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Bad News for Soil Carbon Sequestration?

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100 times that in the surrounding aqueous medium. Similar droplets were also observed when these proteins were overexpressed in cells. Notably, the concentration needed for the phase transition into fluid droplets correlated with the valency of these interacting proteins. The importance of this (*12*) and other in vitro work (*8*) is that it allows the study of the molecular basis of liquid phase separations in cells. It also shows that phase transitions in cytoplasm are not confined to assemblies that contain RNA, suggesting that phase separations could have a general role in organizing cellular biochemistry. There are many other candidate molecules with low-affinity polyvalency that could lead to liquid-liquid demixing, such as polyADP ribose, glycogen, and ubiquitin chains.

Taken together, these studies reveal a number of interesting features of liquid phase transitions in cells. They can occur in two or three dimensions, they involve the assembly of small macromolecular complexes through multivalent interactions, and they can form mesoscale to micrometer-scale fluid phases (*13*). Furthermore, high concentrations of solutes may also contribute to mesoscale organization in certain biological systems (*14*). The concentration of complexes that form the more condensed phase is apparently regulated close to the threshold of phase transition. This may reflect a general tendency of biological systems to be poised near a phase transition and thus promote large responses to small changes in the environment (*15*). More generally, multivalent weak interactions between proteins, or proteins and RNAs, provide the properties for liquid-like states, perhaps explaining their prevalence.

The idea of liquid-like states that either separate from the cytosol or occur in cell membranes is a powerful way to think about cellular compartments (*16*). Changes in valency of interaction by regulatory events such as phosphorylation would allow a phase transition in which the components become rapidly concentrated in one place in the cell. Entry of proteins or other regulators into condensed phases could lead to fast disassembly of liquid compartments. A small increase in the concentration of components could allow reactions to start without any other regulatory event, as the concentrations rise above the Michaelis constant (K_m) for the reaction. Depletion of components from the cytoplasm as they segregate into the condensed phase could stop reactions in the cytoplasm. One could envisage developing drugs that partition directly into fluid phases, thus changing their separation behavior.

Many cellular compartments form rapidly and are disassembled when not required. Also, a surprising number of proteins involved in metabolism and stress responses form cytoplasmic puncta in yeast (*17*). It will be fascinating to examine each one of these compartments to ask whether their formation also represents examples of liquid phase separation, and then to determine the criteria for liquid-liquid demixing. More generally, phase transitions may have important implications in disease. Because they can undergo such large-scale changes in arrangement of molecules, defects in their organization are likely to have major effects on cell viability. For instance, the large number of protein aggregates seen in neurodegenerative disease could be a product of unwanted or misregulated phase transitions.

References and Notes

1. Compartments can refer to organelles such as mitochondria, or nonmembrane-bound organelles such as nucleoli. More generally, compartments can also correspond to local concentration of molecules in specific biochemical processes such as P granules or stress granules and other subcompartments such as domains in cellular membranes.
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ECOLOGY

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Arbuscular mycorrhizal fungi may stimulate additional decomposition of organic carbon in the soil, resulting in a net source of carbon dioxide.

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Rising atmospheric carbon dioxide (CO_2) concentrations are expected to increase plant photosynthetic activity and the transfer of fixed carbon belowground, providing a potential buffering mechanism against elevated CO_2 (*1*). Arbuscular mycorrhizal fungi (AMF) are central to this potential extra carbon sequestration. AMF form symbioses with most land plants, in which the fungi supply the plant with nutrients in exchange for carbohydrates (*2*, *3*). But to what extent will this extra fixed carbon stay sequestered in the soil (*1*)? On page 1084 of this issue, Cheng *et al.* (*4*) show not only that the extra soil carbon is respired back to the atmosphere, but also that AMF activity stimulates additional decomposition of soil organic carbon. Increased carbon fixation by plants and transport of this carbon to the soil via AMF may thus result in a net source of CO_2, rather than the sink we might have hoped for.

Plants may drive this AMF-dependent decomposition to gain access to nitrogen from soil organic matter (*4*). Available nitrogen often limits gross primary production and growth responses to elevated CO_2 (*5*). Thus, increased translocation of nitrogen to the plant by AMF, specifically sequestered in the form of ammonium and not nitrate (*4*), may enhance plant growth. However, if enhanced plant growth leads to further increases in carbon transfer belowground, the net effect will be increased turnover of total carbon and nitrogen, rather than increased storage. Clearly, to understand the responses of terrestrial carbon cycling to climate change, interactions between the car-

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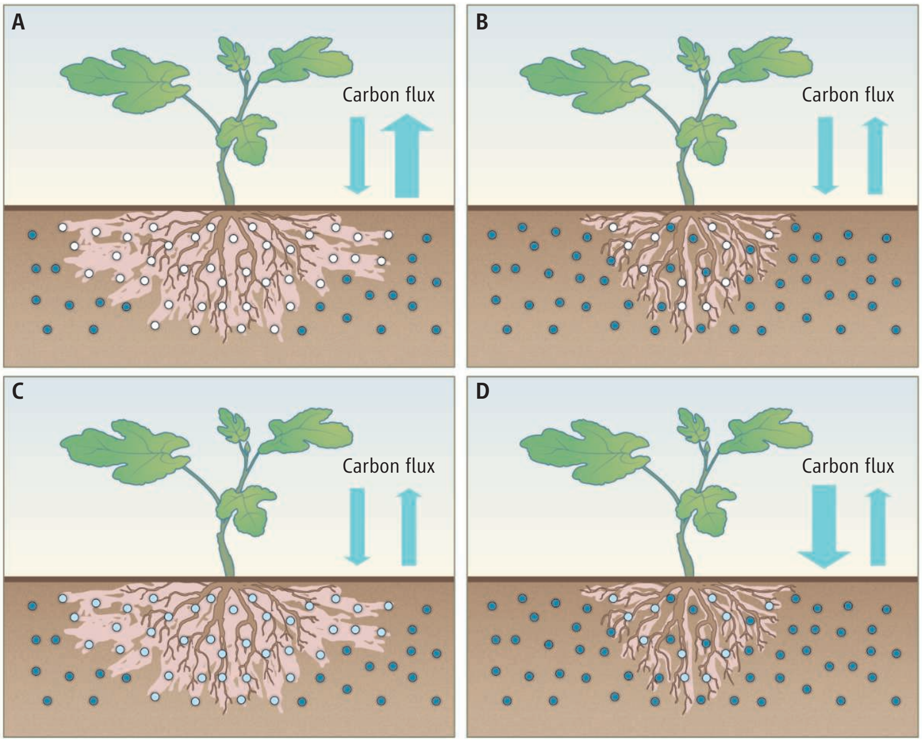

Carbon sink or source? Pink shaded areas are the zones in which soil saprotrophs are influenced by organic compounds exuded from roots or AMF. Dots represent patches of soil organic matter in which the organic matter remains intact (solid blue), partially degraded (lightly shaded), or fully decomposed (blank). Blue arrows depict the fluxes of carbon to and from the belowground compartment. The impact of soil microbes on carbon fluxes depends on the specific interactions involved in the plant-soil systems. (**A**) Efficient AMF colonization and efficient simulation of soil organic matter decomposition, as observed by Cheng *et al*., results in a net carbon source; (**B**) poor or no AMF colonization is carbon neutral; (**C**) poor stimulation of resident saprotrophs by AMF or presence of a poorly adapted saprotrophic community is also carbon neutral; and (**D**) no or poor AMF colonization and a poorly adapted saprotrophic results in a carbon sink.

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bon and nitrogen cycles must be taken into account (*6*).

Cheng *et al*. show that AMF stimulate increased decomposition of soil organic matter, especially under elevated atmospheric CO_2 conditions, but the mechanism behind this increase and the key players in these effects are not yet clear. Although AMF may play a direct role in carbon and nitrogen mineralization (*7*), these processes generally result from complex interactions between numerous bacterial and fungal species specialized in organic matter degradation (saprotrophs). AMF appear to increase decomposition of soil organic matter by stimulating the resident microbial communities, a classic case of the "priming effect" (*8*). In cases of such priming, soil microbes are stimulated by the addition of organic substrate, resulting in degradation of the added substrate and of additional organic matter in the soil. This leads to more soil respiration than can be explained by consumption of the added substrate.

Priming can be a very handy strategy for the degradation of organic pollutants, whereby biostimulation of microbes by addition of substrate leads to increased pollutant degradation (*9*). However, it can have a negative effect on the retention of (supplemented) soil organic matter, which is essential for soil structure and quality (*10*), or in relation to mitigating rising atmospheric CO_2 levels.

The stimulation of decomposition by AMF observed by Cheng *et al*. presumably results from the activation of soil-borne microbes by the increased flux of AMF-derived substrates. This allows the newly stimulated soil microbes to degrade other organic matter sources in the soil (*3*, *11*). AMF can influence soil bacterial communities, and elevated atmospheric CO_2 conditions have been shown to alter these interactions (*3*, *12*, *13*), but knowledge of the affected organisms and genes remains limited. These relationships will determine net carbon sequestration, making this knowledge essential for predicting the impacts of climate and land-use changes on the carbon balance of plant-soil systems.

AMF may impact soil carbon dynamics in several ways. If soil microbes are well adapted to the stimulation by AMF-derived substrates and the degradation of organic matter species in the soil, AMF will induce a net loss of carbon from the soil, and this effect will be enhanced under elevated atmospheric CO_2 conditions (*7*) (see the figure, panel A). Without AMF colonization, or with maladaptive AMF associations (*14*), a more carbon-neutral situation may occur (panel B). Similarly, if soil saprotrophs are not well adapted to stimulation by AMF-derived substrates, or if they are ill-equipped to degrade the organic matter present in the soil, no net losses of carbon are expected (panel C). However, soil-borne saprotrophs are typically well equipped to degrade the types of organic matter most prevalent in their local habitats (*15*). The best scenario from the carbon sequestration perspective would be a combination of no or poor AMF associations with poorly adapted saprotrophs, leading to net carbon sequestration (panel D).

The findings by Cheng *et al*. may undermine some assumptions of plant-soil systems as potential sinks for atmospheric CO_2, but all is not lost. Through manipulations of soil nitrogen, organic matter quality, and field management, the balance of soil decomposition patterns can be tipped in a more positive direction. However, we require mechanistic understanding of decomposition processes and how they are influenced by changing environmental factors and land management. Interdisciplinary approaches that use the emerging environmental "-omics" toolbox, coupled with robust field and glasshouse experiments, seem to represent the best options for garnering this necessary knowledge.

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