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They also generated mutant lines of the fungus with CRISPR-Cas9–mediated deletion of *MoNUDIX*. Both interventions resulted in reduced virulence of *M. oryzae* in rice and barley. The authors also deleted the conserved Nudix hydrolase effector genes in the fungi *Colletotrichum higginsianum* and *Colletotrichum graminicola*, which cause anthracnose disease of *Arabidopsis thaliana* and maize (*Zea mays*), respectively. They found that the role of Nudix hydrolase effectors in promoting virulence was conserved across all three fungi.

McCombe *et al.* used crystallography to solve the structure of MoNUDIX. It was highly similar to that of human diphosphoinositol polyphosphate phosphohydrolase 1, a well-characterized Nudix hydrolase that hydrolyzes PP-InsPs. The authors showed that MoNUDIX and *C. higginsianum* NUDIX hydrolyze a specific PP-InsP in vitro. To understand whether MoNUDIX is translocated from the fungus into the plant cell, the authors transgenically expressed a version of MoNUDIX tagged with a red fluorescent protein in *M. oryzae*. They found that MoNUDIX is translocated from *M. oryzae* into barley and rice cells and that it localizes to the host cell cytoplasm as well as the biotrophic interfacial complex (BIC)—a site in the infecting hypha (branching filament that penetrates the host) that secretes effectors (*9*).

When McCombe *et al.* expressed MoNUDIX, PHRs, and SPX proteins in the leaves of the heterologous model system *Nicotiana benthamiana*, MoNUDIX disrupted the interaction between PHRs and SPX proteins and thus promoted the transcription of phosphate starvation genes. This did not occur when the authors used a mutant version of MoNUDIX that cannot bind PP-InsPs and is thereby unable to hydrolyze them, leaving them available for binding to SPX. Similarly, RNA sequencing of rice leaves infected with either wild-type *M. oryzae* or *M. oryzae* with a *MoNUDIX* deletion revealed that the group of genes with higher expression in the wild-type infected plants was enriched for phosphate starvation response genes. This indicates that *M. oryzae* promotes phosphate starvation responses in its natural host, rice, through the action of the Nudix hydrolase effector (see the figure).

Effectors with Nudix hydrolase domains have been described before in the flax rust fungus *Melampsora lini*, the oomycete *Phytophthora sojae*, and the bacterium *Ralstonia solanacearum* (*10*–*12*). However, other biochemical functions were ascribed to them. McCombe *et al.* now provide evidence that Nudix hydrolase effectors from pathogenic fungi can interfere with phosphate sensing by selectively hydrolyzing PP-InsPs.

How a manufactured state of cellular phosphate starvation promotes the success of *M. oryzae* remains an open question. On the basis of previous evidence from studies in *A. thaliana* (*8*), it is possible that the release of PHRs from inhibition by SPX proteins not only promotes phosphate starvation responses but also suppresses the expression of genes associated with defense against pathogens, for example, those encoding proteins that induce the death of infected cells to prevent pathogen spread. This hypothesis is supported by the observation of McCombe *et al.* that, compared with wild-type *M. oryzae*, infection of rice with *M. oryzae* lacking *MoNUDIX* results in a greater amount of reactive oxygen species in leaves, which is indicative of a stronger pathogen defense response. Alternatively, the reduction of PP-InsPs and resulting phosphate starvation response might lead to an increase in phosphate uptake and accumulation in plant cells. This extra phosphate could feed the fungus or modify plant cell metabolism in a way that favors the fungus.

Regardless of the underlying mechanisms, the study by McCombe *et al.* emphasizes the major role of plant phosphate signaling in regulating plant disease and highlights a route by which pathogens can exploit the cross-talk between nutrient signaling and immunity. More research into the connection between plant nutrient signaling and plant immunity might provide strategies to integrate fertilization with the management of plant disease in agriculture. ■

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HYDROGELS

Hot and cold hydrogel with still water

Carbon chains immobilize water molecules, making a hydrogel elastic across temperatures

By **Zhaohan Yu** *and* **Shaoting Lin**

The soft polymer network of a hydrogel is infiltrated with water molecules, a hydrated state that makes hydrogels useful in biomedical research and in a range of consumer products, such as contact lenses and wound dressing. In contrast to polymers that transform between different states when heated or cooled, a hydrogel generally does not undergo polymeric phase transition because of its hydration. However, a change in temperature can evaporate or freeze mobile water molecules within the polymer networks, which modifies the hydrogel's mechanical properties (*1*). This compromises elasticity of a hydrogel and makes it easily breakable. On page 967 of this issue, Zhang *et al.* (*2*) report a way to control water molecules in polymer networks and produce a temperature-tolerant hydrogel that maintains its elasticity across a wide range of temperatures from −115° to 143°C. This unlocks potential applications that were deemed impossible because of the operation conditions.

The primary challenge in making a hydrogel with temperature-tolerant elasticity lies in effectively immobilizing water molecules within polymer networks. One strategy to address this problem is to engineer functional groups on polymer networks (*3*). A group of atoms with distinct chemical properties can bind to water molecules that are in close vicinity while other water molecules flow freely within the network (*4*). An alternate method is incorporating hygroscopic salts—compounds that absorb moisture from the surrounding environment—into a hydrogel (*5*, *6*). This approach reduces the overall mobility of water molecules by promoting their interaction with ions present in the salts. However, hygroscopic salts cannot completely lock water

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on the networks because they also move around within a hydrogel.

Zhang *et al.* used the sulfuric carbonization reaction to make a hydrogel temperature tolerant. In this reaction, sulfuric acid extracts water to produce a carbon-rich residue on a material. This method successfully immobilizes water molecules in polymer networks by forming sulfuric acid hydrates. However, the reaction breaks down polymers, which leads to fragmentation of polymers and thus degrades a hydrogel. To solve this problem, Zhang *et al.* created a hydrogel with two interpenetrating meshes of polymer chains in which one of them is a sacrificial network that primarily reacts with sulfuric acid to produce a carbon layer on the other polymers for protection and water immobilization (see the figure). The design of double-network hydrogels is known for enhanced toughness (*7*, *8*) but has not been implemented for temperature tolerance.

Two polymers with distinct properties are needed to achieve selective carbonization reaction. Alginate (a natural polysaccharide) forms a network through ionic interactions. By contrast, polyacrylamide (a synthetic polymer) is linked by covalent bonds. In the sulfuric carbonization reaction of Zhang *et al.*, sulfuric acid primarily reacted with the alginate network to produce short chains of carbon (carbon snakes) while preserving the structural integrity of cross-linked polyacrylamides. The carbonization reaction was confirmed by an observed exothermic peak at a temperature of around 143°C. The carbon snakes adhered to and encapsulated the main chains of the polyacrylamide networks and acted as a shield to protect the polymers from excessive reaction and degradation. The resulting hydrogel comprised a single network of polyacrylamide coated with sulfuric acid–bound carbons that immobilized adjacent water molecules. No phase transition was observed in either fragmented alginate chains or polyacrylamide networks across a wide range of temperatures. This confirmed the ability of carbon snakes to effectively lock water molecules within the hydrogel. Additionally, Zhang *et al.* did not observe an exothermic reaction associated with evaporation of water molecules, which is often present in conventional hydrogels at high temperatures (*9*). Consequently, the temperature-tolerant hydrogel maintained its elasticity between –100° and 140°C.

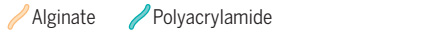
The selective carbonization strategy requires a sacrificial network, so it is intuitive to think that the method cannot be applied to a single-network hydrogel. To demonstrate the generality of the approach, Zhang *et al.* performed the reaction on a hydrogel made of one type of polymer. The synthetic polymer, poly(*N*-vinylpyrrolidone), forms reactive side chains under acidic condition. Sulfuric acid primarily reacted with these short auxiliary chains to form carbon snakes that encapsulated the long chains that comprise the main network. The resulting hydrogel exhibited similar temperature-independent mechanical behavior between –112° and 135 °C.

Although the study of Zhang *et al.* confirms the broad applicability of the water immobilization strategy, additional analysis is needed to further elucidate the underlying mechanisms of temperature tolerance in hydrogels. For example, the differential scanning calorimetry used by Zhang *et al.* measures thermal transitions on the basis of the amount of heat absorbed or released by a sample, which shows absence of phase transitions within the hydrogels at extreme temperatures. Zhang *et al.* presented a plausible hypothesis of the immobilized water molecules suppressing phase transitions of polymers and water within the hydrogel. However, how water molecules that are far away from the polymer chains behave remain to be solved. Additional characterizations such as superresolution Raman microscopy (*10*) could potentially provide details of the underlying pictures.

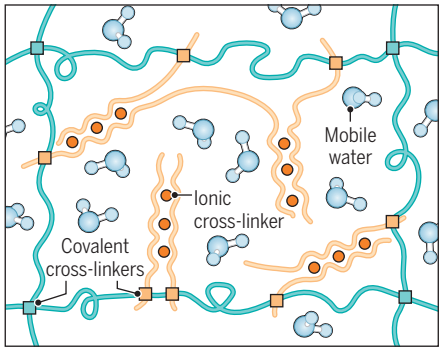
The findings by Zhang *et al.* could have far-reaching implications. Research in developing high-performance hydrogels primarily focuses on exploiting the design of constituent polymer networks (*11*). Little attention has been given to water molecules within a hydrogel because they are generally considered to have negligible influence on mechanical properties. The strategy by Zhang *et al.* opens a new path for designing high-performance hydrogels by strategically engineering water molecules to immobilize them within the polymer networks. The ability to precisely manipulate water molecules in hydrogels could bring previously inaccessible advanced technologies, including but not limited to tissue preservatives and fire retardants. ■

Temperature-tolerant hydrogel

A hydrogel that consists of two distinct networks of polymers can effectively immobilize water molecules without deteriorating its structural integrity. Locked moisture maintains the hydrogel's elasticity in a broad range of temperatures.

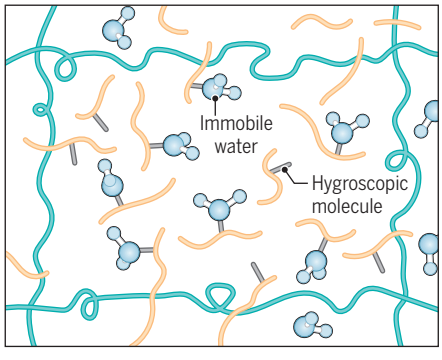


Double-network hydrogel



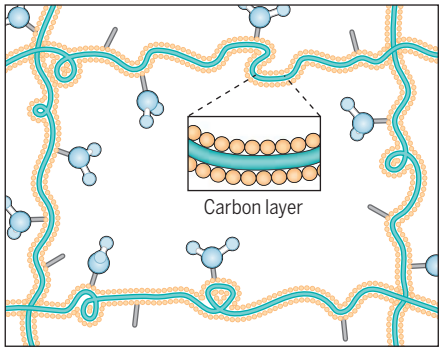
Alginates form a mesh through ionic interactions, whereas polyacrylamide chains are linked by covalent bonds. The two polymer networks are cross-linked covalently.

Water immobilization



Alginates selectively react with hygroscopic molecules that immobilize water within the hydrogel. This causes fragmentation of the polymer network.

Selective carbonization



The reaction between alginates and hygroscopic molecules creates a protective carbon layer on the polyacrylamide network.

GRAPHIC: K. HOLOSKI/*SCIENCE*

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