

classes of promoter. Three types of animal promoter have been identified⁹: type I and type III promoters regulate genes that act during distinct stages in development, whereas type II promoters direct ubiquitous gene expression. Sebé-Pedrós and colleagues detected type II promoters in *Capsaspora*, but not types I or III. Therefore, type I and III promoters might be animal innovations.

It will be exciting to explore what these findings mean for animal origins and early evolution. Future investigations into the thus-far-uncharacterized gene-regulatory landscapes of sponges, comb jellies (ctenophores) and choanoflagellates promise to help pinpoint how and when long-range enhancers and type I and III promoters first evolved. However, the evolutionary distance between these organisms and the model animals that form the basis of our understanding of animal gene regulation may render conserved

molecular mechanisms unrecognizable by functional-genomic approaches. Moreover, other evolutionarily important gene-regulatory mechanisms may lie undiscovered in *Capsaspora*, choanoflagellates and animals that branched off early in the evolution of animals.

Fully reconstructing gene regulation in the progenitors of animals will require studies in diverse relatives, integrating modern functional genomics with forward and reverse genetics — which respectively reveal the genes responsible for a particular trait, and the changes brought about by disrupting the function of a particular gene. Fortunately, armed with the functional-genomics insights from this study, and the establishment of forward genetics in choanoflagellates¹⁰, this goal may be achieved in the not-too-distant future. ■

David S. Booth and Nicole King are at the Howard Hughes Medical Institute and in the

Department of Molecular and Cell Biology, University of California, Berkeley, Berkeley, California 94720-3200, USA. e-mails: dbooth@berkeley.edu; nking@berkeley.edu

1. Knoll, A. H. *Annu. Rev. Earth Planet. Sci.* **39**, 217–239 (2011).
2. Sebé-Pedrós, A. *et al. Cell* **165**, 1224–1237 (2016).
3. Erwin, D. H. *Biol. J. Linn. Soc.* **50**, 255–274 (1993).
4. Richter, D. J. & King, N. *Annu. Rev. Genet.* **47**, 509–537 (2013).
5. Levine, M., Cattoglio, C. & Tjian, R. *Cell* **157**, 13–25 (2014).
6. Sebé-Pedrós, A. *et al. eLife* **2**, e01287 (2013).
7. Lolas, M., Valenzuela, P. D. T., Tjian, R. & Liu, Z. *Proc. Natl Acad. Sci. USA* **111**, 4478–4483 (2014).
8. Hurlin, P. J. *Cold Spring Harb. Perspect. Med.* **3**, a014332 (2013).
9. Lenhard, B., Sandelin, A. & Carninci, P. *Nature Rev. Genet.* **13**, 233–245 (2012).
10. Levin, T. C., Greaney, A. J., Wetzell, L. & King, N. *eLife* **3**, e04070 (2014).

This article was published online on 15 June 2016.

BIOGEOCHEMISTRY

Synergy of a warm spring and dry summer

An analysis suggests that high carbon uptake by US land ecosystems during the warm spring of 2012 offset the carbon loss that resulted from severe drought over the summer — and hints that the warm spring could have worsened the drought.

YUDE PAN & DAVID SCHIMEL

Warmer springs and drier summers are an expected consequence of climate change¹. Warmer springs should increase the carbon uptake of terrestrial ecosystems by lengthening the growing season, whereas drier summers should reduce uptake because of poor plant growth, especially in drought years. In 2012, the continental United States had the warmest spring on record, and one of the worst summer droughts in decades. What did these extremes do to the land carbon budget? The answer matters because terrestrial carbon uptake helps to remove anthropogenic carbon dioxide emissions from the atmosphere. Writing in *Proceedings of the National Academy of Sciences*, Wolf *et al.*² conclude that the increased carbon uptake during the spring essentially offset the carbon lost during the summer — although the details of this phenomenon are rather complex.

The effects of interactions between spring warming and summer drought on carbon budgets at continental and local scales have been reported previously^{3,4}, but it is only in the past few years that multiple data sources with which to evaluate large-scale climate effects and their local variations have become

widely available. The authors arrived at their conclusions by comparing three data sets: eddy-covariance data that measure carbon exchange between the lowest part of the atmosphere (the boundary layer) and land biospheres over areas of approximately 1 square kilometre, gathered by 22 towers scattered across the United States; satellite estimates of the timing of plant growth; and regional carbon-budget estimates from CarbonTracker, a modelling system that uses observations of atmospheric CO₂ levels and gradients to infer surface fluxes of the gas over land. So what do the data show?

The severe drought that occurred during the summer of 2012 encompassed more than half of the continental United States, with most of the affected regions falling into the two worst categories as defined by the US Drought Monitor (extreme and exceptional)⁵. Accordingly, most of the towers reported a loss of carbon from their sites during this period, and recorded that the annual carbon budgets did not balance. Meanwhile, CarbonTracker suggested that carbon gain during the spring (0.24 petagrams of carbon; 1 Pg is 10¹⁵ grams) and carbon loss during the summer (0.23 Pg) were almost equal for the continental United States as a whole.

However, there was considerable variability

within that picture. Eastern temperate forests (Fig. 1a) vigorously sequestered carbon during the spring, and this carbon gain (0.18 Pg) slightly more than offset the summer carbon loss (0.16 Pg) from the Great Plains (Fig. 1b) — the area most affected by drought, and which accumulated significantly less carbon than in an average year. Overall, carbon uptake for the lands of the continental United States had increased, rather than reduced, by the end of the year (a rise of 0.11 Pg C yr⁻¹), with the surplus resulting from increased carbon uptake during the autumn.

Wolf and colleagues propose that the spring warming and summer drought were physically coupled through interactions between the land surface and atmosphere. Simply put, ecosystems entered the summer with a relative water deficit because water was used up earlier than normal during the warmer spring. The deficit led to a reduction in evaporative cooling, which increased the effects of summer heating, causing water stress.

The authors go on to suggest that early warming might even have reinforced weather patterns, increasing the probability or the severity of summer drought. Confirming this will require a more comprehensive analysis and diagnosis, including measurements from more eddy-covariance towers, but is well within the realm of possibility. Clear evidence of such a link would undoubtedly help the public, policy-makers and resource managers to prepare strategies for adapting to droughts in the future.

A strength of Wolf and co-workers' study is that it combines *in situ* eddy-covariance measurements, atmospheric observations and remote-sensing data. The eddy-covariance data provide the most direct evidence for seasonal changes in terrestrial carbon uptake, and are the only data that directly constrain

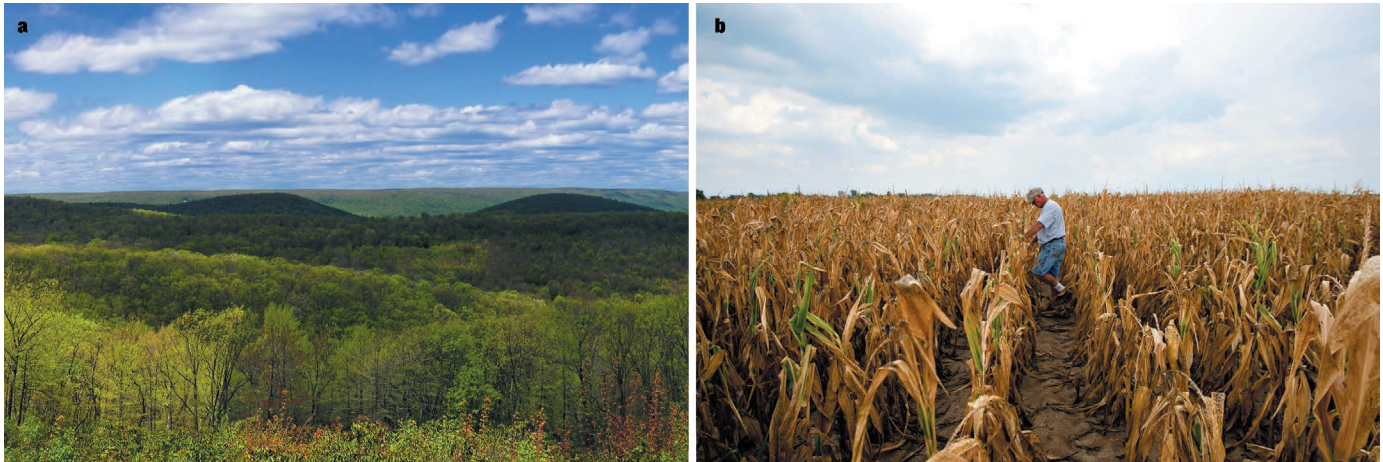


Figure 1 | Seasonal and regional variations of carbon uptake in the continental United States. **a**, Eastern temperate forests grew vigorously during the warm spring of 2012, and took up more carbon than normal for this season. **b**, The subsequent hot, dry summer caused crops to fail in the Great Plains, and carbon uptake in this region was lower than normal. Wolf *et al.*² report that the spring carbon uptake offset the summer carbon losses across the continental United States.

the CarbonTracker and satellite estimates, by quantifying both the carbon flux and the full energy balance of water–temperature interactions. The remote-sensing data provide the best insight into the timing of biological activity across the continent, whereas the atmospheric analyses allow the local fluxes and processes to be understood in the context of the overall carbon budget. In the future, a more sophisticated synthesis of the different data will greatly improve the accuracy of analyses of carbon and water exchange between the land and atmosphere.

A limitation of the study is that the tower sites weren't specifically placed to sample the dominant carbon-flux anomalies that were revealed by CarbonTracker and the satellite data. For instance, the largest region of spring-time carbon-uptake anomalies occurred in the southeastern United States, where there are no flux towers. The largest region of midsummer carbon-loss anomalies occurred in the Great Plains, where the two sites used in the study represent grasslands, rather than the dominant agricultural landscapes of this region.

In addition, the current tower network isn't dense enough to cover climate events such as the extreme year of 2012. A facility called the National Ecological Observatory Network (with which one of us, D.S., was associated for several years), designed to sample climate conditions optimally, will come online in the next few years⁶ and provide uniform coverage of the continental United States. Climatologists have long designed networks to study spatial patterns, whereas ecologists have tended to rely on local field studies and extrapolated their findings to larger areas on the basis of vegetation types or other classifications. A reference network that covers all spatial components and biomes is essential for this type of extrapolation in future studies.

Wolf and colleagues' work shows how important systematic, continental-scale sampling is, because no one site — and not even

several sites — could tell the entire story of a perturbation such as the one that occurred in 2012. As ecologists attempt to understand problems at ever larger scales, they will increasingly direct their creative energies towards problems that require massively more data than individual research laboratories can collect. Information obtained from infrastructural monitoring systems and openly available data will therefore have a crucial role in advancing the science of climate impacts, as they already do in other disciplines. ■

Yude Pan is in the Research Unit of Climate, Fire and Carbon Cycle Sciences, US Department of Agriculture Forest Service, Newtown Square, Pennsylvania 19073, USA.

David Schimel is at the Jet Propulsion Laboratory, California Institute of Technology, Pasadena, California 91109, USA. e-mail: ypan@fs.fed.us

1. Melillo, J. M., Richmond, T. C. & Yohe, G. W. (eds) *Climate Change Impacts in the United States: The Third National Climate Assessment* <http://dx.doi.org/10.7930/J0Z31WJ2> (2014).
2. Wolf, S. *et al. Proc. Natl Acad. Sci. USA* **113**, 5880–5885 (2016).
3. Angert, A. *et al. Proc. Natl Acad. Sci. USA* **102**, 10823–10827 (2005).
4. Hu, J., Moore, D. J. P., Burns, S. P. & Monson, R. K. *Glob. Change Biol.* **16**, 771–783 (2010).
5. Rippey, B. R. *Weath. Clim. Extremes* **10**, 57–64 (2015).
6. Keller, M., Schimel, D. S., Hargrove, W. W., Hoffman, F. M. *Front. Ecol. Environ.* **6**, 282–284 (2008).

This article was published online on 15 June 2016.

STRUCTURAL BIOLOGY

When sperm meets egg

Sperm–egg binding is mediated by two cell–surface proteins. Structural analysis of these proteins, separately and in complex, provides insight into the recognition process and the subsequent sperm–egg fusion. SEE LETTERS P.562 & P.566

KARSTEN MELCHER

An interaction between two proteins — Izumo1, which is produced by sperm, and Juno, its receptor on eggs — enables human fertilization. However, the details of this interaction have been elusive. In two papers, Aydin *et al.*¹ (page 562) and Ohto *et al.*² (page 566) present the structures of Izumo1, Juno and the two proteins in complex, determined by X-ray crystallography at atomic-level resolution.

Following human copulation, motile sperm move towards eggs in the female's Fallopian tubes. The acidic environment of the female

reproductive tract triggers an activation step, in which sperm become hypermobile and penetrate the outer protective layer of the egg. A second activation step occurs when or shortly before the sperm binds to the zona pellucida — the tough inner layer that surrounds the egg. During this step, the acrosome — an organelle at the tip of the sperm head — releases digestive enzymes that break down the zona pellucida. This acrosome reaction allows the sperm to bind to Juno on the egg membrane, following which the two cells' membranes fuse and the cells merge. In turn, the egg releases enzymes that crosslink glycoproteins of the zona pellucida to make it impenetrable,