Will Plants Profit From High CO_2?

Increasing atmospheric CO_2 concentrations may help crops grow better, but the jury is out on how plants in natural ecosystems will respond

Duke Forest in North Carolina is a pleasant place, home to lush stands of sweet gum, loblolly pine, and dogwood. But anyone visiting one particular experimental patch in the next few years may find a forest even more verdant than usual, where the trees are taller and the canopy denser. The elixir that's expected to spark this extra growth: carbon dioxide, pumped into a circular patch of forest by the ton.

Duke's charmed circle is intended to be a window on the future, one of many efforts now under way to predict the effects of rising atmospheric CO_2 concentrations on the plant world. For although debate still rages over whether CO_2 and other greenhouse gases are warming the globe, no one disputes that atmospheric CO_2 is rising. The concentration has climbed from about 270 parts per million (ppm) in 1870 to about 360 ppm today. And CO_2 is more than a greenhouse gas—it's also an essential nutrient for vegetation, an "aerial fertilizer" providing the carbon that plants use to make sugars, carbohydrates, and the other compounds they need to live.

In the agricultural realm, experimental evidence suggests that higher CO_2 concentrations may be a boon, helping many crops grow faster and yield more. In natural ecosystems, the effects are less clear. Although William Schlesinger, co-director of the Duke project, says he expects the trees in Duke Forest to do well, he and others have hundreds of questions about how the rest of the forest, from soil microbes to poison ivy, will respond. Finding the answers demands sophisticated and time-consuming field and lab experiments—like transforming the air inside a patch of forest. "We have some ideas about how CO_2 affects plants , but we're just beginning to figure out what CO_2 does to an ecosystem," says Schlesinger.

The results have ramifications far beyond the botanical world. If higher CO_2 levels stimulate plant growth, plants may absorb even more CO_2 from the air and so buffer the world against additional atmospheric change. In the tally of today's global carbon budget, more than 1 billion metric tons of atmospheric carbon are unaccounted for, and there's evidence that growing forests in the Northern Hemisphere are already taking up some of this missing carbon.

Also, CO_2 has such a profound effect on plants that higher concentrations, even without any associated climate change, could dramatically change the composition of ecosystems. "Virtually every aspect of the structure and function of terrestrial ecosystems—from flowering times to microbial activity to species diversity—has the potential to be changed," says ecologist James Teeri of the University of Michigan.

One reason the composition of ecosystems is likely to change is that not all plant species react in the same way to high levels of CO_2. Modern vegetation has adopted two major pathways for assimilating carbon during photosynthesis. One, the C3 pathway (in which the first products of photosynthesis are three-carbon compounds), wastes half the carbon the plant takes in; the other, the C4 pathway (in which the first products are four-carbon compounds), conserves carbon.

HARVARD UNIVERSITY

Growth bonus. These Texas wildflowers fared better in high CO_2 *(right)* than in ambient concentrations.

C3 plants are sensitive to higher CO_2 and typically respond with a burst of photosynthesis and growth; C4 plants don't respond so dramatically. But even within these two groups, species react differently, says biologist and CO_2 expert Fakhri Bazzaz of Harvard University. For example, his group found that seedlings of American beech trees nearly doubled their biomass under high-CO_2 conditions, while seedlings of white pine—also C3 plants—showed only a 20% increase.

Farm friendly

For agriculture, the generally higher response of C3 plants may be good news. Many major crops, including wheat and rice, belong to the C3 group and are expected to yield more grain in high-CO_2 air. They may also outcompete some C4 weeds. Overall, many agriculture experts say rising CO_2 levels will have a beneficial effect. "Almost every experiment that's been done basically shows that when there's more CO_2 in the air, plants grow better," says Sherwood Idso, who studies CO_2's effects on crops at the U.S. Department of Agriculture's (USDA's) Water Conservation Laboratory in Phoenix. Estimates of yield increases range from 10% to 50% or even more.

For the past 7 years, for example, Idso and his colleagues have been studying the effects of doubling the ambient CO_2 level on sour orange trees grown with plenty of water and fertilizer in open-topped chambers in the field. This experiment is one of the longest running of its kind, and in the first few years, trees grown in high CO_2 were taller than controls. Now both sets of trees are the same height, but those exposed to high CO_2 levels are bushier—and consistently yield twice as much fruit as the controls, says Idso.

Another experiment in central Arizona, co-directed by Idso's USDA colleague Bruce Kimball, pumps CO_2 directly onto crop fields. This technique—the one used in Duke Forest—is called Free Air Carbon Enrichment, or FACE, and is considered by many to be the most realistic way to create high CO_2 conditions. Designed by George Hendrey of Brookhaven National Laboratory, FACE takes CO_2 research into the realm of big science, as each experiment costs more than $1 million and involves a diverse research team. But Hendrey and others feel it's the only way to find out for sure how plants will respond in the field.

FACE studies a few years ago showed dramatic yield increases in cotton—as much as 50%; the latest results, as yet unpublished, show that wheat yields also increase, although more modestly, by about 10%. "On the whole, this is very good news for agriculture," says Kimball. Indeed, Duke's Boyd Strain estimates that up to 10% of the increased crop yields in the past century was due to higher CO_2 levels rather than to new crop varieties or fertilizers and insecticides.

But like every benefit, this one may have its costs. To take full advantage of the CO_2 bonus, farmers may have to use more fertilizer to make sure that lack of other nutrients doesn't limit crop growth. Developing nations, unable to afford extra fertilizer, may not reap all the benefits, says Strain, who notes that "all the problems of agricultural technology are likely to increase."

Air rich in CO_2 is likely to spark other, as-yet-unpredictable changes in agriculture, involving insects, weeds, and livestock. Some important C4 crops, such as corn and sugarcane, may not fare so well against C3 weeds, for example. And because plants grown under high-CO_2 conditions typically have less nitrogen per unit leaf area, forage crops may provide less protein to livestock. For example, sheep grazing on prairie grasses in high-CO_2 enclosures ate poorer quality forage than did controls, according to an experiment done by Clenton Owensby and colleagues at Kansas State University. But overall, most researchers agree with Hugo Rogers of the USDA Soil Dynamics Laboratory in Auburn, Alabama, who says he's "guardedly optimistic, at least about C3 crops," in a high-CO_2 world.

Counting carbon

When it comes to balancing the global carbon budget, though, the crucial component is not farms but forests and other natural ecosystems, which can store tons of carbon, points out Schlesinger. And even though studies have shown that trees and other plants—many of which are C3—increase photosynthesis and growth under high-CO_2 conditions, many uncertainties remain. "Overall, the world may be somewhat of a greener place," says Ohio State University's Peter Curtis. "But there's no guarantee that will be good for biodiversity."

Of course, the basic effect of high CO_2 on plants—making carbon more readily available for photosynthesis—is the same whether plants grow in the wild or in a plowed field. But long-term experiments show that plants in natural ecosystems don't always respond to high CO_2 levels the way crops do.

For starters, in many natural systems—although not all—the increased photosynthesis sparked by air rich in CO_2 levels off over time. For example, a team led by Walter Oechel of San Diego State University showed that after an initial burst of growth, tundra vegetation returned to previous levels of photosynthesis after only 6 weeks or so. The same thing appears to happen in trees. In an as-yet-unpublished meta-analysis combining the data from 38 studies, Curtis found that the growth response of trees to high CO_2 levels was much greater in short-term studies than in long-term ones. "The initial great increase in carbon fixation just doesn't last," sums up Duke's Strain.

Botanists have good physiological mechanisms to explain this "acclimation" to higher

WILL OWENS

Pumped up. The towers are used to pump CO_2 into Duke's experimental forest plot.

levels of CO_2. But the phenomenon typically doesn't appear in crop experiments—Idso's sour orange trees are still growing like gangbusters after 7 years, for example. And not all natural ecosystems show the effect, either. Grasses in the Chesapeake Bay salt marsh ecosystems studied by Bert Drake and colleagues at the Smithsonian Institution have kept up high rates of photosynthesis for years. "How the CO_2 effect plays out in the long run remains a very big mystery," says Teeri.

Idso, who has described rising CO_2 levels as "the single best thing that could ever happen to the biosphere," is convinced that acclimation is simply an artifact of experimental design. He believes that plants grown under less-than-ideal conditions respond more to high CO_2 and speculates that next century, natural ecosystems will burgeon even more than his orange trees.

But most ecologists favor a different explanation for the conflicting long-term results. They think plant responses to CO_2 depend on the availability of other essential factors, such as light, water, and nitrogen. Crops, nurtured with water and fertilizer and protected against insects and weeds, can take advantage of extra atmospheric carbon indefinitely. But in natural ecosystems, plants face limits of many kinds that eventually curb their growth, so they show only a short-term jump in photosynthesis, explains Curtis. If so, predicting the effects of high CO_2 in natural systems requires a detailed understanding of how CO_2 interacts with the cycling of other key factors. So CO_2 researchers have shifted their focus to complex questions of nutrient cycling and soil microbe ecology. While the work is at an early stage, some clues are emerging.

Idso appears to be right with regard to one stress: drought. In long-running experiments on tall grass prairie, Owensby and colleagues found that during wet years, prairie grasses grew no better in high CO_2 than they did in control chambers. But in normal and dry years, high-CO_2 plants responded dramatically, with up to 40% more above-ground biomass. "In our system, the key effect of CO_2 is to reduce water use," says Owensby. Similar results have emerged from ongoing work in California grasslands.

Physiological studies have shown why: Air rich in CO_2 helps plants save water. Water evaporates from plant leaves through the same pores (called stomata) used to exchange CO_2 and oxygen. And because it's easier for plants to take in CO_2 when atmospheric concentrations of the gas are high, stomata stay partially closed and evaporate less water in high CO_2 conditions. Other studies show that plants grown in high CO_2 have fewer stomata per leaf and close them faster.

Nutrient needs

Although there's some agreement that plants under drought stress respond more to CO_2, the consensus frays when other vital factors enter the picture. When it comes to nutrients, most ecologists don't buy Idso's argument that less makes more. "That idea does not make sense," says Bazzaz. "If one nutrient is limiting, how can plants respond more to the addition of a different factor, carbon?"

Ecologists suspect that lack of nutrients may ultimately limit plant growth in natural ecosystems under high CO_2. Even in the short term, there's evidence that scarce nutrients curb plants' responses to high CO_2. For example, when Duke's Richard Thomas and colleagues grew loblolly pine seedlings with abundant nutrients under high-CO_2 conditions, photosynthesis increased. But when either nitrogen or phosphorus was limited, high CO_2 had no effect.

But the literature is confusing; other studies show that high CO_2 helps plants make the most of available nutrients—thereby helping them grow. To sort out the situation, researchers are tracing the intricacies of the nitrogen cycle—much of which happens underground—and testing competing hypotheses as to whether high CO_2 makes more or less nitrogen available.

Teeri and colleagues found evidence of a positive feedback in experiments on aspen. Under high CO_2 levels, seedlings pumped some of the compounds made from the extra carbon into their roots and eventually into the soil. That boosted populations of the soil microbes that make nitrogen available to plants by decomposing plant litter. Also, many studies have shown that high CO_2 levels generally stimulate root growth, allowing plants to exploit soil nitrogen more efficiently. All this is "a jazzing up of the whole below-ground component," says Strain—with a net effect of spurring plant growth.

In contrast, other studies suggest that soil microbes themselves might use any extra nitrogen produced; in that case, plant growth will eventually be limited, says Kurt Pregitzer of Michigan Technical University, who works on the problem with Teeri. And in the long term, high CO_2 levels could slow the nitrogen cycle: If there is less nitrogen per leaf, leaf litter may decay more slowly and limit the amount of nitrogen available to plants, says Pregitzer. For now, there's evidence for both cycles. "It may be that both positive and negative cycles can occur," says Bazzaz. "The trick for us is to find out which scenario operates under which conditions and ecosystems."

Despite all these uncertainties, most ecologists expect terrestrial ecosystems to absorb some—but not all—of the extra carbon that will be pumped into the air in the next century. Bazzaz estimates the global response to doubled CO_2 will be no more than a 10% to 20% growth increase. In that case, plants will almost certainly not be able to balance the carbon budget.

As for ecosystems, although researchers can't predict the effects of high CO_2 in detail, they do forecast change. Even if global warming never comes, if you take a walk in a northern Michigan forest 50 years from now, you'll probably find a changed world, with a different mix of trees and other species, says Teeri. Denser forest canopies may favor shade-tolerant species, and the identity of key pathogens may shift as various insects decline, prosper, or switch from one plant to another under high-CO_2 conditions. In some species, high CO_2 can also trigger earlier flowering, which could disrupt insect pollinators. Researchers are just beginning to explore such changes in Duke's ring of 21st-century air, as well as in other facilities.

For now, there's consensus that air rich in CO_2 will be a boon for many farmers, at least in developed nations. But many ecologists believe it's too soon to say whether humans will celebrate or mourn the biodiversity shifts triggered by our changing atmosphere. One thing seems certain: Whether air enriched in CO_2 warms the globe or not, the gas will alter the growth of green plants and so act as a potent force for global change.

–Elizabeth Culotta

Additional Reading

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INTELLECTUAL PROPERTY

Sweeping Patents Put Biotech Companies on the Warpath

In October 1992, the U.S. Patent and Trademark Office (PTO) stunned the agricultural biotechnology community by awarding a patent to a single company, Agracetus Inc. of Middleton, Wisconsin, for rights to all forms of genetically engineered cotton—no matter what techniques or genes are used to create them. "It was as if the inventor of the assembly line had won property rights to all mass-produced goods, from automobiles to washing machines," says Jerry Caulder, chief executive officer of San Diego–based Mycogen Corp.

While the patent's breadth took the plant biotech community by surprise, what happened next was less surprising: a round of legal challenges that hasn't ended yet. And it would not be the last such battle. At least three major legal tussles over the awarding of broad patents for genetically altered plants are now tying up agricultural biotechnology companies, and more such conflicts are on the horizon. "It's like the Superfund program," says Neil Hamilton, director of Drake University's Agricultural Law Center, referring to the U.S. Environmental Protection Agency's embattled program to clean up toxic waste sites. "Instead of money getting spent to benefit society, it's getting diverted to fights over ownership and liability."

These test cases—along with some similarly broad patents issued in Europe—are being closely followed in the biotech industry. For Agracetus and other companies, the outcomes of these patent decisions could significantly affect their bottom lines. Some smaller companies could even be forced out of business if they have to pay licensing fees for use of the patented technologies. According to Caulder, for example, Agracetus has asked $1 million for a license to exploit its cotton technology—a significant sum for a small start-up company. (Agracetus refused to confirm the figure.)

A budding dispute. Since the early 1980s, the PTO has awarded 112 patents for genetically engineered plants and recombinant DNA approaches to manipulating plants. But the legal skirmishes have been touched off by a handful of patents that stand to be real moneymakers: high-value crops or technologies experts expect to be widely used.

In addition to Agracetus's cotton patent, these include a patent awarded on 2 March 1993 to biochemist Masayori Inouye of the State University of New York, Albany, who now works at the University of Medicine and Dentistry of New Jersey. The patent, licensed to New York City's Enzo Biochem Inc., gives the firm broad rights to use novel RNAs, called antisense RNAs, to block the activity of specific genes in any crop. On the same day PTO issued the patent, Enzo sued Calgene Inc., a Davis, California–based company that uses an antisense gene it patented to produce the Flavr Savr tomato, a vine-ripening tomato that resists spoiling. And in March 1994, the European Patent Office (EPO) granted broad rights to Agracetus for all forms of genetically engineered soybeans. This patent, too, is under legal challenge.

While none of these cases may have the longevity of Jarndyce and Jarndyce, all of them are likely to be long-running. The story of the cotton patent, in fact, is already a decade old. About 10 years ago, a team of Agracetus scientists led by Paul Umbeck launched a program to develop a system for inserting foreign genes into cotton, using as a carrier the bacterial pathogen *Agrobacterium tumefaciens*. This bacterium easily infects cotton, and in the course of the infection, transfers a plasmid, a small circular piece of DNA, into the plant cells, where the plasmid DNA splices itself into the cellular genome. A foreign gene inserted into the plasmid will also be incorporated in the host plant's DNA, and after plant scientists infect cotton cells in culture with *A. tumefaciens* carrying such a modified plasmid, they can regenerate whole plants carrying the new gene from the single cells transformed by the bacterium.

A Tale of Four Broad Patents

1992

October
U.S. Patent and Trademark Office (PTO) awards patent to Agracetus granting rights to all forms of genetically engineered cotton.

1993

March
PTO awards patent, licensed to Enzo Biochem, granting rights to antisense technology used in crops; Enzo sues Calgene for infringing its antisense patent.

Enzo Biochem vs. Calgene

But when Umbeck filed an application for a patent on the technique in August 1990, he claimed to have invented more than just a modified *Agrobacterium* technique for use in cotton: He claimed "cottonseed capable of germination into a cotton plant comprising in its genome a chimeric recombinant