plants with 250 ml of Hoagland's solution containing either 0, 80, 160 or 240 mM concentrations of NaCl every two days until the end of the 28-day study.

This work revealed, as the six Spanish scientists report, that "under ambient CO₂ conditions, 80, 160 and 240 mM NaCl reduced the total plant biomass by 12%, 30% and 44%, respectively," while "growth at elevated CO₂ levels led to 24%, 20% and 33% higher total biomass than under ambient CO₂ levels for 80, 160 and 240 mM NaCl, respectively." And, therefore, Perez-Lopez *et al.* concluded that "barley plants subjected to elevated CO₂ levels will likely overcome mild saline

¹⁵ http://www.co2science.org/articles/V15/N50/B1.php

¹⁶ http://www.co2science.org/articles/V16/N24/B3.php

conditions," which is very good news, for with the need to produce approximately *twice* the amount of food that is produced now to adequately feed the projected human population of the planet by mid-century (Running, 2012), we are going to need all the help we can get; and the documented boost in barley productivity (as well as that of many other crop plants) provided by mankind's CO_2 enrichment of the atmosphere will be *crucial* if we are to be successful in this endeavor.

Most recently, Perez-Lopez et al. (2014)¹⁷ measured uptake and translocation rates, nutrient contents, and nutrient concentrations in whole plants and in individual plant organs, as well as whole-plant nutrient use efficiency and nutrient selectivity in barley seedlings grown under non-saline (0 mM NaCl) and saline (80, 160 and 240 mM NaCl) conditions at 350 and 700 ppm atmospheric CO₂ concentrations. And in doing so they found that "elevated CO₂ caused adjustments in root size and activity that could change the nutrient uptake and transport efficiency to match the demand for the nutrients analyzed." And they indicate, in this regard, that "under combined conditions of salt stress and elevated CO₂, barley seedlings were able to maintain increased uptake and translocation rates for almost all nutrients," with the end result that "this ability allowed the seedlings to adapt to a higher demand under elevated CO₂ and to grow more rapidly by allocating more photo-assimilates to the roots, which increased root growth and active nutrient uptake and translocation."

In concluding this brief review of the scientific literature, it would appear to be safe to say that barley – and many other crop plants as well -- should continue to respond positively to continued increases in the air's CO₂ content, even in situations where significant stresses may be present due to high soil salinity levels.

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¹⁷ http://www.co2science.org/articles/V17/dec/a8.php

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