FACE EXPERIMENTS AND GRASSLAND SPECIES

CO2SCIENCE & SPPI ORIGINAL PAPER ♦ November 20, 2014

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Citation: Center for the Study of Carbon Dioxide and Global Change. "FACE Experiments and Grassland Species." Last modified November 20, 2014. http://www.co2science.org/subject/f/summaries/face grass.php.

In atmospheric CO_2 enrichment experiments, nearly all plants almost always exhibit increases in photosynthetic rates and biomass production when environmental conditions are optimal for growth. Even when conditions are less than favorable (low soil moisture, poor soil fertility, high soil salinity, high air temperature), many plants still exhibit a CO_2-induced growth enhancement; and that *relative* or *percentage* enhancement is sometimes (more often than not, in fact) *greater* than what it is under ideal growing conditions. It is sometimes suggested, however, that results obtained from CO_2-enrichment experiments conducted in growth cabinets, greenhouses and other enclosures may not reflect real-world plant responses to atmospheric CO_2 enrichment due to perturbations in microclimate caused by the enclosures. Thus, *Free-Air CO_2 Enrichment* or FACE technology was developed as a means to enrich the air with CO_2 around vegetation while having minimal effects on the surrounding microclimate; and the following paragraphs of this summary document describe the results of some of those experiments that were conducted on various grassland species, many of which were growing naturally in pastures.

In the study of Nitschelm *et al.* (1997)[1], 18-m-diameter circular plots of white clover were established at a field station of the Swiss Federal Institute of Technology near Zurich and exposed to atmospheric CO_2 concentrations of 350 and 600 ppm; and after one season of growth, the four researchers were able to report that elevated CO_2 increased aboveground biomass production by a whopping 146%. In addition, the extra 250 ppm of CO_2 increased carbon inputs to the soil by 50% while decreasing root decomposition by 24%, thereby enhancing the carbon sequestration capacity of the soils in the CO_2-enriched plots.

In another Swiss experiment, Luscher *et al.* (1998)[2] studied 9 to 14 genotypes of *each* of 12 native grassland species collected near Zurich that were transplanted into FACE arrays maintained at atmospheric CO_2 concentrations of 350 and 700 ppm. And in doing so, they learned that twice-ambient concentrations of CO_2 generally increased aboveground biomass in all twelve species included in the experiment, while showing no preferential effects on any specific genotype of any of the studied species.

In a study by Rogers *et al.* (1998)[3], swards of perennial ryegrass were grown as a frequently-cut herbage crop in a FACE experiment having atmospheric CO_2 concentrations of 360 and 600 ppm. And in this case, the researchers reported that photosynthetic rates were about 35% higher in the CO_2-enriched plots than in the ambient-air plots, *regardless of soil nitrogen content*. Similarly, in a study of nutrient-poor chalk grassland swards, Bryant *et al.* (1998)[4]

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[1] http://www.co2science.org/articles/V2/N21/C4.php.

[2] http://www.co2science.org/articles/V1/N6/B2.php.

[3] http://www.co2science.org/articles/V1/N5/B3.php.

[4] http://www.co2science.org/articles/V1/N5/B2.php.

found that elevated CO_2 increased photosynthetic rates in two of three perennial species by 28%.

Moving into the 21st century, Luscher *et al.* (2000)[5] grew effectively- and ineffectively-nodulating lucerne (*Medicago sativa*) plants in 18-meter diameter FACE plots near Zurich, Switzerland, for multiple growing seasons at atmospheric CO_2 concentrations of 350 and 600 ppm. In addition, half of the plants in each CO_2 treatment received a high soil nitrogen supply, while the other half only received minimal amounts of soil nitrogen. Thus, the authors studied the interactive effects of elevated CO_2 and soil nitrogen supply on biomass production in lucerne plant lines that are both strongly and weekly adept at facilitating symbiotic N_2-fixation.

Results indicated that elevated CO_2 increased the yield of *effectively*-nodulating plants by about 50%, regardless of soil nitrogen supply. In contrast, atmospheric CO_2 enrichment caused a 25% yield reduction in *ineffectively*-nodulating plants subjected to low soil nitrogen, yet produced an intermediate yield stimulation of 11% for the same plants under conditions of high soil nitrogen. These results suggest that the ability to symbiotically fix nitrogen is important in eliciting strong positive growth responses to elevated CO_2 under conditions of low soil nitrogen supply. Atmospheric CO_2 enrichment also increased the percentage of nitrogen derived from symbiosis in effectively-nodulating plants. At high soil nitrogen, for example, elevated CO_2 *doubled* the percentage of symbiotically-derived nitrogen in plant tissues from 21 to 41%. Moreover, at low soil nitrogen, where total plant nitrogen was mostly derived symbiotically, elevated CO_2 still increased its symbiotically-derived percentage from 82 to 88%.

These results suggest that the ability to symbiotically fix nitrogen is important in eliciting strong positive growth responses to elevated CO_2 under conditions of low soil nitrogen supply.

These observations indicate that symbiotic N_2-fixation *per se* is responsible for facilitating significant CO_2-induced growth enhancements in lucerne, particularly under field conditions of inadequate soil nitrogen content. Thus, as the air's CO_2 content rises, it is likely that lucerne species will exhibit significant enhancements in their rates of net photosynthesis. However, it is also likely that these enhancements in carbon uptake will only cause significant biomass increases if the species are adept at symbiotic N_2-fixation. If they are poor nitrogen-fixers, they may exhibit intermediate to negative growth responses, depending upon available soil nitrogen content.

Edwards *et al.* (2001)[6] described how they established a FACE experiment utilizing atmospheric CO_2 concentrations of 360 and 475 ppm on a sheep-grazed pasture in Manawatu, New Zealand, in a study of the long-term effects of elevated CO_2 on community dynamics in this important

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[5] http://www.co2science.org/articles/V3/N23/B3.php.

[6] http://www.co2science.org/articles/V4/N25/B1.php.

dry-land ecosystem; and in this particular paper, they described what they learned about the effects of elevated CO_2 on seed production, seedling recruitment and species compositional changes within the pasture community following two-years of daytime atmospheric CO_2 enrichment. And what was it they found?

In both years of the experiment, the extra 115 ppm of CO_2 was found to increase seed production and dispersal in seven of the eight most abundant pasture species, including the grasses *Anthoxanthum odoratum*, *Lolium perenne* and *Poa pratensis*, the legumes *Trifolium repens* and *Trifolium subterranean*, and the herbs *Hypochaeris radicata* and *Leontodon saxatilis*. More specifically, the three researchers reported that all of the species studied exhibited CO_2-induced increases in the number of reproductive structures per unit area, while in some species the elevated CO_2 also increased the number of seeds per reproductive structure (inflorescences). And these increases in seed production contributed to CO_2-induced increases in the numbers of species present within the CO_2-enriched experimental plots. Greater biodiversity, for example, was found in CO_2-enriched plots due to the presence of several short-lived annual species that were absent from plots exposed to ambient air. In addition, atmospheric CO_2 enrichment helped maintain biodiversity by increasing the number of *H. radicata*, *L. saxatilis*, *T. repens*, and *T. subterranean* seedlings that survived for at least seven months in both study years, while it additionally lengthened the survival time of *A. odoratum* and *L. perenne* in the initial year of experimentation.

As the atmospheric CO_2 concentration increases, therefore, dry-land pasture plants common to New Zealand will likely grow more robustly due to increased seed production, dispersal and extended seedling survival periods, in spite of repeated grazing by sheep. Thus, these pastures will likely increase their carbon-sequestering prowess as the CO_2-mediated changes continue to occur. In addition, the rising CO_2 content of the air should help to maintain, and even *increase*, the biodiversity of these unique pasture communities by increasing the numbers of both the common and uncommon species they contain.

One year later, Billings *et al.* (2002)[7] enclosed naturally-occurring vegetation in the Mojave Desert of Nevada, USA, within FACE plots maintained at atmospheric CO_2 concentrations of 350 and 550 ppm in order to study the effects of elevated CO_2 on this desert community that is dominated by the perennial shrub *Larrea tridentat*a. And at the end of their study, the six scientists reported the results of their measurements of plant nitrogen isotopic composition, which they had made with the objective of determining if elevated CO_2 affects nitrogen dynamics in this arid desert ecosystem.

Over a seven-month sampling period, the amount of ^{15}N within ambiently-grown and CO_2-enriched vegetation increased by 34 and 58%, respectively; and the researchers suggested that the larger CO_2-induced enhancement of plant ^{15}N concentration was due to atmospheric CO_2 enrichment helping soil microbes to overcome soil carbon limitations, thus enabling microbial activity to increase and enhance the availability of soil nitrogen to plants. And, therefore, in many desert areas, where the productivity of natural ecosystems is limited by low soil carbon concentrations, the ongoing rise in the air's CO_2 content should result in greater

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[7] http://www.co2science.org/articles/V5/N18/B2.php.

inputs of carbon to soils via enhanced plant root exudation and litter production that in turn will likely stimulate soil microbial activities, which should increase the amount of soil nitrogen that is available to plants. And this phenomenon, in turn, should allow desert plants to produce even more biomass, with the result that the productivity of carbon-limited ecosystems, such as deserts, will likely rise significantly as the CO_2 content of the atmosphere continues its upward trajectory.

In many desert areas, where the productivity of natural ecosystems is limited by low soil carbon concentrations, the ongoing rise in the air's CO_2 content should result in greater inputs of carbon to soils via enhanced plant root exudation and litter production that in turn will likely stimulate soil microbial activities, which should increase the amount of soil nitrogen that is available to plants.

Simultaneously, Suter *et al.* (2002)[8] grew perennial ryegrass (*Lolium perenne* L.) in field plots, as part of a FACE experiment, where ambient and elevated CO_2 concentrations were maintained for approximately two months at 350 and 600 ppm, respectively; and in doing so, they found that the elevated CO_2 treatment increased total dry matter production by 65%, while it enhanced root dry weight by 109%, which led them to conclude that as the CO_2 content of the air increases, swards of perennial ryegrass will likely exhibit increased rates of photosynthesis and dry matter production that should favor the growth of belowground organs, such that the carbon sequestering prowess of grasslands dominated by perennial ryegrass is likely to increase with future increases in the air's CO_2 content.

One year later, in introducing their study of the subject, Richter *et al.* (2003)[9] noted that the productivity of earth's temperate grasslands is often limited by the availability of soil nitrogen (Vitousek and Howarth, 1991); and they remarked that both empirical and modeling studies had suggested that the magnitude and duration of grassland growth responses to rising levels of atmospheric CO_2 may be constrained by limiting supplies of soil nitrogen, citing Rastetter *et al.* (1997), Luo and Reynolds (1999) and Thornley and Cannell (2000). And in light of this mix of *real-world observations* and *theoretical implications*, it would seem only natural to *believe*, as Richter *et al.* (2003) *hypothesized*, that "increased below-ground translocation of photo-assimilates at elevated pCO_2 would lead to an increase in immobilization of N due to an excess supply of energy to the roots and rhizosphere," which would ultimately lead to a reduction in the size of the growth-promoting effect of elevated atmospheric CO_2 that is nearly universally manifest in short-term CO_2 enrichment experiments.

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[8] http://www.co2science.org/articles/V5/N21/B3.php.

[9] http://www.co2science.org/articles/V6/N49/B1.php.

To test this hypothesis, Richter *et al*. measured gross rates of N mineralization, NH_4^+ consumption and N immobilization in soils upon which monocultures of *Lolium perenne* and *Trifolium repens* had been exposed to ambient (360 ppm) and elevated (600 ppm) concentrations of atmospheric CO_2 for *seven years* in the Swiss FACE study conducted near Zurich. And in doing so, in the words of the five researchers, they found that "after seven years of exposure to elevated CO_2, gross mineralization, NH_4^+ consumption and N immobilization in both the *L. perenne* and the *T. repens*s wards did not show significant differences." In addition, they found that the size of the microbial N pool and immobilization of applied mineral ^{15}N were not significantly affected by elevated CO_2.

Richter *et al*. thus concluded that the results of their study "did not support the initial hypothesis," but that they indicated that "below-ground turnover of N, as well as N availability, measured in short-term experiments are not strongly affected by long-term exposure to elevated CO_2." And they also concluded that "differences in plant N demand and not changes in soil N mineralization/immobilization are the driving factors for N dynamics in these meadow grassland systems." Therefore - as in the studies of Finzi and Schlesinger (2003) and Schafer *et al*. (2003) dealing with trees - their work provided no evidence that the growth responses of earth's grasslands to atmospheric CO_2 enrichment will ever be significantly reduced from what is suggested by moderate-term studies of a few to several years' duration.

Concluding this topical summary are a few remarks on the study of van Groenigen *et al.* (2003)[10], who studied, as they described it, "the effects of *Trifolium repens* (an N_2-fixing legume [white clover]) and *Lolium perenne* [L.] [perennial ryegrass] on soil N and C sequestration in response to 9 years of elevated CO_2 under FACE conditions." This work was conducted at the grassland FACE facility of the Swiss Federal Institute of Technology in Eschikon 20 km northeast of Zurich, where control FACE plots were maintained at the CO_2 concentration of the ambient air (~350 ppm) and CO_2-enriched plots were maintained at a concentration of 600 ppm. In addition, each FACE plot was split into a low- and high-N soil fertility treatment by applying either 140 kg N ha^{-1} or 560 kg N ha^{-1}, respectively, to the soil following periodic cuttings of the swards. And what did they thus learn?

As the atmosphere's CO_2content continues to rise, grassland productivity, growth and carbon sequestration should all increase right along with it.

The five scientists reported that as observed in other studies (Hu *et al*., 2001; Kimball *et al*., 2002), they too "found a trend of increased total soil C under elevated CO_2." But they also reported that "although N_2 fixation was a major source of N for *T. repens*, the presence of N_2 fixation *per se* did not lead to higher soil N and C content compared with a low-N-fertilized *L. perenne* system." Hence, they concluded that "factors other than N_2 fixation exert a higher control on soil C and N stabilization in the *T. repens* system." And it is also thereby to be noted that the findings of this study did not support

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[10] http://www.co2science.org/articles/V7/N7/B1.php.

the claim of Hungate *et al*. (2003), in that these real-world observations demonstrated that extra nitrogen provided in the form of either fertilizer-applied N or biologically-fixed N was not needed to enhance the CO_2-induced sequestration of carbon in the soil of this experiment.

In summary, the results obtained from the several FACE experiments described above clearly demonstrate that the increasing CO_2 content of the air will positively impact photosynthetic rates and biomass production in grassland plants, even if they are growing under stressful conditions imposed by poor soil fertility. Thus, as the atmosphere's CO_2content continues to rise, grassland productivity, growth and carbon sequestration should all increase right along with it.

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