The Woodwide Web

or Capitalism and Socialism in the Forest

by Susan Goldhor

For a long time I thought of the forest as the ultimate in capitalist ecosystems, where the capital was sunlight and the trees reaching the canopy were the plutocrats. Or, as I privately termed them, the Donald Trunks. As for those below... well, every system has its losers, right? It's just the unavoidable underside of having winners.

Maybe everyone thought of the forest this way until researchers looking at soil discovered that the above-ground capitalism of the forest had a social services underground, with a complicated fungal web connecting plants together by their roots, taking from the Haves to give to the Have-Nots. A fungal safety net! Fungi as Robin Hoods! The Woodwide Web! And this was the point at which Capitalism, Red in Tooth and Claw, showed its soft underbelly and—at least in the minds of those of us attuned to such matters—morphed into the safety net of social services delivery. Or, partnership (which might be a better way of looking ar the relationship between government and its citizens). As put by Bonfante and Genre in their brilliant review, "As lichens clearly show, combining an organism that can exploit light and atmospheric CO_2 with one that can efficiently exploit the substrate represents a fruitful adaptation to habitats at the soil–atmosphere interface." Insert "communities" into that sentence and you can see where my brain was heading.

What were we all thinking when we pictured the big trees as robber barons? How did we think the rest of the forest survived? In some estimates, big trees lose/donate as much as 40% of their sugars from their roots and, although some of that goes to feed the soil's other inhabitants, most of it goes directly to the trees' fungal partners. These partners (and one tree can have more than twenty different fungal partners) are attached to the roots so thickly as to cover them, but they also maintain connections to others of the same species and to other plants. It's this network, which some clever person has termed the "wood-wide web" which keeps those understory plants and light-deprived seedlings alive on the forest floor. That tiny hemlock tree that doesn't even reach your knee and has a stem thinner than a pencil? It might be a hundred years old. Supported by the web, it's waiting for an ice storm or a hurricane or a logger to open up the canopy and give it sun and space to grow. And how did we think the big trees survived without that underground source of physical support from healthy soil and nutrient supply from fungal partners? No tree is an island. No tree lives by sunlight and carbon dioxide alone. Tree roots exist for physical support. They're really not very good at accessing water and nutrients; the N-P-K that gardeners supply as fertilizer. It's the fungal web that can find distant patches of water; that can leach phosphorus from minute mineral particles; that rots debris and kills insects to get nitrogen, and then shares all this with the big trees in exchange for sugar.

Pinesap, *Monotropa hypopitys*, courtesy S. Trudell.

Are there welfare cheats? Of course. Take Indian Pipes or Pinesaps or the other monotropes. These small plants have no chlorophyll of their own, and can only get sugars from their fungal partners which, in turn, get it from trees that (presumably) don't know about these little parasites. Or perhaps they do know, and either don't care or can't figure out how to cut off that supply without depriving themselves of the greater mycorrhizal benefits (a hypothesis originally suggested by Bidartondo and Bruns in 2001). A lot of energy has gone into figuring out what monotropes might contribute to their partners, and so far, they seem to be the lilies of the wood; they toil not, neither do they spin. Peripheral as monotropes may be to the big forest picture, it was a study of Pinesaps (*Monotropa hypopithys*) and their partners (*Tricholoma* species) that led to the first intimation of the WWW when, more than a half century ago, E. Bjorkman injected radioactive glucose and phosphorus into the phloem of pine and spruce trees under which the epiparasite grew. He found that the radioactivity passed from tree to fungi to monotrope and that separating the Pinesap from trees stunted its growth. (While Bjorkman's 1960 work may have provided proof of C transfer, it's astounding—at least to me—to realize that Franz Kamienski had concluded that monotropes were nourished by fungi connected to tree roots in the early 1880s, thus underlining the statement by Martin Bidartondo, "To examine the early history of mycorrhizal research is to immerse oneself in the biology of myco-heterotrophic plants".)

Close to a quarter of a century later, David Read, together with his colleagues and graduate students of Sheffield University was, to the best of my knowledge, the first to show uni-directional flow of C between chlorophyllous plants. But not until the August 7, 1997 issue of *Nature* appeared, almost forty years after Bjorkman's work, did the words "The wood-wide web" appear in print, signaling the first paper (Simard et al.) to show that the flow of C between plants in the field is bi-directional, via an ectomycorrhizal network. Although I had assumed that Suzanne Simard or one of her co-authors had come up with this catchy phrase, it does not appear in the paper. It was Melanie Jones and Dan Durall who clued me into the fact that it was the brainchild of one of *Nature*'s (unsung) editors, who blazoned it on that issue's cover, signaling the importance of what lay within.

No revolutionary idea generates immediate acceptance, and the role of challenger fell to the Scottish mycologists, Robinson and Fitter, who pointed out that although labelled carbon was detected in the recipient plant roots, it was not detected in shoots. Therefore, they suggested that it was likely that the C in question was being hoarded in fungal structures within the roots, unavailable to the plants, yet separated only by membranes—shades of Tantalus! Additionally, since no fine mesh filter separated the donor and recipient plants, transfer via soil was possible. "Carbon transfer via an AM network" they declared, "does not allow 'resource sharing' among linked plants" going on to say that if plants really could share C, "Interactions between neighbors would then be less of a struggle for a meagre resource than a communal enterprise in which everyone (at least those in the common mycorrhizal network) got their share." That would change fundamentally our view of an important influence over the structure and dynamics of plant communities." So I guess I wasn't the only one who thought of plant communities as capitalist systems.

This paper, like all good challenges, laid out for the more left-leaning mycologists what their next experiments needed to do; i.e., cut off the possibility of significant soil transfer, and show that labelled C did indeed make it into shoots and leaves. Within a couple of years, Sylvain Lerat and colleagues from Quebec had carried out a very ingenious (and, to me, very surprising) experiment, which showed that, not only was C transferred from one plant species to another through an AM network, but that the transfer was bi-directional depending upon who was photosynthesizing at that time, according to what is called a source-sink relationship. The partners in this case (planted in large pots in a local maple forest) were trout lilies and sugar maples—two very different plants, but ones that fulfilled four requirements: they grew locally; they were found together in nature; they were both colonized by AM fungi and could share a network; and the ephemeral lily put out leaves and photosynthesized in early spring while the canopy was still leafless, but built up its underground corms later in the season, when it was shaded by the actively photosynthesizing maple canopy.

I'm sure you've guessed the result. The lilies passed C to the maple seedlings during leaf expansion of the latter, and the maples passed C to the lilies late in the season, when they were storing nutrients in their corms. This is pretty amazing. It's one thing to think that the WWW allows trees to nourish seedlings of the same species; seedlings that might even carry their very own genes, but this is two wildly different genera helping each other get through hard times. And, unlike the work on reciprocity between plant and fungus ("I'll give you sugar if you give me phosphorus and nitrogen"), this reciprocity occurs with big time gaps between the gifts. So there's an intriguing implication of trust. Incidentally, while they were at it, the Quebecois group showed that it wasn't C transfer through soil, by planting ectomycorrhizal birch seedlings in the same pots. Since the birches didn't glom onto the AM network, they didn't receive any C.

Since then, further work, done on ectomycorrhizal networks, has shown complex natural networks with hubs at large trees, linked to seedlings and smaller trees. (Such work can only be done on ectomycorrhiza because only ectomycorrhizals can be identified genetically. AMs, with their mingled cytoplasm and their lack of comprehensible (to us) sexuality, simply can't be identified very clearly.) Examples of this EM work, such as that by Teste and by Beiler (both from Simard's lab) have concentrated on Douglas-fir, with all trees (although not all fungi) being single species. This has conformed more to our view of the WWW allowing bigger, older trees to nurture their seedlings (and provides yet one more reason why it's bad forestry to remove the larger trees or to think that a plantation of seedlings constitutes a healthy forest), although it seems likely that the Web is maintaining much of the understory vegetation-genetic relationships notwithstanding.

Beiler's paper (entitled, "Architecture of the Woodwide Web") extended our understanding of the structure of natural webs by looking at two species of *Rhizopogon* fungi, each of which exhibited slightly different web structure, with *R. vesiculosus* linking larger numbers of trees and inhabiting a greater depth than *R. vinicolor*. The ability to access deeper strata could be useful when resources are scarce. The Teste paper showed the complexity of the web in nature, finding a total of 32 EM fungal taxa linked to the adult trees and seedlings studied, linkage to the web and C-sharing was helpful to the survival and development of seeds planted in the experimental forest plot, but did not appear to assist transplanted seedlings. (Teste et al. conclude that the strength of the sink outweighs the strength of the source.) And, just to complicate the picture, the larger the donor in this Douglas-fir plot, the less C it shared. (Back to Capitalism here—or, as the Italians say, "If you need money, ask the poor".)

Edwin Hubble once said that the history of astronomy is a history of receding horizons. Of course, that is true of all scientific knowledge. But it's striking to me that the horizon of outer space has receded by parsecs, while that of soil is receding—very slowly and incompletely—by inches.

I've also been struck by the preponderance of Canadian researchers in this field. This might be just the founder effect of a small number of labs that happened to be in Canada. But I can't help wondering if it has to do with the fact that Canada has a strong social safety net for its citizens, and the U.S. doesn't. If we were to decide that taking care of the weak and the young was a national priority, would there be more U.S. research on the interconnectedness of ecosystems, and the benefits of resource sharing? I semi-jokingly shared this thought with an old friend, John Klironomos, a Canadian mycologist who'd just returned from the international mycorrhiza conference in India, and he emailed back, "You have a very keen sense of observation. At the meetings, the biggest critics of resource sharing through mycorrhizal networks did seem to be a few Americans... hmmm..."

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Note: At some point in the latter half of the twentieth century the spelling of *Monotropa hypopitys* changed to *M. hypopithys*. So, it's not a misprint.