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INSIDE

Science FINDINGS

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"Science affects the way we think together."

Lewis Thomas

Nutritional Hotspots and the Secret Life of Forests

Rhonda Mazza

Piloderma*, a genus of mat-forming fungi found in the organic soil layer of Pacific Northwest coniferous forests, influences soil processes that make nitrogen available for plant growth and enhances phosphorus uptake.*

IN SUMMARY

The floor of a Douglas-fir forest may be rich in organic matter, but nutrients essential to plant growth are locked within the decomposing needles, leaves, and fallen wood. Before nitrogen, phosphorus, and other nutrients can be cycled back through the forest system, they need to be further broken down into forms accessible to plants. Understanding how nutrients become available to plants has long been of interest in the Pacific Northwest because the productivity of the region's conifer forests is often thought to be limited by the availability of nitrogen.

In some Douglas-fir forests, a single genus of mat-forming fungi, Piloderma*—which has a symbiotic relationship with nearby trees—covers up to 40 percent of the forest floor. These mats, as well as the surrounding forest soil, harbor a diverse suite of microbes. Scientists analyzed samples of mat and non-mat soils from the H.J. Andrews Experimental Forest for biochemical activity linked to nutrient cycling. They found that the presence of the ectomycorrhizal mats enhanced enzyme activity that likely makes soil nitrogen available for plant uptake. The researchers also found chemical compounds in the mat samples that suggests* Piloderma *helps cycle phosphorus, making it available to plants.*

Ectomycorrhizal mat-forming fungi play another essential role in forest ecosystems: The fruiting bodies they produce, such as mushroom or truffles, serve as a major food source for many forest mammals.

"Each soil is an individual body of nature, possessing its own character, life history, and powers to support plants and animals."

—Hans Jenny

From sprouting seedlings, to towering trees, to rotting logs—these are the stages of life found above ground in a mature forest. But scratch the surface by probing beneath a decomposing log, or brush away an inch or so of debris from the forest floor and the signs of another realm appear. Fungal networks weave through the floors of Pacific Northwest forests and are a critical component of the forest ecosystem.

The critical ecological roles that fungi and other soil organisms play are often overlooked in natural resource management because their functions have remained largely mysterious. But the ongoing development of modern molecular techniques now enables scientists to explore the dynamics of the subterranean world at increasingly finer resolution.

Some of the revelations have been startling. For example, researchers discovered a 2,400-acre site in eastern Oregon populated by a once-contiguous growth of mycelia—masses of branching, threadlike hyphae that represent the vegetative part of a fungus—estimated to be at least 2,200 years old. And, studies are uncovering evidence that chemical signals may induce mycelia to transport nutrients between trees.

Research spanning more than 20 years has revealed that fungi growing in distinctive, dense mats commonly occur in coniferous forest soils of the Pacific Northwest. Intriguingly, mats formed by a single fungal genus, *Piloderma,* cover as much as 40 percent of the forest floor in some Douglas-fir forests. Studies by research botanist Jane Smith, of the Pacific Northwest Research Station (Corvallis, Ore.), and others showed that the presence of *Piloderma* corresponds with the amount of forest floor covered by downed wood in advanced stages of decay.

The notion that such prevalent organisms must play a significant ecological role in their habitat has led Smith, soil scientist Laurel Kluber of the Oak Ridge National Laboratory (Knoxville, Tenn.), and soil microbiology Professor David Myrold of Oregon State University to investigate the biological workings of *Piloderma* mats and their associated communities of bacteria and other fungi. Kluber, an Oregon State University doctoral student at the time of the study, teased out key details of the ecological role of mat-forming fungi such as *Piloderma*.

KEY FINDINGS

- Forest soils colonized by mat-forming ectomycorrhizal fungi are associated with distinctive physical and biochemical properties, compared to surrounding non-mat soils.
- The presence of ectomycorrhizal mats in Douglas-fir forests influences soil processes by enhancing rates of enzymatic activity, making nitrogen available for plant growth, and increasing the production of organic acids that enhance phosphorus uptake.
- Ectomycorrhizal fungal mats commonly occur in the organic soil layer of Pacific Northwest coniferous forests. *Piloderma* mats cover up to 40 percent of the forest floor in some Douglas-fir forests. The fungal and bacterial communities inhabiting *Piloderma* mats differ significantly from the communities found in non-mat soils.
- Across the seasons, *Piloderma* mats examined in the study showed consistently higher activity levels of chitinase—the enzyme that breaks down the nitrogen-containing protein chitin and releases nutrients—than non-mat soils, although this activity varied over time. The fungal and bacterial populations in mats and non-mat soils fluctuated throughout the year while the community composition of each remained stable.

IT TAKES A "VILLAGE"

During their lifetimes, plants manufacture an amazing array of compounds necessary for growth and maintenance. To do so, they need basic elements such as nitrogen and phosphorus in accessible forms. "Although forest ecosystems have an abundance of organic matter, nutrients such as nitrogen and phosphorus often occur in complex organic forms that plants cannot directly take up," Kluber notes.

Enter the fungi—legions of them. As Smith explains, fungi inhabit a range of niches and possess strategies for extracting and releasing nutrients: "Saprophytes, otherwise known as decomposers or wood-rotters, include certain mushrooms, cup fungi, and shelf fungi. Parasitic fungi attack living organisms, while mycorrhizal fungi—such as many of the large, fleshy, showy mushrooms and below-ground truffles—have developed a mutualistic relationship with plants."

In this ingenious partnership—forged over evolutionary time and believed to have aided aquatic plants in adapting to terrestrial environments—the fungus colonizes the host plant's roots. Super-fine fungal hyphae are better able to penetrate nutrient-rich areas in the soil than are plant roots. **Endo**mycorrhizal fungi use their hyphae to channel these essential ingredients directly into root cells. **Ecto**mycorrhizal fungi such as *Piloderma* fashion a robust sheath around the root and insinuate their hyphae between and around the root cells. It's here that nutrients and water delivered by the fungal hyphae are exchanged for nourishing plant-produced sugars. Some ectomycorrhizal mats, such as *Piloderma,* occur in the top, organic layer of the soil, which is often 2 to 3 inches deep in mature Northwest forests, while other ectomycorrhizal mats inhabit the underlying, mineral horizon of the soil.

Jane E. Smith

Piloderma *mats are yellowish or cream-colored, making them some of the more visually striking fungal mats.*

"Most tree species in Pacific Northwest forests depend on ectomycorrhizal fungi, both matformers and non-mat formers. The notable exceptions are redwoods and cedars which are colonized by endomycorrhizal fungi," Smith notes.

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NUTRITIONAL HOTSPOTS

Questions about the availability of plant nutrients have long been of interest in the Northwest, because coniferous forests here have been considered nitrogen-limited—a condition that constricts forest productivity and has repercussions for the entire ecosystem. During the late 1980s, studies that measured concentrations of nitrogen and carbon in Northwest forest soils suggested that soil areas with ectomycorrhizal mats were richer in these essential elements than non-mat soils. The mats also appeared to be sites of greater enzyme activity. These findings hinted that, rather than being fairly homogeneous in terms of nutrients, the forest floor is peppered with "nutritional hotspots."

Rama Ghimire

Researchers gather soil samples in the H.J. Andrews Experimental Forest.

To gain a better understanding of the system underpinning such hotspots, Kluber focused on *Piloderma* mats in eight Douglas-fir stands of various ages in the H.J. Andrews Experimental Forest in western Oregon. "Ectomycorrhizal mats are densely populated with microorganisms—bacteria and other fungi—so studying the highly abundant *Piloderma* mats provided us with the opportunity to begin to understand how mat hyphae and their associated microbes influence enzyme activity in the surrounding soil," Kluber explains.

During summer 2005 her team collected plugs of mat and non-mat soils at each of the eight stands and used DNA sequencing to classify the mat-forming fungi. The researchers also analyzed the samples for indicators of chemical and biochemical activity, such as enzymes involved in the cycling of carbon, nitrogen, and phosphorus.

The results were telling. "The types of enzymatic activity occurring in mat versus non-mat soils were distinctly different," Kluber reports. For example, one key indicator was chitinase, the enzyme that breaks down chitin, a structural compound produced by insects and bacteria and found in the walls of fungal hyphae. "Fungi produce chitinase to 'recycle' their own hyphal material, and also to prey on other fungi for their nutrients," says Kluber. The mat samples had higher levels of chitinase activity than non-mat samples; however, it is difficult to know whether it's the bacteria and fungi living within the *Piloderma* mats, or the mat-forming fungi themselves that are responsible, she says. Nonetheless, "The fungal hyphae within mats are a source of chitin, which contains nitrogen, and thus mats potentially represent a significant nitrogen source to support forest soil productivity," she concludes.

The researchers also discovered that, compared to the non-mat soil samples, the mat soil contained 2.7 times more oxalate—an organic acid manufactured and exuded by fungi to extract phosphorus from rocky material—which made the soils significantly more acidic. "The higher oxalate levels suggest that mats play a role in cycling phosphorus and making it available for plants," Kluber says. Overall, the results provided evidence that ectomycorrhizal mat fungi such as *Piloderma* can alter biogeochemical processes in Douglas-fir forests by creating a unique soil environment with distinct microbial activities, as compared to non-mat soils.

A YEAR IN THE LIFE OF *PILODERMA* MATS

In follow-up research in 2006, Kluber and colleagues returned to the experimental forest to probe more deeply into the links between *Piloderma* mats and their attendant microbial communities. The previous study had utilized samples collected only in summer, so it yielded no insights on possible seasonal changes. "We considered the mats as relatively static structures, but soil samples are like snapshots in time, and without repeated sampling you can't know whether biological activity will be the same two months down the road," she explains. Kluber continues, "Enzymatic and microbial activity are generally driven by temperature and moisture, which vary dramatically throughout the year. So, I was curious to explore whether the mix of microbes and their population sizes also fluctuate over the seasons, and how such changes might affect levels of microbial activity."

Thus, for this round of study, Kluber's team gathered mat samples and non-mat soil samples during each of the four seasons in five old-growth stands at the H.J. Andrews, where mats are particularly well developed. Once again they quantified the levels of nitrogen-liberating chitinase activity over time. But in this study they went a step further and utilized molecular techniques to identify the bacteria and fungi in the samples to gauge the scope of their diversity.

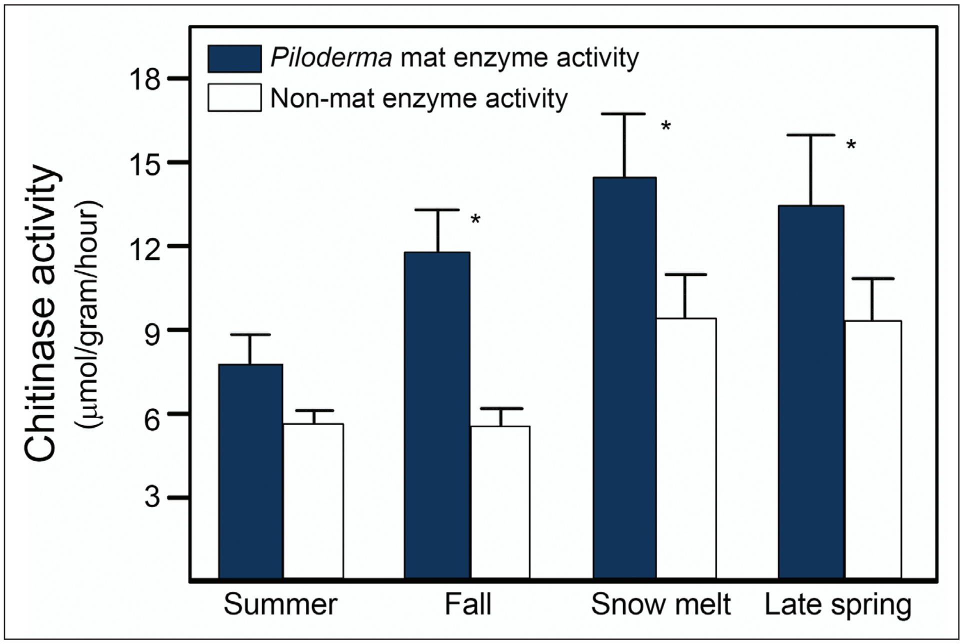
Matt Trappe

Piloderma *mats cover up to 40 percent of the forest floor in some Douglas-fir forests.*

"As with the first study, we saw that throughout the year the *Piloderma* samples had consistently greater chitinase activity—on average about 1.4 times more—than the non-mat soils. However, this activity varied according to the season. The largest difference between mat and non-mat soils occurred in fall, when conditions are at peak dryness," Kluber reports. The team found significantly different communities of fungi and bacteria associated with the mats versus the non-mat soils. Intriguingly, the overall size of the respective microbial populations fluctuated throughout the year while the community composition of each remained stable over the course of the year.

One big surprise was the similarity between the two groups in the overall quantity of fungal biomass, as calculated in terms of fungal genetic material in the samples, Kluber says. "*Piloderma* heavily colonizes the soil with thick yellowish or cream-colored, cord-like bundles of hyphae, and this makes their mats some of the most visually striking ones you can find. Since previous studies have shown that *Piloderma* material accounted for half of the dry weight in the mat samples, we expected to see more fungal DNA in them than the non-mat samples. But not all fungal cells contain nuclear DNA, so that could explain the finding." Nonetheless, the quantity of fungal biomass in both sets of samples did change over the study year. "Interestingly, both fungal and bacterial biomass peaked around the period of snowmelt. Despite the cold temperatures during that time, moisture is relatively high, it's beginning to warm up, and anything that has died off becomes food to fuel microbial growth," she adds.

These results paint a picture of two distinct microbial communities inhabiting the forest floor of Douglas-fir stands. "The size and activity of the microbial populations wax and wane in response to seasonal changes in environmental factors," Kluber concludes. "The make-up of their respective communities seems to be linked to physical and chemical aspects of their micro-habitats, but overall, it appears to remain stable."



Analysis of soil samples with and without Piloderma *mats revealed that* Piloderma *samples had higher levels of an enzyme that frees soil nitrogen from organic matter. The largest difference was in fall, which is when the soil was driest. The figure above shows the mean and standard errors for enzyme activity sampled throughout a year. Enzyme activity in summer differed statically from enzyme activity during snowmelt and late spring. The asterisks indicate statistical differences between mat and non-mat samples within a given season.*

ECOSYSTEM SERVICES OF MAT-FORMING FUNGI

The insights gleaned from Smith's and Kluber's work on ectomycorrhizal fungi highlight their beneficial role in sustaining trees and other forest plants. In the Northwest, some 120 plant species from 19 families and 41 genera serve as hosts for ectomycorrhizal fungi, and these plants depend on this symbiosis for their growth and survival. However, by decomposing organic matter, cycling and retaining nutrients, and transferring energy through soil food webs, these fungi also contribute to the wider health, resiliency, and sustainability of forest ecosystems.

A prime example is the bounty of food that ectomycorrhizal fungi provide. Although the fruiting bodies of *Piloderma* species are small and inconspicuous, most mat-forming fungi produce nutritious, aromatic mushrooms and truffles—vital nourishment for numerous animals, including deer, elk, bear, smaller mammals, slugs, and insects. In turn, these animals disperse mushroom and truffle spores, via their feces, throughout the forest.

A growing number of people are also forest fungi aficionados, regularly collecting

Jane E. Smith

Other types of fungi also play important roles in the forest ecosystem. The mushrooms (Chrysomphalina aurantiaca) *shown above are part of the decomposition process, helping to cycle nutrients through the forest food web.*

mushrooms and truffles for recreation, study, and delectables for their dinner tables. The two largest mushroom societies in Oregon boast more than a thousand members and the expanding harvest of truffles in the region is leading to the development of a truffle industry.

Conserving these fungal communities and maintaining their functions are keys to wise management of forest resources, and Kluber's and Smith's work is contributing to this effort by raising the awareness of the public and resource managers on the intricacies of fungal mats.

"Along with conserving old-growth environments and forests that include trees of varying ages, we can manage for fungal diversity by developing management strategies that maintain the accumulation of natural organic matter essential to thriving mat communities and overall ecosystem health," Smith says.

MANAGEMENT IMPLICATIONS

- Maintaining habitat diversity within forest stands and across landscapes is critical for sustaining mat-forming fungi. These fungi have evolved within the shifting mosaic of forest age classes, plant community dynamics, and periodic disturbances that have occurred in the Pacific Northwest over millennia.
- Mat-forming fungi inhabit a wide variety of forest types—from young to old-growth, wet to dry, and frequently to infrequently disturbed. Their scattered distribution throughout the forest is likely a response to different habitat niches, microclimatic differences, and fungal species competition.
- Allowing logs to remain on the forest floor supports significant ecosystem functions. The logs store water and nutrients and create habitat for *Piloderma*, other mat-forming fungi, and many plant and wildlife species.
- Maintaining soil productivity is essential to sustainable forest management. Mat-forming fungi contribute to soil productivity by cycling nutrients and making the nutrients available to plants.

"I place soils and ecosystems, the nature museums, on par with art museums ...colleges, and temples."

–Hans Jenny

Jane E. Smith

The Piloderma *hyphae penetrate between the root cells of trees to deliver nutrients and water; in exchange, the fungus receives plant-produced sugars.*

FURTHER READING

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