ECOLOGY

Fungal Carbon Sequestration

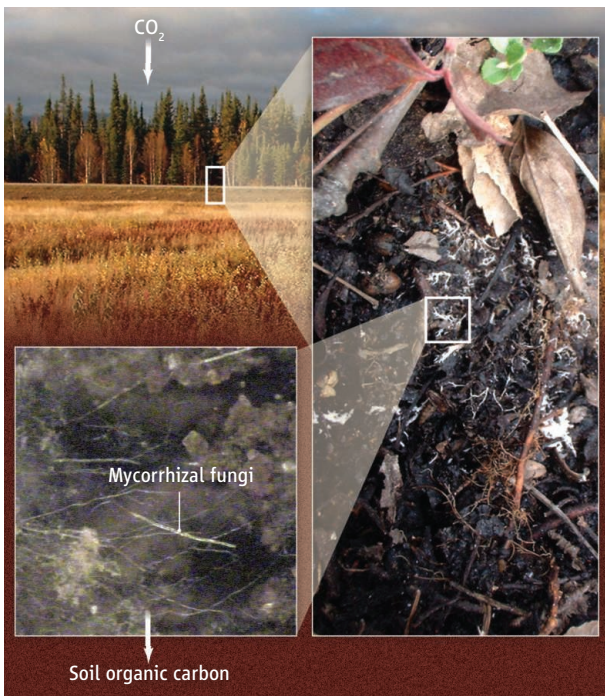
Mycorrhizal fungi associated with plant roots may contribute to carbon sequestration in soils.

Kathleen K. Treseder and Sandra R. Holden

Many soil fungi consist of small, delicate hyphae that permeate a complex matrix of soil particles (see the figure). They are easily damaged, making it difficult to directly observe their activities under undisturbed conditions. On page 1615 of this issue, Clemmensen *et al.* (*1*) use isotopic and molecular techniques to infer that a common group of fungi, the mycorrhizal fungi, can sequester carbon in the soil. This is important because carbon stored in soil over long periods can help to offset the release of greenhouse gases to the atmosphere. Most fungal species act as decomposers that elicit a net release of CO_2 to the atmosphere, but mycorrhizal fungi could be a notable exception.

Mycorrhizal fungi form symbioses with most plant roots, helping the plants to take up nutrients from soil. As a result, plants that are colonized by these fungi often grow much faster (*2*). Essentially, the fungi augment the removal of atmospheric CO_2 by their plant hosts (see the figure). A portion of that carbon is then allocated to the mycorrhizal fungi, which use it to build hyphae that extend into the soil (*3*). Once these hyphae die, the carbon in their tissues could be quickly decomposed by other soil microbes, or it could remain in the soil for years to decades. The longer the mycorrhizal carbon remains in the soil, the greater the potential contribution to soil carbon sequestration. Thus, it is critical to understand the fate of mycorrhizal carbon in ecosystems.

To address this issue, Clemmensen *et al.* investigated a set of boreal forest islands that differ in their wildfire history and soil carbon accumulation. They used a mathematical model to partition soil carbon stocks into carbon derived from aboveground plant litter or from roots and root-associated fungi. This modeling approach revealed that as much as 70% of soil carbon was root-derived, particularly deeper in the soil where root densities were highest. The model findings were corroborated by molecular analyses, which showed that mycorrhizal and other root-associated fungi dominated deeper soils, whereas decomposer fungi were only abundant in shallow soils. Furthermore, stable isotope signatures of soil organic matter most closely resembled that of mycorrhizal fungi.



The role of mycorrhizal fungi. Plants remove carbon dioxide from the atmosphere during photosynthesis and direct a portion of this carbon belowground to roots, where it is transferred to mycorrhizal fungi. The fungi then incorporate some of this carbon into hyphae. Once hyphae die and decompose, residues of the carbon are converted to organic material in the soil. Clemmensen *et al.* suggest that this process may contribute to long-term carbon storage in soils. Mycorrhizal fungi are the white filamentous structures in both soil photos.

These findings highlight the central role of mycorrhizal fungi in soil carbon sequestration in boreal forests. Historically, ecosystem ecologists have focused on how quickly the carbon in dead plant leaves is converted to CO_2 by decomposers. Yet recent work indicates that the carbon compounds that remain in the soil over the long term have been produced by fungi and other microbes, not by plants (*4*). These microbially derived compounds are extremely diverse and are thus difficult for decomposers to target (*5*). They can include remnants of cell walls, such as chitin, glucans, peptidoglycans, or polysaccharides (*6*). Microbial residues react with one another and with other components of the soil to form materials that cannot be easily converted to CO_2. It makes sense that organic compounds produced by mycorrhizal fungi would fit this scenario.

Mycorrhizal fungi are a dominant component of the microbial community in soils. Changes in their abundance (and hence in their contribution to carbon sequestration) could therefore have global consequences (*7*). Two groups of mycorrhizal fungi, ericoid and ectomycorrhizal fungi, are especially common in high-latitude systems (*8*). They dominated the deeper soils in the study by Clemmensen *et al.* At least some of these fungi respond to elements of global change. For instance, ectomycorrhizal fungi tend to proliferate when exposed to elevated concentrations of atmospheric CO_2 and decline after nitrogen enrichment (which is common in ecosystems surrounding urban and agricultural areas) (*7*). Any ectomycorrhizal contributions to carbon sequestration could change in concert.

In northern forests, wildfires may also alter the ability of mycorrhizal fungi to sequester carbon in soil on short and long time scales. Wildfires decrease the abundance of ectomycorrhizal fungi, and reduced fungal abundance after wildfires can persist for several years (*9*). On millennial time scales, Clemmensen *et al.* found that mycorrhizal fungi make smaller contributions to soil carbon in more frequently burned boreal forests, potentially because dead fungal tissues decay faster in these soils. Given that climate warming is likely to increase the occurrence of wildfires in northern forests (*10*), mycorrhizal contributions to soil carbon sequestration may decline in these regions.

Many questions remain regarding the influence of mycorrhizal fungi on carbon cycling within ecosystems. For example, it remains to be shown whether certain residues of ericoid or ectomycorrhizal fungi consistently contribute to soil carbon storage. The

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glycoprotein glomalin produced by arbuscular mycorrhizal fungi (another major group) is thought to reside for decades in the soil (*11*). It is not clear whether analogous compounds are constructed by other mycorrhizal fungi and under what conditions. Another open question is whether ericoid and ectomycorrhizal fungi conduct decomposition themselves. Many members of these groups have the physiological capacity to break down and take up soil organic material (*8*), which could ultimately result in the production of CO_2. Finally, the extent to which mycorrhizal fungi improve plant growth can also determine how much carbon is deposited in the soil via dead plant material. It is the sum of these three processes—deposition of mycorrhizal residues, decomposition by mycorrhizal fungi, and augmentation of plant growth—that determines how mycorrhizal fungi affect carbon storage.

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BIOCHEMISTRY

A Protease for the Ages

Structures of membrane metalloproteases provide the basis for understanding mutations associated with premature aging.

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Mutations in the genes encoding the nuclear scaffold protein lamin A or the zinc metalloprotease ZMPSTE24 cause the devastating premature aging disorder Hutchinson-Guilford progeria syndrome (HGPS) and the related progeroid disorders restrictive dermopathy (RD) and mandibuloacral dysplasia (MAD-B) (*1*–*4*). Children with HGPS, for example, manifest accelerated aging symptoms, including failure to thrive, hair loss, joint ailments, lipodystrophy, and cardiovascular disease, typically dying from the latter in their mid-teens. In all of these progeroid disorders, a persistently farnesylated and methylated form of lamin A is the "molecular culprit," exerting dominant-negative effects that promote aging-related symptoms (*1*). On pages 1604 and 1600 of this issue, Quigley *et al*. (*5*) and Pryor *et al*. (*6*) report the three-dimensional crystal structures of the human zinc metalloprotease ZMPSTE24 and its yeast homolog, Ste24p. These proteases play critical roles in two steps of the posttranslational maturation of human lamin A and the yeast mating pheromone **a**-factor, respectively (*7*–*9*). ZMPSTE24 and Ste24p are multispanning membrane proteins and as such, determining their structures by x-ray crystallography represents a substantial accomplishment. The structures should lead to a better understanding of how these enzymes function and how they are associated with aging.

The ZMPSTE24 substrate lamin A maintains the structural integrity of the nucleus. It is synthesized as a precursor, prelamin A, that terminates in a C-terminal CAAX motif (where C is cysteine, A is generally an aliphatic amino acid, and X is any residue). Like all CAAX proteins, prelamin A undergoes three sequential posttranslational modifications including isoprenylation of cysteine with a farnesyl lipid moiety, endoproteolytic removal of the -AAX peptide by ZMPSTE24 (or by RCE1), and carboxyl methylation (*1*, *2*) (see the figure). Unlike most other CAAX proteins, however, prelamin A undergoes a second cleavage event, also mediated by ZMPSTE24, to yield mature lamin A. This second cleavage removes the last 15 amino acids of the protein, including the newly modified C terminus (*4*, *7*–*9*). The

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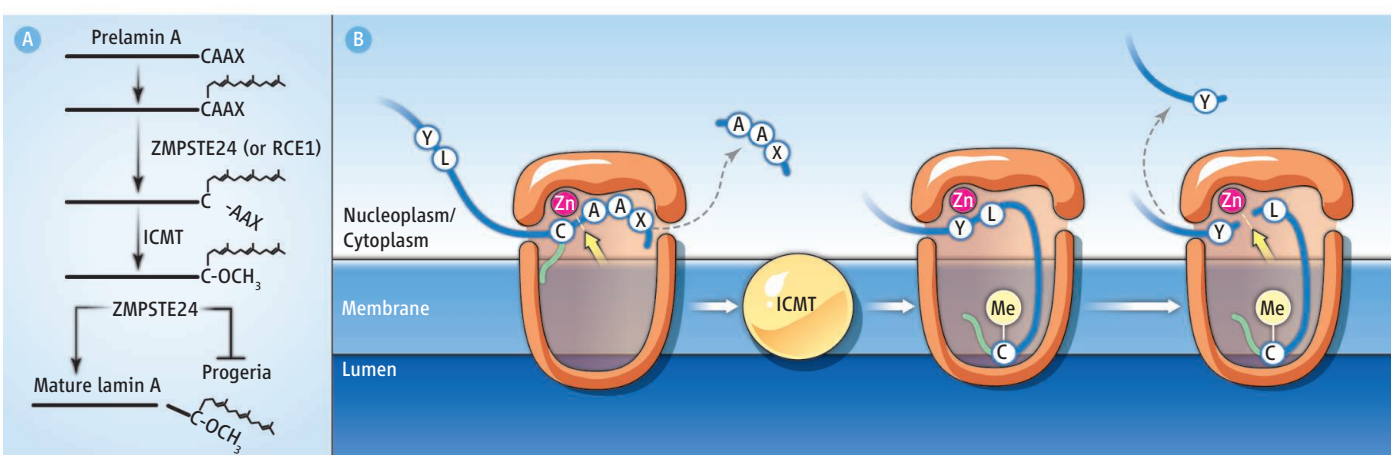

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In the hollow. (**A**) In the posttranslational modification of lamin A, the zinc metalloprotease ZMPSTE24 (or RCE1) mediates processing of the -CAAX motif; ZMPSTE24 then makes a second cleavage. (**B**) ZMPSTE24 is a membrane protein with a large hollow barrel-shaped chamber enclosing the active site. In the hypothetical reaction scheme shown, the C terminus of lamin A (blue), which has been modified with a farnesyl moiety (green line), enters the cavity through a gap in the chamber wall between two transmembrane spans, and aligns in the Zn^{2+} active site. ZMPSTE24 removes the -AAX peptide. The membrane protein ICMT then methylates (Me) lamin A. This is followed by removal of the modified C terminus by ZMPSTE24 and the release of lamin A.

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