CLIMATE CHANGE

Past and Future Global Biospheric Productivity

Large changes in global ecosystem productivity are set in motion by CO_2 rise and climate change

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The response of terrestrial and marine ecosystems to rising CO_2 levels and climate change is one of the key scientific questions of our times. Ecosystems are responsible for storing vast amounts of carbon, which, if destabilized, could amplify climate change (*1*). Ecosystems also provide multiple services to society, from food and shelter to recreation and wellbeing. Changes in ecosystems and their productivity at the global scale could have fundamental implications for society. On page XXX of this issue, Yang and al. (*2*) reconstruct changes in global biosphere productivity during the past eight glaciations, providing unique insights into the sensitivity of global ecosystems to CO_2 levels and climate change.

Several processes influence the productivity of terrestrial and marine ecosystems. For terrestrial ecosystems, the concentration of CO_2 in the atmosphere is a major limiting factor (*3*). At higher CO_2 levels, plants become more efficient at using water because their stomata need to open less to capture the CO_2 needed for photosynthesis. Eventually as CO_2 rises, this “CO_2 fertilization” effect becomes less important as other resources become limiting, in particular water and nutrients. At lower CO_2 levels, CO_2 fertilization acts in the reverse direction, decreasing productivity (see the figure). It has been difficult to quantify globally the exact extent of CO_2 fertilization in recent decades because it is difficult to separate the fertilization effect from the regrowth of vegetation following the abandonment of agricultural land and other management processes (*4*, *5*). For the ocean, there is no widespread CO_2 fertilization effect because marine ecosystems are primarily limited by nutrients, although ecosystems respond to ocean acidification resulting from rising CO_2 in ways that are not fully understood (*6*).

Climate change also affects terrestrial and marine ecosystems and their productivity in multiple different, and often opposing, ways (*7*). On land, changes in temperature, rainfall, and associated changes in weather and land cover regulate nutrient cycling, ecosystem composition and productivity, and ultimately the carbon stored in biomass and soils (*4*, *8*). In the ocean, the uptake of CO_2 by the oceans today mainly results from the dissolution of CO_2 in the ocean surface and its transport to the deep ocean (*9*). However, changes in temperature, winds, and rainfall influence ocean circulation, surface stratification, nutrient cycling and availability, marine productivity, and ultimately changes in the storage of carbon in the deep ocean (*10*, *11*). The effect of climate change can be profound, but because climate influences so many processes it has been difficult to quantify (*1*, *12*). The effect of climate change on the storage of carbon in the land and oceans is one of the largest sources of uncertainties for the projection of future climate change.

Glacial cycles offer a natural laboratory to study the large-scale response of ecosystems to changing CO_2 levels and climate. Glacial cycles have been triggered by small changes in the Earth’s orbit that led to increased snow and ice coverage, more reflected sunlight, colder oceans storing more carbon, and lower CO_2 levels in the atmosphere causing further cooling. Much of our knowledge on glacial cycles is known from measurements of air trapped in ice cores and from the analysis of marine sediments. These natural archives provide unique opportunities for understanding what we today call "Earth System" processes, referring to processes that involve complex exchanges between the natural environment, including the storage of carbon in the land and ocean, and climate.

Yang et al analyzed the isotopic signature of oxygen in ancient air bubbles trapped in ice cores over the past 800,000 years covering eight glacial cycles. They use the oxygen isotopes to reconstruct past changes in global gross primary productivity (GPP) – the amount of atmospheric CO_2 absorbed (or O_2 produced) during photosynthesis by the oceanic and terrestrial ecosystems combined. Heavy isotopes are discriminated against during photosynthesis because of their mass, and leave a specific signature behind. However, the biological signal is compounded by exchanges between the troposphere and the stratosphere, where the isotopic signature also differs from that of background air at the Earth's surface. *Yang et al.* isolated the influence of photochemical reactions in the stratosphere from the biological signal induced by the past global biosphere productivity using two simple models that differed in the formulation of the stratospheric effect. Their analysis suggests large decreases in productivity during glacial periods, estimated between 55% and 87% of the present global GPP.

The reduced productivity inferred by *Yang et al.* during glacial periods is for the terrestrial and marine productivity combined (*13*). However, the timing of the decrease in global productivity cannot be strictly explained by processes that were operating in the ocean at that time. During glacial periods, some marine photosynthesizers were limited by a reduction in the supply of essential nutrients induced by reduced ocean ventilation. Meanwhile, the increase in atmospheric dust deposition was a large source of iron (a limiting nutrient) to the ocean, although it was limited to the Southern Ocean in the later stages of the glaciations (*14*). By using several local records of past marine biosphere productivity, *Yang et al.* confirmed the diversity of responses of the oceanic biosphere to the glacial climates, and they exclude the ocean as the main cause of the large decreases in GPP inferred from oxygen isotopes.

In contrast, the changes in productivity inferred by Yang et al. occurred systematically in response to changes in atmospheric CO_2 concentration, pointing to the effect of CO_2 fertilization on the terrestrial biosphere. The coinciding changes in productivity and atmospheric CO_2 between glacial and interglacial periods were also observed within glacial periods thanks to their new high-temporal-resolution index of the past global GPP. During glaciations, CO_2 fertilization acted as a negative (damping) feedback, because productivity decreased as atmospheric CO_2 levels decreased, leading to less uptake of CO_2 by the biosphere and leaving more CO_2 in the atmosphere where it reduced the initial effect. Yang et al. tested the CO_2 fertilization hypothesis using GPP reconstructed with a process model output from an Earth System Model over the Last Glacial Maximum. The model results confirm that the inferred GPP changes during glaciations are consistent with estimates based on current knowledge of plant physiology and their responses to changes in CO_2 fertilization. Moreover, the reduced atmospheric CO_2 fertilization effect on the terrestrial biosphere productivity during glacial periods was supported also by pollen records from Europe and SE Africa. Finally, the global GPP increases observed at mid-glacial stages could also be explained by an enhanced terrestrial productivity due to the CO_2 fertilization and, secondly, increases in the tropical precipitation.

CO2 emissions from human activities causing a rise in atmospheric CO2. The fertilizing effect of CO2 leads to an increase in terrestrial productivity and carbon storage (*4*) which will continue some time in the future (*1*), providing a strong negative feedback that greatly slows down the rate of climate change. The analysis of Yang et al. confirms its importance and provides constraints on its size. Deforestation, in addition to releasing the carbon stored in existing biomass, also reduces the sink potential from this important CO_2 fertilization effect (*15*). The comparison between glacial and future changes in productivity has limits, because glaciations do not provide information on the level at which CO_2 fertilization ceases, which depends on the limitation by water, nutrients and on physiological factors. More importantly, the growing and pervasive warming of the climate system caused by human activities are known to cause positive (amplifying) feedbacks as the terrestrial biosphere and the ocean respond to a changing climate. Although many uncertainties remain, it is already clear that the damping feedback of CO_2 fertilization will decrease while the amplifying feedback of climate on carbon storage will grow in the future.

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CO_2-PRODUCTIVITY-CLIMATE INTERACTIONS

During glaciations, global productivity decreased because of the effect of low CO_2 fertilization on terrestrial ecosystems. The ongoing rising CO_2 from human activities fertilize global ecosystems but has limits, while climate change reduces global ecosystem productivity and amplifies warming.