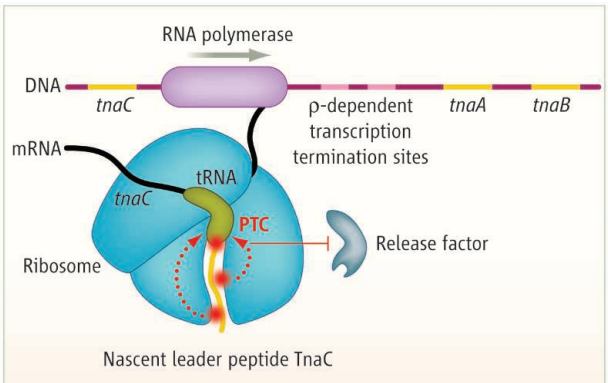


Regulation of the bacterial tryptophanase operon. At low tryptophan concentrations, ribosomes are released from the mRNA after translating the TnaC leader peptide. This allows rho helicase to terminate transcription at sites upstream from the *tnaA* and *tnaB* genes, which encode tryptophanase and tryptophan permease. In the presence of high tryptophan concentrations, the interaction of the nascent leader peptide with the tunnel stalls translation by preventing the action of release factors in the peptidyl transferase center. The ribosome remains bound to the mRNA, thus preventing termination of transcription by rho helicase and allowing complete transcription of the tryptophanase operon. Seidelt *et al*. now report a cryo-EM structure of a ribosome stalled during the translation of TnaC. The structure shows specific interactions between the nascent chain and the tunnel, and the authors propose relay pathways to the peptidyl transferase center.

The large surface of the large ribosomal subunit apposed to the ER membrane may provide additional binding sites for enzymes such as signal peptidase and oligosaccharyl transferase, which work cotranslationally in concert with the protein-conducting channel to form the "translocon." In fact, one of the previously characterized ribosome-binding proteins, ribophorin, is part of the oligosaccharyl transferase complex. The interaction of these and other integral membrane proteins of the translocon with the protein-conducting channel and the apposed large ribosomal subunit surface must not interfere with lateral opening of the channel, so that transmembrane segments of nascent integral membrane proteins can exit into the lipid bilayer.

In the second paper, Seidelt *et al*. (page 1412) (*2*) assembled an RNC containing the "leader" peptide (*11*) of the tryptophanase operon, a cluster of genes in bacteria that are transcribed as one messenger RNA (mRNA). In the presence of high concentrations of tryptophan, the leader peptide of the tryptophanase operon causes stalling of translation and thereby allows complete transcription of the operon (*12*) (see the second figure). This is an example of regulation of translation-coupled transcription in bacteria by the nascent peptide. The 6 Å resolution of this complex allowed the nascent chain to be traced in the tunnel and its interactions with surrounding nucleotides and ribosomal proteins to be delineated (*2*). Seidelt *et al*. suggest how the conformational changes induced by these interactions are relayed to the peptidyl transferase center, where the authors observed distinct conformations of individual bases that are incompatible with the termination of translation by release factors (*2*).

The tunnel in the large ribosomal subunit is clearly not just a passive conduit for the nascent chain, but rather a compartment in a dynamic molecular dialogue with the nascent chain. This interplay might not only affect the structure and function of the ribosome and associated factors, but also the conformation and folding of the nascent chain. Once emerged from the ribosome, nascent chains containing a single peptide can engage the SRP, the protein-conducting channel and other downstream factors in translation-coupled translocation.

References and Notes

1. T. Becker *et al*., *Science* **326**, 1369 (2009); published online 29 October 2009 (10.1126/science.1178535).
2. B. Seidelt *et al*., *Science* **326**, 1412 (2009); published online 29 October 2009 (10.1126/science.1177662).
3. M. Halic *et al*., *Nature* **427**, 808 (2004).
4. M. Halic *et al*., *Science* **312**, 745 (2006).
5. R. Beckmann *et al*., *Cell* **107**, 361 (2001).
6. K. Mitra *et al*., *Nature* **438**, 318 (2005).
7. J. F. Menetret *et al*., *J. Mol. Biol.* **348**, 445 (2005).
8. B. Van den Berg *et al*., *Nature* **427**, 36 (2004).
9. S. M. Simon, G. Blobel, *Cell* **65**, 371 (1991).
10. S. M. Simon, G. Blobel, *Cell* **69**, 677 (1992).
11. The synonymous use in the literature of the terms "leader" peptide and "signal" peptide should be discouraged, as a signal peptide is exclusively involved in targeting the nascent chain for membrane translocation, whereas a leader peptide regulates translation-coupled transcription in bacteria.
12. F. Gong, C. Yanofsky, *Science* **297**, 1864 (2002).

10.1126/science.1183690

ECOLOGY

Biodiversity Under Global Change

A long-term experiment into plant community responses to elevated carbon dioxide and nitrogen yields surprising results.

Scott L. Collins

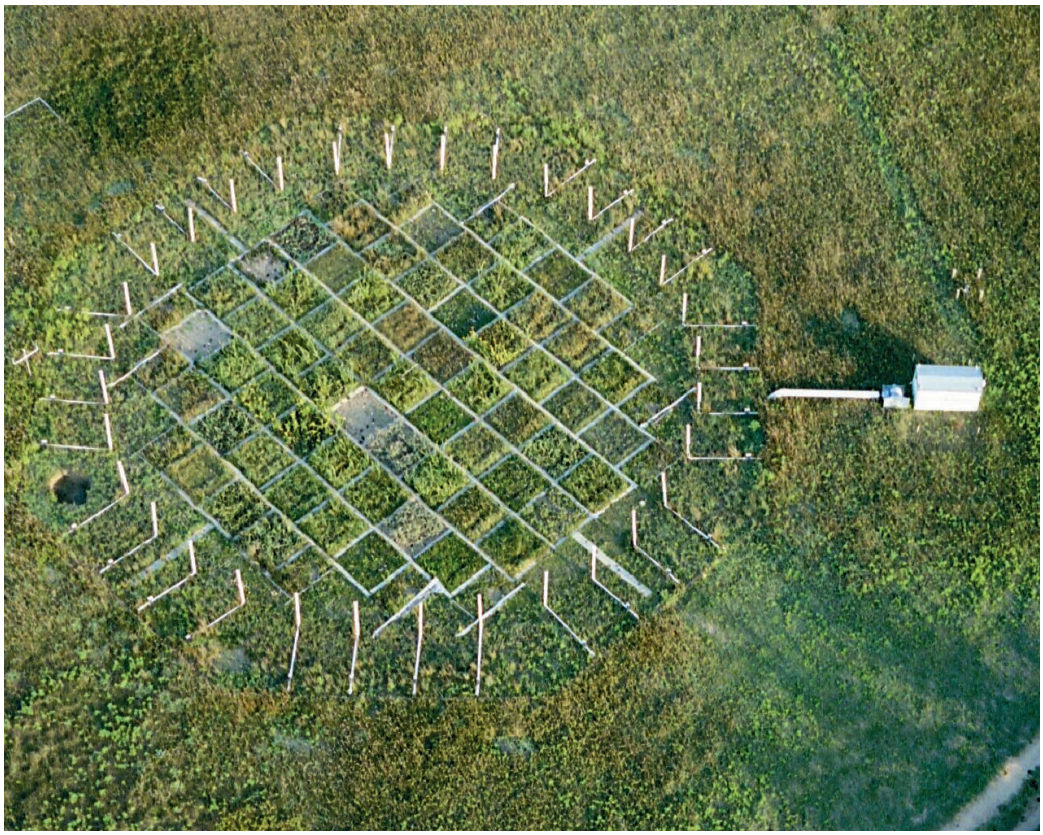
Many common plant species, such as prairie grasses, have evolved traits for the efficient capture and use of two key resources that limit terrestrial productivity: nitrogen (N) and carbon dioxide (CO_2). Over the past 60 years, human activity has vastly increased the availability of these resources. Atmospheric CO_2 concentration has increased by 40%, and N availability has more than doubled. These changes are likely to have important consequences for species interactions, community structure, and ecosystem functioning. On page 1399 of this issue, Reich investigates one important consequence, biodiversity loss, based on a long-term elevated CO_2 and nitrogen fertilization experiment (*1*).

The individual consequences of either elevated CO_2 or N on ecosystem structure and function have been studied intensively. Numerous experimental and empirical studies have shown that higher N availability increases aboveground net primary production and decreases species diversity (*2*, *3*). Higher aboveground net primary production intensifies competition for aboveground resources, such as light. As production increases, light availability beneath the canopy falls, leading to a loss of understory species and a decline in diversity (*4*). Elevated CO_2 can also increase aboveground net primary production (*5*). Yet, we know little about the impact of increased CO_2 on species diversity (*6*), and next to nothing about the interactive effects of N and CO_2 on plant community structure.

Reich now presents the results of 10 years of experimental addition of CO_2 and N on plant community structure in synthetic grassland communities at the Cedar Creek LTER (Long Term Ecological Research) site in Minnesota. Like the somewhat sim-

Department of Biology, University of New Mexico, Albuquerque, NM 87131, USA. E-mail: scollins@sevilleta.unm.edu

CREDIT: ADAPTED BY P. HUEY/*SCIENCE*



The BioCON experiment at the Cedar Creek LTER site in Minnesota.

ilar experiment in annual serpentine grassland at Jasper Ridge, California (*5*, *6*), the Biodiversity, CO_2, and Nitrogen (BioCON) experiment at Cedar Creek (see the figure) is one of the few long-running field experiments investigating the interactive effects of increased CO_2 and N on ecosystem structure and function. In the current study, Reich focuses on the interactive effects of CO_2 and N on plant species diversity. The results are noteworthy, important, and surprising.

Given that both N and CO_2 increase production independently and synergistically in this system (*7*) and that higher aboveground net primary production generally decreases diversity, one might predict the combined effects of N and CO_2 on diversity to be additive or even synergistic. Indeed, Zavaleta *et al*. (*6*) found that effects of multiple global change factors on diversity were additive in California grassland. Instead, Reich found that although elevated CO_2 reduced diversity by 2% and N addition reduced diversity by 16%, in combination, N and CO_2 reduced diversity by only 8%. Elevated CO_2 has been shown to counteract N effects on aboveground net primary production (*5*), but this is the first study to show that elevated CO_2 can reduce biodiversity loss.

What are the mechanisms behind this surprising response? Essentially, N and CO_2 differentially affect key processes that drive the productivity-diversity relationship. First, CO_2 increases aboveground net primary production, which increases N uptake by the vegetation, and at elevated N supply reduces plant-available N in the soil. Second, N fertilization leads to dominance by nitrophile plants, and this change in species composition in higher-N plots results in no net decrease in light penetration through the canopy. Moreover, CO_2 and N fertilization have opposing effects on the C:N ratio in plant tissues. Increasing both resources reduces progressive N limitation (*8*), a phenomenon that limits aboveground net primary production under elevated CO_2 alone. Finally, CO_2 and N have opposing effects on soil water content. Plants grown in elevated CO_2 experience reduced water stress, whereas elevated N in this case leads to higher root biomass, higher water uptake by plants, and therefore lower soil water content. Thus, together CO_2 and N have opposing rather than synergistic or additive effects on community structure.

The BioCON design has limitations. The synthetic communities contain 16 species, with four species each from four functional groups (C_4 grasses, C_3 grasses, legumes, and nonlegume forbs). This design is often used to determine how species diversity affects ecosystem functioning. It is less effective for studying biodiversity loss as a result of changing ecosystem structure. The amelioration of species loss in combination, relative to N addition alone, is a counterintuitive and somewhat encouraging outcome, but its generality must be challenged with additional experiments in other plant communities and with other limiting resources.

Conservation of biodiversity remains a high priority for ecological research. Biodiversity has many benefits, including increased community stability, increased resistance to invasive species, and higher resistance to diseases (*9*). Individually, many global change drivers negatively impact biodiversity. However, when such drivers have opposite effects on mechanisms controlling community structure, multiple global change drivers in some cases may actually increase community stability.

The BioCON experiment is a rare gem in long-term ecological research, and the results generated thus far have been highly informative when addressing aggregate properties, such as the impact of species diversity and resource availability on ecosystem processes. More work on different plant communities is needed, however, before we can comfortably extrapolate the results to other communities and other global change drivers. There is thus an urgent need for more multifactor experiments to better understand how ecosystems will respond as human activities continue to alter global biogeochemical cycles.

References

1. P. B. Reich, *Science* **326**, 1399 (2009)
2. C. J. Stevens, N. B. Dise, J. O. Mountford, D. J. Gowing, *Science* **303**, 1876 (2004).
3. K. N. Suding *et al*., *Proc. Natl. Acad. Sci. U.S.A.* **102**, 4387 (2005).
4. Y. Hautier, P. A. Niklaus, A. Hector, *Science* **324**, 636 (2009).
5. M. R. Shaw *et al*., *Science* **298**, 1987 (2002).
6. E. S. Zavaleta *et al*., *Proc. Natl. Acad. Sci. U.S.A.* **100**, 7650 (2003).
7. P. B. Reich *et al*., *Nature* **410**, 809 (2001).
8. P. B. Reich, B. A. Hungate, Y. Lui, *Annu. Rev. Ecol. Evol. Syst.* **37**, 611 (2006).
9. D. Tilman, *Ecology* **80**, 1455 (1999).

10.1126/science.1183271

CREDIT: CEDAR CREEK ECOSYSTEMS SCIENCE RESERVE