In this respect though, it is puzzling that some of the most plastic ecotypes they observed were from the Mediterranean Sea, which tends to have relatively low variability in CO_2 concentrations, compared with the extremes in CO_2 levels typical of upwelling regions[7], for instance. Their general hypothesis about the fitness advantages of CO_2-related plasticity also hinges on whether CO_2 actually has a large role in determining the outcome of intraspecific competition. Other factors, such as differential responses to nutrients and light, certainly influence the genotypes that win or lose in phytoplankton populations. It will be interesting to see what range of plastic responses exists in algal species with respect to these other key environmental variables (most of which are also in flux due to climate change[6,8]), and what effect this might in turn have on the relative fitness of phytoplankton ecotypes in the future.

Although plenty of open questions remain, clearly this work has important lessons for the science community. We need to do a much better job of considering the full range of biodiversity in natural populations of marine species than we have done in the past, with our too-narrow focus on a few model culture isolates. Their results also offer us a ray of hope in a discipline that often seems to deal mostly with bad news for ocean ecosystems. The unexpected diversity of plastic responses to ocean acidification within this single species suggests the possibility that, in many phytoplankton populations, there may be enough existing genetic variation to allow them to cope with the profound environmental challenges they will be faced with in the future.

Schaum *et al.*[1] have opened the door to a broader discussion of the role of plasticity in the responses of marine organisms to a changing ocean. For instance, how does the concept of plasticity-related fitness apply to other relevant factors, such as warming, or shifts in light and nutrient availability? Can plastic responses encompass the types of complex synergistic and antagonistic interactions[8] that are known to occur between these and other variables under climate change? And what will be the relative importance of plasticity, acclimation and adaptation as the biota are confronted with all of these simultaneous changes? These are the kinds of questions that will need to be answered if we are to fully understand how ecologically critical functional groups of phytoplankton will respond to a rapidly changing ocean environment. ❐

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BIOGEOCHEMISTRY

Limits on carbon uptake by plants

Increased concentrations of carbon dioxide in the atmosphere support greater plant biomass in grasslands, but this response is constrained in the long term by soil nitrogen availability.

Pamela H. Templer

Human activities, including deforestation and burning of fossil fuels, have led to increased concentrations of CO_2 in the atmosphere over the past two centuries[1]. Carbon dioxide is an essential compound for plant growth, but it is also a greenhouse gas, with greater concentrations leading to potentially warmer global temperatures and other consequent changes in climate. Plants convert CO_2 to sugars and oxygen during photosynthesis and this process provides the source of energy that most life on our planet relies on. Increased concentrations of CO_2 in the atmosphere are known to fertilize plants and increase their rates of growth; an outstanding question is whether this 'CO_2 fertilization effect' will continue indefinitely, or be limited by the availability of other nutrients essential for plant life, including nitrogen. Nitrogen is an essential constituent of DNA, enzymes and proteins in all living organisms. If the CO_2 fertilization effect were to continue indefinitely, the result would be a win-win for the planet. Plants would increase their rates of productivity, humans would have more food to eat and concentrations of CO_2 would be diminished in the atmosphere. Unfortunately, a new study by Reich and Hobbie[2] in *Nature Climate Change* indicates that nitrogen availability does indeed constrain the CO_2 fertilization effect over the long term, at least for grassland plants.

Many experiments have been established to examine the interaction between nitrogen availability and the effect of elevated atmospheric concentrations of CO_2 on photosynthesis and plant biomass. However, very few studies have investigated this relationship with open-air CO_2 enrichment for a period longer than 5 years[2–4]. In this type of experiment, CO_2-enriched air is pumped into an ecosystem to expose plants and soils to increased concentrations of CO_2. Reich and Hobbie[2] present results from their grassland experiment at the Cedar Creek Ecosystem Science Reserve in Minnesota: they used a complete factorial design — where all possible combinations of the inputs are investigated — with half of the plants receiving ambient CO_2, and the other half exposed to higher concentrations (180 μmol mol^{-1} above background). In each of these two groups, half received ambient levels of soil nitrogen, and the other half were provided with an additional 4 g N m^{-2} yr^{-1}. The authors measured biomass by clipping and weighing plant tissue in 296 open-air plots over a 13-year period. They found nitrogen availability had no effect on plant biomass during the first three years of the experiment. However, over the next 9 years, they found that plant biomass doubled when plants were provided with greater amounts of nitrogen. These results indicate that nitrogen availability in soils can constrain the ability of plants to take up CO_2 in the long term, thereby influencing the carbon balance between plants, soils and the atmosphere. Reich and Hobbie[2] argue that nitrogen availability should therefore be incorporated into a greater number Earth system models.

One of the strengths of their study lies in the fact that it is one of the longest running experiments of its kind, with 13 years of published data so far. As Reich and Hobbie point out, similar investigations in other grasslands — as well as other ecosystem types — are needed to make predictions for the future. Their results highlight the positive effects of enhanced nitrogen availability on the ability of plants to take up CO_2 and increase their biomass. However, it should be noted that future CO_2 uptake by plants could also be constrained by negative effects of enhanced nitrogen availability, as has been demonstrated by studies examining large N additions through atmospheric deposition[5]. In other words, a small increase in nitrogen acts as a fertilizer, and can stimulate uptakeof CO_2 and plant growth, but too much nitrogen leads to a variety of negative effects, including nutrient imbalances in plants, reduced rates of productivity and acidification of soils and nearby aquatic ecosystems.

Other human-mediated changes in the environment are also known to reduce rates of CO_2 uptake by plants, and these should be considered in Earth system models as well[6]. A key example is increased concentrations of ground-level (tropospheric) ozone — caused by photo-oxidation of nitrogen oxides (NO_x) released due to human activities — that reduce rates of CO_2 uptake by plants[7] and net primary productivity[8]. Ozone is a strong oxidant that enters plant leaves through stomata and leads to degradation of plant chlorophyll, which is required for photosynthesis. Tropospheric ozone concentrations are projected to increase worldwide up to 42% by 2100 (relative to 2000)[9], making it imperative that interactive effects of CO_2 uptake, nitrogen availability and ozone pollution on plants be examined (Fig. 1). All of these constraints that affect the ability of plants to remove CO_2 from the atmosphere need to be incorporated together into Earth system models to make more accurate predictions about the potential role of plants as sinks for CO_2. Although this will make the models more complex, and possibly more unwieldy, both the positive and negative effects of nitrogen availability — and other human-induced changes in the environment — should be accounted for to avoid bias in one direction or the other. Reich and Hobbie[2] take us a step closer to making these predictions more accurate in the future. ❐

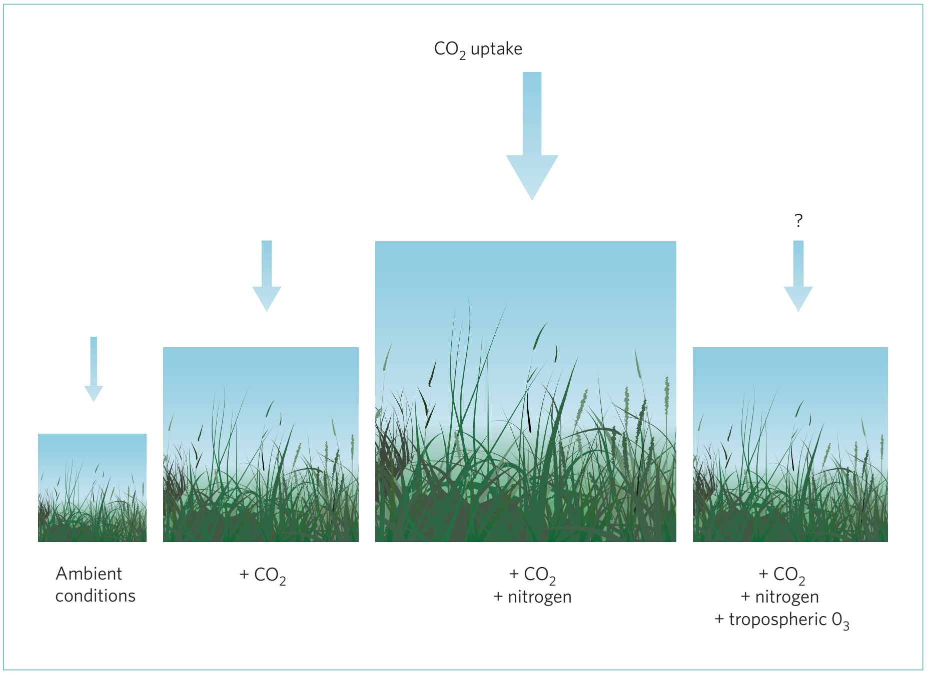

Figure 1 | Schematic representation of some of the environmental controls on plant productivity. Increased atmospheric CO_2 concentrations can enhance plant productivity, but this CO_2 fertilization effect is constrained by nitrogen availability, and offset by increased concentrations of tropospheric ozone and other pollutants. The relative size of each arrow is proportional to the flux of CO_2 taken up by plants, and the question mark indicates that CO_2 uptake is less well undertood under these conditions. The relative size of each ecosystem is proportional to the biomass and rate of productivity within it.

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