INTERACTIVE EFFECTS OF CO$_2$ AND PATHOGENS ON LEGUMES

Will plants suffering from various pathogenic diseases be able to reap the benefits of atmospheric CO$_2$ enrichment?
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As the air's CO$_2$ content continues to rise, nearly all of Earth's plants should continue to exhibit increasing rates of photosynthesis and, as a result, increased biomass production. But what about plants that are suffering from various pathogenic diseases? Will they be able to reap the benefits of the many positive effects of atmospheric CO$_2$ enrichment?

In the words of Chakraborty and Datta (2003)

There are a number of CO$_2$-induced changes in plant physiology, anatomy and morphology that have been implicated in increased plant resistance to disease and that "can potentially enhance host resistance at elevated CO$_2$," among which phenomena they list "increased net photosynthesis allowing mobilization of resources into host resistance (Hibberd et al., 1996a); reduced stomatal density and conductance (Hibberd et al., 1996b); greater accumulation of carbohydrates in leaves; more waxes, extra layers of epidermal cells and increased fiber content (Owensby, 1994); production of papillae and accumulation of silicon at penetration sites (Hibberd et al., 1996a); greater number of mesophyll cells (Bowes, 1993); and increased biosynthesis of phenolics (Hartley et al., 2000), among others." In what follows, we summarize the findings of some additional studies that have dealt with these and other related phenomena with respect to legumes.

Returning to the study of Chakraborty and Datta (2003), the two researchers studied the aggressiveness of the fungal anthracnose pathogen *Colletotrichum gloeosporioides* by inoculating two isolates of the pathogen onto two cultivars of the tropical pasture legume *Stylosanthes scabra* (Fitzroy, which is susceptible to the fungal pathogen, and Seca, which is more resistant) over 25 sequential infection cycles in controlled-environment chambers filled with air of either 350 or 700 ppm CO$_2$. By these means they were able to determine that the aggressiveness of the pathogen was reduced at the twice-ambient level of atmospheric CO$_2$, where aggressiveness is defined as "a property of the pathogen reflecting the relative amount of damage caused to the host without regard to resistance genes (Shaner et al., 1992)." As they describe it, "at twice-ambient CO$_2$ the overall level of aggressiveness of the two [pathogen] isolates was significantly reduced on both cultivars."

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Simultaneously, however, pathogen fecundity was found to increase at twice-ambient CO₂. Of this finding, Chakraborty and Datta report that their results "concur with the handful of studies that have demonstrated increased pathogen fecundity at elevated CO₂ (Hibberd et al., 1996a; Klironomos et al., 1997; Chakraborty et al., 2000)." How this happened in the situation they investigated, according to Chakraborty and Datta, is that the overall increase in fecundity at high CO₂ "is a reflection of the altered canopy environment," wherein "the 30% larger S. scabra plants at high CO₂ (Chakraborty et al., 2000) makes the canopy microclimate more conducive to anthracnose development."

In view of the opposing changes in pathogen behavior induced by the elevated level of atmospheric CO₂ employed in this experiment -- reduced aggressiveness but increased fecundity -- it is difficult to determine the ultimate impact of atmospheric CO₂ enrichment on the pathogen-host relationship of this particular plant. One year later, however, the publication of new research swung the pendulum in a favorable direction.

Also studying the Fitzroy cultivar of Stylosanthes scabra, Pangga et al. (2004)² grew well-watered and fertilized seedlings within a controlled environment facility maintained at atmospheric CO₂ concentrations of either 350 or 700 ppm, where they inoculated six-, nine- and twelve-week-old plants with C. gloeosporioides. Then, ten days after inoculation, they counted the anthracnose lesions on the plants and classified them as either resistant or susceptible.

Adherence to this protocol revealed, in their words, that "the mean number of susceptible, resistant, and total lesions per leaf averaged over the three plant ages was significantly (P<0.05) greater at 350 ppm than at 700 ppm CO₂, reflecting the development of a level of resistance in susceptible cv. Fitzroy at high CO₂." In fact, with respect to the plants inoculated at twelve weeks of age, they say that those grown "at 350 ppm had 60 and 75% more susceptible and resistant lesions per leaf, respectively, than those [grown] at 700 ppm CO₂."

In terms of infection efficiency (IE), the Australian scientists say their work "clearly shows that at 350 ppm overall susceptibility of the canopy increases with increasing age because more young leaves are produced on secondary and tertiary branches of the more advanced plants." However, they report that "at 700 ppm CO₂, IE did not increase with increasing plant age despite the presence of many more young leaves in the enlarged canopy," which finding, in their words, "points to reduced pathogen efficiency or an induced partial resistance to anthracnose in Fitzroy at 700 ppm CO₂." Consequently, as the air’s CO₂ content continues to rise, it would appear that (at least for the Fitzroy cultivar of this

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pasture legume) *Stylosanthes scabr*a will indeed acquire a greater intrinsic resistance to the devastating anthracnose disease.

Working with a different pasture legume, Lau et al. (2008) measured the amounts of pathogen damage done to the common prairie plant *Lespedeza capitata* growing in ambient and elevated (560 ppm) CO$_2$ treatments in the seventh and eighth full years (2004 and 2005) of the BioCON study (Reich et al., 2001) conducted at the Cedar Creek Natural History Area in Minnesota (USA), where the CO$_2$ treatments were applied during the daylight hours of each growing season.

With respect to pathogen damage, Lau et al. report that disease incidence "was lower in the elevated CO$_2$ environment, although this difference [10% less in 2004 and 53% less in 2005] was statistically significant only in 2005 (P < 0.01)." The importance of this finding is illustrated by the authors statement that "because disease caused major reductions in reproductive output, the effects of CO$_2$ on disease incidence may be important for *L. capitata* evolution and population dynamics," which phenomena should significantly benefit this species in a high-CO$_2$ world of the future. In addition, they note that Strengbom and Reich (2006), "working in the same experimental site ... also found that elevated CO$_2$ ... reduced disease incidence on *Solidago rigida*." Writing as background for their study on a legume of great global importance, Eastburn et al. (2010) say that "globally, soybean is the most widely planted dicot crop and has economic significance due to its wide variety of uses, ranging from food and health products to printing inks and biodiesel [fuels]," but they say that "little to no work has evaluated the influence of future atmospheric conditions on soybean diseases" in spite of the fact that "worldwide yield losses to all soybean diseases combined are about 11% (Wrather et al., 1997), which is equivalent to more than 24 million metric tons based on current production."

Against this backdrop, Eastburn et al. evaluated the individual and combined effects of elevated carbon dioxide (CO$_2$, 550 ppm) and ozone (O$_3$, 1.2 times ambient) on three economically important soybean diseases -- downy mildew, Septoria brown spot and sudden death syndrome (SDS) -- over the three-year period 2005-2007 under natural field conditions at the soybean free-air CO$_2$-enrichment (SoyFACE) facility on the campus of the University of Illinois (USA).

Results of the analysis indicated that "elevated CO$_2$ alone or in combination with O$_3$ significantly reduced downy mildew disease severity by 39-66% across the three years of the study." On the other hand, the five researchers who conducted the study say that "elevated CO$_2$ alone or in combination with O$_3$ significantly increased brown spot severity in all three years," but they add

that "the increase was small in magnitude." Last of all, they say that "the atmospheric treatments had no effect on the incidence of SDS."

Examining the effects of atmospheric CO$_2$ enrichment on another soybean pathogen was Braga et al. (2006)$^5$, who conducted three independent experiments. Specifically, the authors grew well-watered soybean (Glycine max (L.) Merr) plants of two cultivars (IAC-14, susceptible to stem canker disease, and IAC-18, resistant to stem canker disease) from seed through the cotyledon stage in 5-liter pots placed within open-top chambers maintained at atmospheric CO$_2$ concentrations of either 360 or 720 ppm in a glasshouse, while they measured various plant properties and processes, concentrating on the production of glyceollins (the major phytoalexins, or anti-microbial compounds, produced in soybeans) in response to the application of β-glucan elicitor (derived from mycelial walls of Phytophthora sojae) to carefully created and replicated wounds in the surfaces of several soybean cotyledons.

Results indicated that the IAC-14 cultivar did not exhibit a CO$_2$-induced change in glyceollin production in response to elicitation -- as Braga et al. had hypothesized would be the case, since this cultivar is susceptible to stem canker disease -- but they found that the IAC-18 cultivar (which has the potential to resist the disease to varying degrees) experienced a 100% CO$_2$-induced increase in the amount of glyceollins produced after elicitation, a response the researchers described as remarkable. As for its significance, Braga et al. say the CO$_2$-induced response they observed "may increase the potential of the soybean defense since infection at early stages of plant development, followed by a long incubation period before symptoms appear, is characteristic of the stem canker disease cycle caused by Dpm [Diaporthe phaseolorum (Cooke & Ellis) Sacc. f. sp. meridionalis Morgan-Jones]." Hence, they say the response they observed "indicates that raised CO$_2$ levels forecasted for next decades may have a real impact on the defensive chemistry of the cultivars."

Further expounding on the importance of glyceollin production was Kretzschmar et al. (2009)$^6$, who introduced their study of the subject by noting that "isoflavonoids constitute a group of natural products derived from the phenylpropanoid pathway, which is abundant in soybeans," and that "the inducible accumulation of low molecular weight antimicrobial pterocarpan phytoalexins, the glyceollins,

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is one of the major defense mechanisms implicated in soybean resistance." The authors next proceeded, as they describe it, to evaluate "the effect of an elevated \( \text{CO}_2 \) atmosphere on the production of soybean defensive secondary chemicals induced by nitric oxide and a fungal elicitor." This they did in a glasshouse study where they grew soybeans from seed for a period of nine days in large well-watered pots placed within open-top chambers that were maintained at atmospheric \( \text{CO}_2 \) concentrations of either 380 or 760 ppm, while they examined changes in the production of phytoalexins and some of their precursors in the activity of three enzymes related to their biosynthetic pathways.

Based on their analysis, Kretzschmar et al. report that "elevated \( \text{CO}_2 \) combined with nitric oxide resulted in an increase of intermediates and diverted end products (daidzein - 127\%, coumestrol - 93\%, genistein - 93\%, luteolin - 89\% and apigenin - 238\%) with a concomitant increase of 1.5-3.0 times in the activity of enzymes related to their biosynthetic routes." Such findings, in the words of the four Brazilian researchers, "indicate changes in the pool of defense-related flavonoids in soybeans due to increased carbon availability, which may differentially alter the responsiveness of soybean plants to pathogens in \( \text{CO}_2 \) atmospheric concentrations such as those predicted for future decades." Put more simply, the ongoing rise in the air's \( \text{CO}_2 \) content will likely increase the ability of soybeans to withstand the attacks of various plant diseases in the years and decades to come, helping the world to better meet the challenge of feeding its still-growing population.

In summation, it would appear from the several findings listed above, and taken in their entirety, that elevated \( \text{CO}_2 \) has the ability to significantly ameliorate the deleterious effects of various stresses imposed upon legume plants by numerous pathogenic invaders. More research, however, would help to further clarify the situation. Nevertheless, the large number of ways highlighted above in which elevated \( \text{CO}_2 \) has been demonstrated to increase plant resistance to pathogen attack gives reason to believe that plants will gain the advantage as the air's \( \text{CO}_2 \) content continues to climb in the years ahead, giving them the ability to successfully deal with pathogenic organisms and the damage they have traditionally inflicted on these important plants.

**REFERENCES**


*Cover photo of soybean seedling uploaded by JMN4 to wunderground.com.*