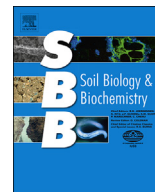




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Chemical communication connects soil food webs



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ABSTRACT

Food webs are conceptual maps of ecosystem matter and energy flows, intended to illustrate the connections between organisms at different trophic and phylogenetic levels. All organisms communicate, most by way of diffusion of chemical signals, often in a density-dependent manner. In this essay, I suggest that food web interactions are regulated by extracellular, inter-species and often inter-domain communication. Defining the web of chemical communication in soils may illuminate new food web interactions and improve our understanding for how disturbances will reverberate through trophic interactions in terrestrial ecosystems.

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If we could hear signaling in soils, it would be loud. All organisms are able to communicate, most by way of diffusion of chemical signals. Chemical communication is the regulation of function by small molecules that are cheaply made and easily diffusible through cell membranes, often in a density-dependent manner. Why do organisms communicate chemically? Generally, signaling is considered a low risk, or inexpensive way of testing whether a high risk or expensive action is worth the investment. Specifically, the reasons for communication are nearly as varied as the organisms themselves: signals protect organisms from predation or stress (Hastings and Greenberg, 1999; Von Bodman et al., 2003); signals hide virulence factors from the host until pathogens are numerous enough to defeat the host immune system (Hentzer et al., 2003; Zhu et al., 2002); signals are inexpensive proxies for testing diffusion of more expensive gene products, like extracellular enzymes, antibiotics or siderophores (Hense et al., 2007; Redfield, 2002). As research in chemical communication has advanced, it has become clear that chemical signals span all domains of life, facilitating interactions within species and between plants and the diverse bacteria and fungi that comprise the rhizosphere (Waters and Bassler, 2005; González and Venturi, 2013; Bonkowski and Clarholm, 2015).

As conceptual maps of matter and energy flows, food webs define interactions between organisms. The nature of organism

interactions as “food webs” was first defined in terrestrial systems with the recognition that all organisms are essentially resource- (or “food”)-limited, and any means by which organisms directly use other organisms for food, including predation or grazing, define the food web (Hairston et al., 1960). It must be the case, the authors argued, that consumers at “higher” levels directly limit herbivores because “the world is green.” Terrestrial food webs are now divided into a root-based (or really, photosynthate-based) branch and a detrital branch, the foundation of this branch being soil organic matter (Hunt et al., 1987). In this essay, I argue that matter and energy flows are also indirectly regulated in both branches by extracellular, inter-species and often inter-domain communication. These indirect interactions are as important as the direct interactions that define classical food webs.

By mapping chemical interactions between soil organisms onto a soil food web diagram, the basic concept of soil food webs as actual interactions is transformed into a map of interaction potentials, where communications mediate risk-benefit analyses on the part of the players whether they want to be involved or not. Signaling occurs within trophic levels as well as across trophic levels, with the chemical interactions highlighting known trophic interactions and suggesting some new ones (Fig. 1). The remainder of this essay describes our current knowledge about these indirect, non-consumptive interactions between organisms in soils, and the extent to which we may be able to extrapolate indirect food web interactions based on our understanding of communication in soils.

Plant signaling touches many trophic levels, and mapping the

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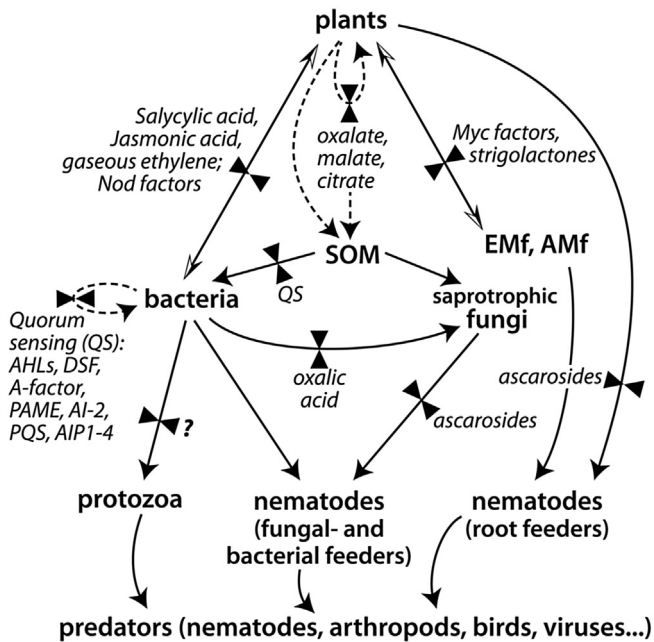


Fig. 1. A map of the soil food web is shown, with known biotic interactions mediated by signaling mapped to the food web interactions. Not shown are the biotic and abiotic factors that control signaling, which are often species- or environmental context-specific and not yet generalizable; see main text for details and references. Solid-line arrows point from a food source to a consumer, and a bowtie on top of the arrow indicates empirical support for a control point in that interaction regulated by extracellular signaling. Dotted-line arrows denote deposition of soil organic matter (SOM), a potential food source in soil food webs.

food web of communication relative to plants shows a network interconnecting the root and detrital branches of the classic terrestrial food web. The plant hormones salicylic acid, jasmonic acid, and gaseous ethylene regulate plant growth and also plant immune responses (Jones and Dangl, 2006), acting as antagonists to rhizosphere bacterial pathogens (Fu and Dong, 2013). Plant hormones are also involved in the assembly of healthy root microbiomes (Lebeis et al., 2015; Pieterse et al., 2012). Plants also produce malate, citrate and oxalate, organic acids part of the photosynthate exuded in the rhizosphere thought to selectively encourage growth of certain populations of bacteria (Shi et al., 2011). Oxalate may also function in facilitating plant-fungal ectomycorrhizal mutualisms as for *Pinus sylvestris* (Van Hees et al., 2006) as well as serve as an attractant for fungus-feeding bacteria (Bravo et al., 2013; Rudnick et al., 2015). Plants and fungi produce oxalic acid in concentrations of up to 27 mM in the soil solution (Guggiari et al., 2011; Sullivan et al., 2012). These organic acids can become stabilized in soils by binding to mineral surfaces (Keiluweit et al., 2015), so that these signals contribute to the SOM pool of the soil food web, meaning that organic acids are part of the detrital-branch as well as the photosynthate-branch of the terrestrial food web.

Microbial signaling systems also regulate plant-microbial symbioses, as with arbuscular mycorrhizal fungi, ectomycorrhizal fungi, and rhizobacteria. Among these beneficial interactions, host ranges may be narrow, with single species of fungi or bacteria associating with single species of plants, or host ranges may be broad, with associated signaling being equally broad (Oldroyd, 2013). For example, nod factors are acylated lipochitooligosaccharides produced by bacteria that regulate interactions between rhizobia and their hosts. Host plants may accept the mutualist based on the positional chemical decorations (acyl, methyl, fucosyl or sulfate groups) of the nod factor, then produce flavonoids to complete the

signal exchange and begin the formation of infection threads to permit the mutualism. A similar exchange happens between mycorrhizae and plants, mediated by fungus-produced Myc factors and plant-produced strigolactones. Plants are also able to monitor and respond to bacterial quorum sensing, the density dependent-control over bacterial gene expression, where bacteria constantly produce (via LuxI synthases) and detect (via LuxR receptors) the signals acyl-homoserine lactones (AHLs) (Engebrecht and Silverman, 1984; Waters and Bassler, 2005). A variety of AHLs induce reproducible plant reactions in *Arabidopsis thaliana*, *Phaseolus vulgaris*, *Medicago trunculata*, and others (Hartmann et al., 2014; Liu et al., 2012; Veliz-Vallejos et al., 2014), including root or root hair formation and elongation, increased metabolism and transpiration, as well as immune response (Schenk et al., 2012; Zhao et al., 2015).

There are numerous studies that describe communications that facilitate food web interactions. For example, bacterial quorum sensing controls production of the extracellular enzymes required for SOM mobilization in rhizosphere food webs (DeAngelis, 2013). Though further evidence in soils is currently lacking, addition of exogenous AHLs increased hydrolytic enzyme activity in particulate organic matter in the ocean (Hmelo et al., 2011). Signaling does not always have a positive effect: alkaline phosphatase enzyme production by the marine cyanobacteria *Trichodesmium* is regulated by signaling, with AHLs associated with increased phosphatase activity and AI-2 associated with attenuated phosphatase activity (Van Mooy et al., 2012). Of the 44 rhizosphere and 85 endophytic bacteria screened in the *Populus deltoides* microbiome (spanning 85 bacterial genera), 40% produced AHLs (Schaefer et al., 2013), with similar prevalence of quorum sensing in the rhizosphere communities of rice (Sessitsch et al., 2011) and wild oat (DeAngelis et al., 2008). Considering that there are a wide variety of signals known for bacterial signaling beyond AHLs, including DSF, PAME, PQS, A-factor, AI-2 and AIP1 through 4 (Waters and Bassler, 2005), we must conclude that signaling within and across species in soil is pervasive, though more work is needed to define the functional control of signaling in food web interactions.

There is also rampant interception of signals for predation and prevention of infection throughout the food web. For example, protoanemonin is produced by *Pseudomonas* to inhibit quorum sensing (Bobadilla Fazzini et al., 2013). Plants interfere with bacterial signaling in the production of enzymes that globally block quorum sensing (Dong et al., 2001). Plant pattern-recognition receptors (PPRs) are surface-localized kinases responsive to a wide range of signals characteristic of other plants and microbes, though PRRs appear not to include bacterial signaling molecules (Zipfel, 2014). PRRs recognize the nematode hormones ascarosides, a family of over 200 different compounds produced by nematodes that regulate nematode development and behavior as well as activate plant immune responses (Manosalva et al., 2015). Fungi that predate nematodes may be able to intercept these same hormones (Hsueh et al., 2013). Protozoa show selective grazing of bacteria, and this preference of protozoa for specific bacteria may be rooted in extracellular signaling among other factors (Matz and Kjelleberg, 2005), though understanding how signaling factors into protozoal grazing and the microbial loop in soils is still mostly conceptual (Bonkowski and Clarholm, 2015).

There are a variety of signal receptor solos, or orphans, in bacterial and plant genomes which indicate an ability to eavesdrop on signaling cascades of other organisms (González and Venturi, 2013). Most signaling systems are coded by two genes or sets of genes: the synthases which produce the signal, and the receptors which detect the signal and transmit downstream changes in gene expression. Among the 129 bacteria screened in the *Populus* microbiome, more had solo homologs of the LuxR receptors than

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