Agriculture, Ecosystems and Environment 210 (2015) 47–49

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

journal homepage: www.elsevier.com/locate/agee

News & views

Signal transduction in edaphic ecosystems governs sustainability

Gamini Seneviratne *

Microbial Biotechnology Unit, National Institute of Fundamental Studies, Hantana Road, Kandy, Sri Lanka

ARTICLE INFO

Article history:
Received 18 February 2015
Received in revised form 11 May 2015
Accepted 18 May 2015
Available online 26 May 2015

Keywords:
Ecosystems
Food web
Microbes
Signal transduction
Sustainability

ABSTRACT

Sustainability of natural and agro ecosystems is governed mainly by soil processes. In these, contributions of the biotic or living constituents are much important. The biotic part is represented by soil food web. Here, I argue that the sustainability of the ecosystems is an outcome of chemical signaling in the food web. Then, I show that it is the microbes living mainly endophytically and in the soil, including fauna, which contribute to ecosystem balance through signaling in complex network interactions. Sustenance of edaphic or soil ecosystems collapses when the signaling is retarded due to human impact and global change. This issue can only be addressed by manipulating soil microbes. I introduce a new term edaphic ecosystem signal transduction (EST), which can summarize the concept explained in this article.

1. Ecosystem sustainability

Sustainability of natural and agroecosystems is governed mainly by soil processes of biotic and abiotic components. Amongst, contributions of the diverse biotic or living constituents towards functional equilibrium are much important (Singh, 2015). Soil food web represents basically the biotic part. It determines cycling processes of major elements across ecosystems, and it is a better predictor of those processes than land use (de Vries et al., 2013). It is now revealed that microbial species interactions in the soil food web could be more important to the soil processes than just species richness and abundance (Lupatini et al., 2014). Such interactions and also nestedness of the soil food web have been reported to reduce interspecific competition and increase the number of coexisting species, and hence biodiversity (Bastolla et al., 2009). Here, I argue that the stability and balanced responses of a large number of individuals in the food web, being such a complex network are attributable to chemical signaling. Because signaling compounds function as messengers for communicating among organisms in the ecosystems for cooperative existence. This idea of the linkage between ecosystem sustainability and chemical signaling has not been established yet. Numerous chemical compounds that act as signaling molecules in the soil-plant system have been identified to date. Cytokinins are one such group of compounds (Giron et al., 2013). They are the key regulators of intricate plant–microbe–insect interactions, and contribute to plant growth-defense compromise in facing to mutualists as well as invaders. Other signaling molecules that have been recognized include indoles, which play an important role in intercellular signaling in microbial communities, plant–microbe interactions and plant growth, ecological balance and possibly human health (Lambrecht et al., 2000; Lee and Lee, 2010; Mabood et al., 2014). As such, chemical signaling plays an essential role in sustenance of ecosystems.

2. Microbes in complex network interactions

In soil bacterial communities, it is a long known fact that bacteria use species specific quorum sensing signals or autoinducers to coordinate gene expression according to the density of their local population. However now, non-species specific autoinducers that are capable of mediating intra- and inter-species communication among different bacteria have been identified (Galloway et al., 2012). Recent evidences demonstrate the roles of those autoinducers, even in plant defense responses and root development (Bai et al., 2012). On the other hand, some higher plants were observed to produce the bacterial autoinducer signal-mimic compounds which mediate interactions between the higher plants and soil bacteria (Teplitski et al., 2000). However, it is reported now that it is the microbes living endophytically in higher plants, which are responsible for producing the mimic compounds and other metabolites (Bérdy, 2005). Therefore, it seems that endophytes are tightly bound to biosynthetic pathways of secondary metabolites in the hosts. A common role of the secondary metabolites in plants is defense mechanisms. As such, I suggest that there could be a close communication between the plants and their endophytes for producing the secondary

* Corresponding author. Tel.: +94 81 2232002; fax: +94 81 2232131.
E-mail address: gaminis@ifs.ac.lk (G. Seneviratne).

http://dx.doi.org/10.1016/j.agee.2015.05.006
0167-8809/

metabolites, when need arises, for example in a pest or pathogen attack. Flavonoid pathway in plants produces a diverse array of compounds with functions in defense against pathogens, signaling in symbiosis, auxin transport regulators and as antioxidants and pigments (Hassan and Mathesius, 2012). In alfalfa, chemotaxis towards the host plant by symbiotic *Sinorhizobium meliloti* has been reported to mediate from sensing of proline secreted by roots (Webb et al., 2014). In the presence of host plant physiological stress, many eukaryotic signal molecules are released and detected by Gram-negative pathogenic bacteria which in return rapidly adapt their physiology for virulence (Lesouhaitier et al., 2009). Here in pathogenesis, plant immune signaling network balances two conflicting demands, vigor against pathogenic perturbations and moderation of negative impacts of immune responses on plant fitness (Sato et al., 2010). Thus, it seems that it is the microbes living endophytically and in the soil, which contribute to ecosystem balance through signaling in complex network interactions.

Recent findings provide further evidence for above, showing intriguing complex interactions mediated by signaling among plant–insect–microbes. Aphid-mediated plant immunity against pathogen infection, particularly the priming of defense responses against different pathogens through hormonal signaling has been found to help prepare the plant for subsequent pathogen attacks (Lee et al., 2012). Further, an exciting study reports that plants can exploit common mycorrhizal networks in the soil for herbivore-induced defense signal transfer and interplant defense communication to activate defense responses more rapidly and aggressively upon insect attack and to increase their insect resistance (Song et al., 2014).

3. Microbes: interface between biotic and abiotic environment

In addition to above, induction of common signaling components in organisms challenged by a change in the environment has been reported. For example, plant rootlets starved of soil nitrogen have been observed to secrete small peptides that are translocated to the shoot and received by specific receptors so that the signaling from the root to the shoot helps the plant adapt to fluctuations in local nutrient availability (Tabata et al., 2014). In this instance, the signaling may induce the action of endophytic nitrogen fixers for compensating short supply of soil nitrogen to the plant. Moreover, in response to high doses of UV-B radiation, signaling molecules such as abscisic acid (ABA), nitric oxide (NO) and Ca^{2+} in plant and animal cells are induced for stress tolerance (Tossi et al., 2012). Also, NO can modulate the activities of cellular and extracellular proteins in various groups of organisms, implementing significant physiological functions (Medinets et al., 2015). Further, NO can play a signaling function to enhance microbial biofilm formation in the soil (Medinets et al., 2015), which renders numerous biochemical and physiological benefits to plant growth (Qurashi and Sabri, 2012). And also, biofilm formation improves soil fertility through aggregate formation (Qurashi and Sabri, 2012) and carbon storage (Seneviratne et al., 2011). It is now known that microbes are an integral part in plants and animals. Microbes in macro-organisms provide their metabolic activity producing an amazing diversity of compounds and signaling molecules for nutrition, protection and development of the hosts (Selosse et al., 2014). Thus, the soil-derived host microbiome acts as the interface between biotic and abiotic environment.

Taking everything into consideration, I introduce a new term edaphic ecosystem signal transduction (EST), which can summarize the facts and the concept explained in this article. The EST is defined as chemical signaling from signaling molecules to trigger a change in the activity or state at and within the edaphic ecosystem, taking the ecosystem as a one unit, like a cell. The EST is mediated by receptors of microbes in soil, plants and animals in the ecosystem through signal-receptor-process-response cascade (Fig. 1). The response could be a signal which again triggers receptors of other counterparts of the ecosystem. This leads to establish a signaling network. However, sustenance of edaphic ecosystems collapses when the signaling network is disrupted due to human impact (e.g. chemical inputs in agricultural practices (e.g. Fox et al., 2007), tillage etc.) and global change. This can further be explained by the case discussed below.

Nitrogen fixers play a key role in the growth and persistence of effective microbial communities in the soil by supplying nitrogen through biological nitrogen fixation (Seneviratne et al., 2011). However, nitrogenous fertilizers in agriculture and forestry suppress the action of microbes, particularly nitrogen fixers in

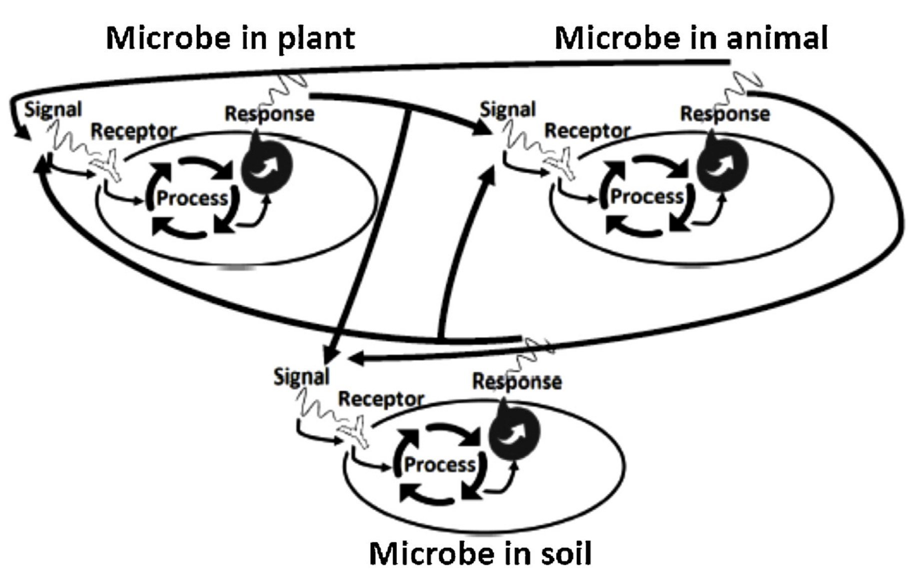

Fig. 1. Interactions among biotic counterparts in edaphic ecosystems. In undisturbed ecosystems like forests, there is a delicate balance among the interacting counterparts, the center of which is represented by microbes. Their cascading effect and chemical signaling networks, as indicated by arrows support the balance and stability of the ecosystems. This concept is introduced as edaphic ecosystem signal transduction (EST). However, in disturbed ecosystems like croplands, particularly chemical inputs weaken the interactions through collapsing the signaling networks, consequently breaking the delicate balance of the ecosystem.

agroecosystems through disruption of the signaling networks. This tends to produce nitrogen-deficient, weak microbial communities with low biomass and activity, due to diminished nitrogen supply from the repressed nitrogen fixers. That leads to collapsed microbial diversity and ecosystem functioning. Under this circumstance, 1) reduced soil fertility and organic matter buildup (Scholes and Scholes, 2013; Bi et al., 2015) leading to low soil moisture retention, and hence drought stress, and also 2) yield decline (e.g. Kumar and Yadav, 2001), possibly due to lack of rhizoremediation, resulting in phytotoxin accumulation (e.g. Dams et al., 2007), which are prevalent in collapsed sustainability, can be observed in the ecosystems. Thus, the question arises here is that, how could the signaling networks be reinstated for reviving the microbial diversity for sustainability? This issue can only be addressed by manipulating soil microbes in the ecosystems for re-establishing communication through EST, but not solely by nutrients and water management, as suggested in conventional agriculture and forestry.

References

Bai, X., Todd, C.D., Desikan, R., Yang, Y., Hu, X., 2012. *N*-3-oxo-decanoyl-L-homoserine-lactone activates auxin-induced adventitious root formation via hydrogen peroxide- and nitric oxide-dependent cyclic GMP signaling in mung bean. Plant Physiol. 158, 725–736.

Bastolla, U., Fortuna, M.A., Pascual-García, A., Ferrera, A., Luque, B., Bascompte, J., 2009. The architecture of mutualistic networks minimizes competition and increases biodiversity. Nature 458, 1018–1020.

Bérdy, J., 2005. Bioactive microbial metabolites. J. Antibiot. 58, 1–26.

Bi, L., Yao, S., Zhang, B., 2015. Impacts of long-term chemical and organic fertilization on soil puddlability in subtropical China. Soil Till. Res. 152, 94–103.

Dams, R.I., Paton, G.I., Killham, K., 2007. Rhizoremediation of pentachlorophenol by *Sphingobium chlorophenolicum* ATCC 39723. Chemosphere 68, 864–870.

de Vries, F.T., Thébault, E., Liiri, M., Birkhofer, K., Tsiafouli, M.A., Bjørnlund, L., Jørgensen, H.B., Brady, M.V., Christensen, S., de Ruiter, P.C., d'Hertefeldt, T., Frouz, J., Hedlund, K., Hemerik, L., Hol, W.H.G., Hotes, S., Mortimer, S.R., Setälä, H., Sgardelis, S.P., Uteseny, K., van der Putten, W., Wolters, V., Bardgett, R.D., 2013. Soil food web properties explain ecosystem services across European land use systems. Proc. Natl. Acad. Sci. U. S. A. 110, 14296–14301.

Fox, J.E., Gulledge, J., Engelhaupt, E., Burow, M.E., McLachlan, J.A., 2007. Pesticides reduce symbiotic efficiency of nitrogen-fixing rhizobia and host plants. Proc. Natl. Acad. Sci. U. S. A. 104, 10282–10287.

Galloway, W.R.J.D., Hodgkinson, J.T., Bowden, S., Welch, M., Spring, D.R., 2012. Applications of small molecule activators and inhibitors of quorum sensing in Gram-negative bacteria. Trends Microbiol. 20, 449–458.

Giron, D., Frago, E., Glevarec, G., Pieterse, C.M.J., Dicke, M., 2013. Cytokinins as key regulators in plant–microbe–insect interactions: connecting plant growth and defence. Funct. Ecol. 27, 599–609.

Hassan, S., Mathesius, U., 2012. The role of flavonoids in root-rhizosphere signalling: opportunities and challenges for improving plant–microbe interactions. J. Exp. Bot. doi:http://dx.doi.org/10.1093/jxb/err430.

Kumar, A., Yadav, D.S., 2001. Long-term effects of fertilizers on the soil fertility and productivity of a rice–wheat system. J. Agron. Crop Sci. 186, 47–54.

Lambrecht, M., Okon, Y., Broek, A.V., Vanderleyden, J., 2000. Indole-3-acetic acid: a reciprocal signalling molecule in bacteria–plant interactions. Trends Microbiol. 8, 298–300.

Lee, B., Lee, S., Ryu, C.-M., 2012. Foliar aphid feeding recruits rhizosphere bacteria and primes plant immunity against pathogenic and non-pathogenic bacteria in pepper. Ann. Bot. 110, 281–290.

Lee, J.-H., Lee, J., 2010. Indole as an intercellular signal in microbial communities. FEMS Microbiol. Rev. 34, 426–444.

Lesouhaitier, O., Veron, W., Chapalain, A., Madi, A., Blier, A.-S., Dagorn, A., Connil, N., Chevalier, S., Orange, N., Feuilloley, M., 2009. Gram-negative bacterial sensors for eukaryotic signal molecules. Sensors 9, 6967–6990.

Lupatini, M., Suleiman, A.K.A., Jacques, R.J.S., Antoniolli, Z.I., de Siqueira Ferreira, A., Kuramae, E.E., Roesch, L.F.W., 2014. Network topology reveals high connectance levels and few key microbial genera within soils. Front. Environ. Sci. 2, 10. doi:http://dx.doi.org/10.3389/fenvs.2014.00010.

Mabood, F., Zhou, X., Smith, D.L., 2014. Microbial signaling and plant growth promotion. Can. J. Plant Sci. 94, 1051–1063.

Medinets, S., Skiba, U., Rennenberg, H., Butterbach-Bahl, K., 2015. A review of soil NO transformation: associated processes and possible physiological significance on organisms. Soil Biol. Biochem. 80, 92–117.

Qurashi, A.W., Sabri, A.N., 2012. Bacterial exopolysaccharide and biofilm formation stimulate chickpea growth and soil aggregation under salt stress. Braz. J. Microbiol. 43, 1183–1191.

Sato, M., Tsuda, K., Wang, L., Coller, J., Watanabe, Y., Glazebrook, J., Katagiri, F., 2010. Network modeling reveals prevalent negative regulatory relationships between signaling sectors in *Arabidopsis* immune signaling. PLoS Pathog. 6 (7), e1001011. doi:http://dx.doi.org/10.1371/journal.ppat.1001011.

Scholes, M.C., Scholes, R.J., 2013. Dust unto dust. Science 342, 565–566.

Selosse, M.-A., Bessis, A., Pozo, M.J., 2014. Microbial priming of plant and animal immunity: symbionts as developmental signals. Trends Microbiol. 22, 607–613.

Seneviratne, G., Jayasekara, A.P.D.A., De Silva, M.S.D.L., Abeysekera, U.P., 2011. Developed microbial biofilms can restore deteriorated conventional agricultural soils. Soil Biol. Biochem. 43, 1059–1062.

Singh, J.S., 2015. Microbes: the chief ecological engineers in reinstating equilibrium in degraded ecosystems. Agric. Ecosyst. Environ. 203, 80–82.

Song, Y.Y., Ye, M., Li, C.Y., He, X.H., Zhu-Salzman, K.Y., Wang, R.L., Su, Y.J., Luo, S.M., Zeng, R.S., 2014. Hijacking common mycorrhizal networks for herbivore-induced defence signal transfer between tomato plants. Sci. Rep. 4, 3915. doi:http://dx.doi.org/10.1038/srep03915.

Tabata, R., Sumida, K., Yoshii, T., Ohyama, K., Shinohara, H., Matsubayashi, Y., 2014. Perception of root-derived peptides by shoot LRR-RKs mediates systemic N-demand signaling. Science 346, 343–346.

Teplitski, M., Robinson, J.B., Bauer, W.D., 2000. Plants secrete substances that mimic bacterial *N*-acyl homoserine lactone signal activities and affect population density-dependent behaviors in associated bacteria. Mol. Plant Microbe Interact. 13, 637–648.

Tossi, V., Cassia, R., Bruzzone, S., Zocchi, E., Lamattina, L., 2012. ABA says NO to UV-B: a universal response. Trends Plant Sci. 17, 510–517.

Webb, B.A., Hildreth, S., Helm, R.F., Scharf, B.E., 2014. *Sinorhizobium meliloti* chemoreceptor McpU mediates chemotaxis toward host plant exudates through direct proline sensing. Appl. Environ. Microbiol. 80, 3404–3415.