this case, the future sperm cells). (This data set can be browsed and downloaded at http://www.human-gastrula.net)

Analysis of the data set revealed several intriguing findings. First, cells of the amniotic ectoderm and the embryonic ectoderm display highly similar gene-expression profiles. The anatomical organization of the disc-shaped human embryo reflects this similarity, with the ectoderm directly bordering the overlying amniotic sac. This is different from the case in mouse embryos, in which these tissues are spatially separated. Further studies are needed to explore this close relationship between the human amniotic ectoderm and embryonic ectoderm in more detail.

Notably, there was no sign of neural induction, a process in which the embryo's ectoderm starts to form neural tissue, suggesting that this occurs later. Furthermore, using algorithms targeted at the detection of rare cell types, a small population of putative PGCs was identified among the cells of the primitive streak, indicating that the future sperm cells had already been set aside. This is in line with findings from *in vitro* cultures of human embryos showing that such cells are specified as early as day 11 after fertilization, before gastrulation[9]. The authors also found pigmented cells in the wall of the yolk sac that they identified as primitive blood-related cells called erythroblasts and haemato-endothelial progenitors, confirming previous evidence that the production of blood cells in humans begins as early as Carnegie stage 7 (ref. 10).

The availability of human embryos is limited owing to ethical, as well as technical, reasons. Thus, embryonic stem cells that are derived from the inner cell mass of human embryos at about six days after fertilization are a crucial tool in researching early development. However, a long-standing debate exists about the exact *in vivo* equivalent of these human embryonic stem cells. Tyser *et al.* compare their data set with gene-expression data from the epiblast of pre-implantation embryos. They conclude that embryonic stem cells maintained in a 'naive' state are most similar in terms of gene expression to epiblast cells of pre-implantation embryos. By contrast, gene expression in conventional 'primed' embryonic stem cells (which resemble more-mature cells ready to differentiate) is more similar to that in the epiblast of the gastrulating embryo.

This comparison also exemplifies the potential use of the authors' data set as an *in vivo* reference for *in vitro* models of early embryonic development. Cell populations previously identified in macaque embryos cultured to day 14 *in vitro*[11] showed close correlation with those in the human gastrulating embryo, validating their correct identification as epiblast, endoderm, embryonic mesoderm, extra-embryonic mesoderm and amniotic ectoderm. Similar studies have used these data to benchmark the changes in gene expression that occur in different cell types in models of gastrulation, in which aggregates of human embryonic stem cells are organized in concentric layers (see, for example, ref. 12).

Given the rapidly growing interest in this research field, several *in vitro* models that mimic human post-implantation development and gastrulation are emerging. Careful evaluation of their fidelity to their counterpart cell types *in vivo* is warranted, to see whether such models hold the promise of opening this black box of embryology to provide mechanistic insights into this stage of human development.

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Climate science

Constraints on the CO_2 fertilization effect emerge

Chris Huntingford & Rebecca J. Oliver

Plants offset a large fraction of Earth's carbon dioxide emissions, but estimating the size of this carbon sink relies on differing terrestrial-biosphere models. Combining multiple models with data has now reduced the uncertainty. **See p.253**

The goal of mitigating climate change requires a global commitment to reducing greenhouse-gas emissions to avoid substantial temperature increases. However, achieving this objective is complicated by uncertainty over how much carbon dioxide will be absorbed naturally by trees and other plants. On page 253, Keenan *et al.*[1] have constrained estimates of this uncertainty by drawing empirical links between observations of the current climate and multi-model predictions of the land-carbon sink. The relationships between these observations and predictions are known as emergent constraints.

Plants draw CO_2 from the atmosphere to grow using photosynthesis. Since the Industrial Revolution, the burning of fossil fuels has increased atmospheric CO_2 concentrations from around 280 parts per million (ref. 2) to 416 parts per million in 2020 (ref. 1). The effect of this increase on plants has been the subject of many investigations — from controlled laboratory experiments to large-scale free-air CO_2 enrichment (FACE) studies, which simulate different concentrations of atmospheric CO_2 accessible to plants growing under realistic field conditions[3] (Fig. 1). The consensus is that photosynthesis increases as CO_2 concentrations rise, a phenomenon known as CO_2 fertilization.

A simple conclusion would be that plants naturally compensate for a substantial fraction of the CO_2 emissions caused by the burning of fossil fuels. However, biological processes are complex: we still have much to learn about everything from the inner workings of a leaf to the dynamics of entire ecosystems. The impact of CO_2 fertilization will depend on how the plant ecosystem adapts as the climate changes. For example, the location-specific availability of water and nutrients will modulate CO_2 fertilization and have varying consequences for different species. The net result of these interactions at the global scale will determine the amount of carbon absorbed by plants and, therefore, the extent to which CO_2 fertilization can help to slow global warming.

Each year, there are updates to the status of the global carbon cycle (see, for example, ref. 4). These updates have been used to infer the land-carbon gain by accounting for all emissions, and then subtracting the carbon held in the atmosphere and the oceans. The first steps towards performing a more direct calculation using land models were taken only last year when the perceived uncertainty associated with these models started to decrease[4].

The effect that increases in atmospheric CO_2 concentrations have on photosynthesis can be measured directly only at the level of the leaves. To quantify the impacts at the plant and ecosystem levels, researchers rely on other estimates taken from models or FACE experiments, or use proxy data from satellite images and ice cores. However, differing projections have emerged from the terrestrial biosphere models that climate researchers have used to simulate the amount of carbon that will be absorbed by plants in the future.

Both modelling and proxy-data approaches yield values that are associated with a high degree of uncertainty when applied to data from recent decades[5]. Satellite data typically suggest that terrestrial biosphere models overestimate the impact of CO_2 on photosynthesis, whereas ice-core measurements imply that these models underestimate its effects.

Keenan *et al.* reduced the uncertainty in estimating the CO_2 fertilization effect in data from past decades using an ensemble of terrestrial biosphere models. They first removed the variation in the models' responses to meteorological factors such as precipitation and water-vapour pressure. They then used these models to identify an emergent constraint that relates a data-led estimate of the amount of carbon absorbed by plants as a result of all factors – for example, weather variation – to the isolated CO_2 fertilization effect.

Emergent constraints are relationships, here applied to terrestrial biosphere models, that link a quantity measured for the present day to a second quantity of interest to climate policy. Keenan and colleagues took independent estimates of the amount of carbon absorbed by plants from the Global Carbon Project (see go.nature.com/3d2exaf), and used the emergent-constraint analysis to predict the projected magnitude of CO_2 fertilization.

The authors estimated that CO_2 fertilization increased global, annual levels of photosynthesis by around 12% (equivalent to about 14 petagrams of carbon per year; 1 Pg is 10^{15} g) between 1981 and 2020. The uncertainty bounds on this value are around 74% lower than those predicted by the same terrestrial-biosphere models without the emergent constraint that decreases the differences in their predictions. The researchers then used this result to constrain estimates of global photosynthesis inferred from data from satellite images and other sources. The overall findings provide better estimates of how fertilization affects atmosphere–land CO_2 fluxes.

Emergent constraints are used widely to reduce variation between models for attributes of Earth's physical, chemical and biological processes[6]. Although they offer much promise, there are potential problems[7]. First, large-scale models might contain common parameterizations, which can result in artificially small confidence bounds on a predicted quantity. A second concern is that all terrestrial biosphere models might incorrectly model, or completely omit, a process that becomes more important as atmospheric CO_2 levels increase, which could give rise to a different emergent constraint for higher CO_2 levels.

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Figure 1 | A free-air CO_2 enrichment (FACE) experiment at the Cedar Creek Ecosystem Science Reserve in Minnesota. CO_2-enriched air is emitted from the vertical vent pipes to simulate artificial CO_2 levels for plants growing under realistic field conditions.

It is thought that non-carbon geochemical cycles become increasingly crucial for limiting plant growth as CO_2 levels increase. The fact that low nitrogen availability might limit the plants' carbon uptake has been described in a number of studies (see, for example, ref. 8). Many terrestrial biosphere models now incorporate the nitrogen cycle, and these models generally predict a lower carbon uptake than do those that omit it[9]. However, representation of the phosphorus cycle is much less common, yet phosphorus availability could eventually become a limiting factor for how much carbon plants can absorb, especially in the tropics[10]. Failure to model the phosphorus cycle might therefore provide an overly optimistic assessment of how much CO_2 is absorbed by plants.

Most terrestrial biosphere models do not take into account evidence suggesting that plants can adjust their optimal temperature for absorbing carbon as their surroundings become warmer[11]. Modelling this effect could result in higher estimates of CO_2-fertilization levels.

Finally, terrestrial biosphere models rely mostly on empirical approaches to simulate where the carbon absorbed by plants goes. If higher rates of photosynthesis generate more carbohydrates, the amount of carbon absorbed will depend on which part of the plant takes up the extra carbon, and how it is allocated to various processes, such as biomass production or respiration, which releases CO_2 back into the atmosphere[12]. Improving models by incorporating these subtleties might lead to more-precise inferences of the sensitivity of photosynthesis to CO_2. Nevertheless, Keenan and co-workers' analysis provides a welcome addition to an ongoing debate.

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Update
The authors wish to alert readers to the fact that the report on which this comment was based, 'A constraint on historic growth in global photosynthesis due to increasing CO_2', has been retracted. Some of the comments in this News & Views relying on the accuracy and reproducibility of these data should therefore be reconsidered.