



## A role for coercion in the evolution of plant-microbe communication

Journal:	<i>Molecular Plant-Microbe Interactions</i>
Manuscript ID	Draft
Manuscript Type:	Current Review
Date Submitted by the Author:	n/a
Complete List of Authors:	Rowe, Shawna; Michigan State University, Department of Plant Biology; Michigan State University, BEACON: An NSF Center for the Study of Evolution in Action Norman, Jeffrey; Michigan State University, Department of Plant Biology Friesen, Maren; Michigan State University, Plant Biology Department; Washington State University, Crop and Soil Sciences; Washington State University , Plant Pathology
Area That Best Describes Your Manuscript:	molecular signaling < Bacteria-plant symbiosis, rhizosphere and phyllosphere ecology < Microbial ecology

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

**TITLE:**

A role for coercion in the evolution of plant-microbe communication

**AUTHOR NAMES AND AFFILIATIONS:**

S.L. Rowe<sup>1\*</sup>, J.S. Norman<sup>1</sup>, and M.L. Friesen<sup>1,2,3</sup>

<sup>1</sup>Plant Biology Department, Michigan State University, East Lansing, MI, USA

<sup>2</sup>Department Department of Plant Pathology, Washington State University, Pullman, WA, USA

<sup>3</sup>Department of Crop and Soil Sciences, Washington State University, Pullman, WA, USA

\*Indicates Corresponding author

**CORRESPONDING AUTHOR CONTACT INFORMATION:**

Shawna L. Rowe (S.L. Rowe)

Email: roweshaw@msu.edu

Mailing address:

Department of Plant Biology

612 Wilson Rd, Room 166

East Lansing MI, USA, 48824

**CONFLICT OF INTEREST STATEMENT:**

The authors declare no conflict of interest.

**ABSTRACT:**

Plants and microbes are dependent on chemical signals as a means of inter-kingdom communication. There are two predicted paths for the evolution of these signals. Ritualization, the evolution of signals from cues, is the oft-assumed pathway for the evolution of plant-microbe communication systems. However, plant-microbe signaling may evolve from coercive interactions as well, a process known as sensory manipulation. Here, we aim to highlight the prevalence of coercive interactions and discuss sensory manipulation in the context of plant-microbe interactions. We present two examples of stabilized coercion: microbial coercion of plants via the release of phytohormones and plant coercion of microbes via manipulation of quorum-sensing compounds. Furthermore, we provide an evolutionary framework for the emergence of signaling from coercive plant-microbe interactions through the process of sensory manipulation. We hope that researchers will recognize the relevance of coercive interactions in plant-microbe systems and consider sensory manipulation as a plausible evolutionary trajectory for the emergence of plant-microbe signaling.

36  
37 **INTRODUCTION**

38       Communication systems in nature provide a foundation for both intra- and interspecific  
39 interactions (Scott-Phillips 2008). Developing an understanding of how communication systems  
40 evolved is therefore key to understanding the evolution of complex relationships between species  
41 including mutualism, parasitism, competition, and commensalism. Plants, a sessile group of  
42 organisms, are dependent on molecular communication events to interact with the diverse  
43 microbial communities present in their environments (Baker et al. 2006). Recent efforts to  
44 uncover the functional significance of the plant microbiome have resulted in a new wave of  
45 questions about the evolution of the complex associations between plants and microbes. Future  
46 advances in this field will depend on a mechanistic understanding of plant-microbe  
47 communication and the evolutionary processes that underlie it. Here we discuss coercion, an  
48 evolutionary precursor to molecular signaling, in the context of plant-microbe interactions.

49       While human communication relies mainly on the production and detection of visual and  
50 auditory stimuli as means of communication, plants and microbes primarily depend on secretion  
51 and detection of “infochemicals” (a term we borrow from Barto et al. 2011) to send and receive  
52 information. A formal definition of the term “infochemical” and others that we introduce can be  
53 found in Table 1; note that the general communication theory we modify for specificity to plant-  
54 microbe interactions was originally presented by Scott-Phillips (2008) and Scott-Phillips et al.  
55 (2012). Infochemicals are secreted by one organism (i.e. the sender) and detected by another (i.e.  
56 the receiver); both plants and microbes can play the role of sender or receiver. The emergence of  
57 novel plant-microbe interactions depends upon two aspects of organismal physiology: 1) both  
58 plants and microbes release a variety of chemicals into the environment; 2) both plants and

microbes have a variety of chemical receptors that allow them to detect myriad chemicals. Random mutation of genes encoding metabolic pathways and of cell-surface proteins therefore allow for changes in the respective complements of chemicals both released and detected by plants and microbes. To the extent that the release and perception of these chemicals is associated with survival and reproduction, natural selection can act upon the release of novel chemicals and novel detection mechanisms favoring either sender or receiver accordingly.

If detection of an infochemical benefits the receiver, without benefit to the sender, the infochemical is classified as a cue. Note that we only use the term “cue” to describe a class of infochemicals throughout this article; colloquial definitions of the term and those that do not deal with infochemicals (*e.g.* “environmental cues” such as sunlight) should not be inferred in the text (Table 1). A recent review by van’t Padje et al. (2016) focused on the prevalence of cues on both sides of plant-microbe interactions. For example, plants are thought to use quorum sensing autoinducers released by rhizosphere bacteria as cues that convey information about bacterial abundance (. Conversely, myco-heterotrophs, parasitic non-photosynthetic plants that extract carbon and nitrogen from arbuscular mycorrhizal (AM) fungi, are thought to use as-of-yet unidentified cues to locate AM fungal hyphae within the soil matrix (Rasmussen et al. 2015).

The prevalence of coercion, a formal definition of which is provided in Table 1, in plant microbe interactions has yet to be investigated to the same degree. Coercive infochemicals are those that benefit the sender, without benefit to the receiver. The release of coercive infochemicals often allows the sender to take advantage of an existing evolutionary response in the receiver, which the sender can use to modify the receiver’s behavior (Figure 1). The prevalence of coercion is an oft-overlooked interaction despite its apparent presence in commonly studied systems. Here we discuss the mechanism of coercion as it applies to plant

microbe interactions, and we provide examples of coercion in natural systems. Furthermore, we discuss the evolutionary outcomes of coercive interactions between plants and microbes focusing on the mechanism by which coercion, which benefits the sender, turns into signaling, which benefits both the sender and receiver, known as “sensory manipulation.” (Scott-Phillips 2008, Scott-Phillips et al. 2012).

**INTERSPECIFIC COERCION**

Although not always recognized as such, many well-characterized molecular interactions between plants and their associated microbes fall into the category of coercion, where the sender benefits at the potential expense of the receiver. Two pervasive types of coercion are plant coercion of microbes via manipulation of quorum sensing and microbial coercion of plants via modulation of phytohormones. In this section we provide specific examples of each behavior within the conceptual framework of communication theory.

**Plant coercion of microbes— Manipulation of quorum sensing**

Rhizosphere microbes use quorum sensing, a form of cell-to-cell communication, to regulate a variety of behaviors including exoenzyme release (*e.g.* Chernin et al. 1998), biofilm formation (*e.g.* Danhorn and Fuqua 2007), and motility (*e.g.* Köhler et al. 2000). Quorum sensing relies on infochemicals known as autoinducers to provide information about the density of microbes that release these chemicals in a given environment or the diffusion environment of the microbes; this ensures that the behaviors of the aforementioned group only occur under optimal conditions. Once enough bacteria are present (or there is a low rate of diffusion, such as when the microbes are adjacent to a root surface) the total amount of autoinducers present will

1  
2  
3 105 exceed the necessary threshold for a bacterial response to occur (Bassler 1999, Redfield 2002).  
4  
5  
6 106 Autoinducers often times directly bind to transcription factors or act upstream of transcription  
7  
8 107 factors and regulate gene expression (Engebrecht and Silverman 1987). Plants can manipulate  
9  
10 108 quorum sensing by releasing molecules that either mimic bacterial autoinducers or interfere with  
11  
12 109 the ability of microbes to produce or detect autoinducers; we provide further examples of these  
13  
14 110 phenomena below. Plants can decouple quorum sensing-controlled behaviors from microbial  
15  
16 111 density thereby ensuring that those behaviors that positively affect plant fitness are favored,  
17  
18 112 while those that negatively affect plant fitness are not. We suggest that the ubiquitous  
19  
20 113 phenomenon of plant manipulation of quorum-sensing is a coercive act.  
21  
22  
23

24  
25 114 Extracts and exudates from plants have been shown to elicit quorum sensing-dependent  
26  
27 115 responses in bacterial indicator strains (*e.g. Chromobacterium violaceum*, which uses quorum  
28  
29 116 sensing to regulate production of the pigment violacin) suggesting that plants produce molecules  
30  
31 117 that mimic bacterial autoinducers; this behavior could prevent biofilm formation which is a key  
32  
33 118 component of pathogenesis for many pathogens (Pérez-Montaña et al. 2013). This type of  
34  
35 119 coercive behavior in higher plants was first demonstrated in pea (*Pisum sativum*) (Teplitski et al.  
36  
37 120 2000) and has since been shown in rice (*Oryza sativa*) (Degraasi et al. 2007, (Pérez-Montaña et  
38  
39 121 al. 2013).), common bean (*Phaseolus vulgaris*) (Perez-Montano et al. 2013), barrel medic  
40  
41 122 (*Medicago truncatula*) (Gao et al. 2003), and a variety of medicinal plants (Tolmacheva et al.  
42  
43 123 2014). Annapoorani et al. (2012) predicted that a variety of compounds produced by plants  
44  
45 124 would bind to quorum-sensing regulator genes suggesting that these compounds were  
46  
47 125 autoinducer mimics. Recently, Corral-Lugo et al. (2016) tested these predicted effects of one  
48  
49 126 such compounds, rosmarinic acid, and showed that this compound activates quorum sensing-  
50  
51 127 controlled behavior by a variety of bacterial indicator strains.  
52  
53  
54  
55  
56  
57  
58  
59  
60

Plants also coerce microbes by interrupting quorum sensing through a variety of processes collectively known as quorum quenching. Mechanisms of quorum quenching found in nature include the release of enzymes such as lactonases and acylases that degrade autoinducers, and the release of inhibitory chemicals that affect the ability of microbes to synthesize, exchange, perceive, and respond to, autoinducers (Grandclément et al. 2016). In higher plants, quorum quenching effects were first demonstrated in pea plants (*Pisum sativum*) (Teplitski et al. 2000), and have since been shown in garlic (*Allium sativum*) (Rasmussen et al. 2005), various medicinal plants (Adonizio et al. 2006) and more-recently in tarragon (*Artemisia dracunculus*), radish (*Raphanus raphanistrum*), and hollyhock (*Althea officinalis*.) (Mahmoudi et al. 2014) among others. Enzymatic degradation of autoinducers in the extracellular environment, a trait common to many bacterial taxa (Rasmussen and Givskov 2006 and references therein), has yet to be shown in plants, though some are capable of intracellular enzymatic degradation of autoinducers (Palmer et al. 2014). However, plants from 21 families produce various phenolics, terpenoids, organosulfur phytochemicals, coumarins, quinones, and alkaloids that inhibit quorum sensing by a variety of mechanisms (Ta and Arnason 2015 and references therein), suggesting that plant coercion of microbes by quorum quenching may be widespread.

**Microbial coercion of plants—Manipulation of phytohormones**

Phytohormones, plant hormones involved in a variety of developmental and regulatory processes, are well documented to be commonly modulated by microorganisms (Chanclud and Morel 2016). While phytohormones can have microbial functions (Glick 2015), most studies have discussed the production of phytohormones by microbes in a mutualistic fashion where microbes are interacting with plants in a beneficial manner that results in equal fitness trade-offs



(Hardoim et al. 2008) Evolutionary theory demonstrates that, to understand these types of traits, we need to take the perspective of the microbial genes and ask how natural selection will act on variation that arises. If a mutation arises that alters a plant's physiology in a way that enhances microbial fitness, then this mutation will spread through the population. Studies showing microbial modulation of plant growth typically focus on plant growth promotion and rarely consider the complex relationship that resulted in a given phenotype. Microbial production of phytohormones is nearly ubiquitous in soil-dwelling organisms and occurs in both prokaryotic and eukaryotic microorganisms including heterotrophs, phototrophs, algae, and fungi (Tsavkelova et al. 2005). However, it can be difficult to tease apart which interacting partner is acting coercively. Below, we offer examples of two phytohormones used by microbes for the manipulation of plants.

Gibberellins (GA) are a group of phytohormones that regulate growth and developmental processes in plants such as germination, senescence, and flowering (Sun 2010). GA were first discovered by Kurosawa (1926) in the fungal pathogen *Gibberella fujikuroi*. GA production was shown to be a critical factor in the excessive stem elongation in rice plants, known as "foolish seedling syndrome," infected with *G. fujikuroi* and GA levels also positively correlate with virulence of the pathogen (Desjardins et al. 2000). Since GA production might be occurring to increase the total biomass available for exploitation, GA production is likely a coercive method used by microbes to facilitate plant growth.

Ethylene, the well-characterized phytohormone responsible for fruit ripening and numerous other plant processes (Bleecker and Kende 2000 and references therein), is another molecule used in coercive plant-microbe interactions. Some pathogenic bacteria produce a molecule called rhizobitoxine that inhibits the rate limiting enzyme in the metabolic pathway

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

174 responsible for ethylene production in plants (Yasuta et al. 1999) and induces chlorosis in leaf  
175 tissue. Surprisingly, some members of the beneficial group of bacteria known as rhizobia  
176 produce rhizobitoxine (Yuhashi et al. 2000). During symbiotic associations between leguminous  
177 plants and their rhizobial counterparts, the inhibition of ethylene biosynthesis results in a  
178 hypernodulation response (i.e. more nodules are formed on root systems when ethylene is  
179 inhibited) (Penmetsa and Cook 1997). Thus, it appears that the production of rhizobitoxine may  
180 be a coercive act on the part of rhizobial partners; decreased ethylene levels increases the ability  
181 of a particular rhizobial strain to colonize the root system of host likely resulting in a net fitness  
182 gain for that particular strain. Furthermore, rhizobitoxine producers are able to hoard carbon  
183 resources in the form of poly-3-hydroxybutyrate while simultaneously reducing plant growth  
184 (Ratcliff and Denison 2009). The fitness gain at the expense of the host strongly indicates that  
185 this interaction is coercive. Developing an improved framework to understand these complex  
186 associations will allow a greater understanding of the directionality of various communication  
187 mechanisms.

**EVOLUTIONARY OUTCOMES OF COERCION**

Coercive interactions currently observable in plant-microbe systems are merely a  
snapshot along an evolutionary trajectory with a variety of possible outcomes. The very  
existence of these interactions indicates a past evolutionary response by the sender. For example,  
while a random mutation may have initially caused a particular plant to excrete a quorum sensing  
mimic, fitness benefits to that plant favored the proliferation of this mutation, therefore  
increasing the prevalence of this coercive behavior in plant populations over time.

Just as evolution has played a role in the emergence of these interactions, evolution of the interacting organisms also determines the eventual fate of coercive plant-microbe interactions. Scott Phillips et al. (2012) introduced a framework by which coercive interactions either remain coercive, disappear, or transform into signaling through the process of sensory manipulation, which depends on evolution of sender and/or receiver. While the evolution of signals from cues, a process known as ritualization, has recently been explored in the context of plant microbe interactions (van't Padje et al. 2016), sensory manipulation, an alternate pathway for the evolution of signaling that we explore here, has not. Both ritualization and sensory manipulation are shown in Figure 1.

### **Stabilized coercion**

Scott-Phillips et al. (2012) posited that coercive interactions can continue indefinitely under a given set of environmental conditions if there is no net effect of coercion on the fitness of the receiver and therefore no evolutionary pressure to change the receiver's behavior. Though, on the surface, coercion seems to benefit the sender at the expense of the receiver, one can imagine plant-microbe interactions where the net fitness of the receiver is unaffected. Building on real examples from the literature, we propose hypothetical scenarios to examine possible evolutionary outcomes. For example, soil microbes may release a phytohormone that increases a plant's growth rate thereby increasing the exudation of carbon subsidies to the soil environment. This increased growth rate may be advantageous to the plant, allowing it to outcompete neighboring plants for light. By increasing phytohormone levels through coercion, microbes have caused both decreases in plant fitness associated with increased carbon costs belowground and increases in fitness due to the competitive advantages associated with increased height

1  
2  
3 219 aboveground; if these fitness effects balance out over time, and environmental conditions remain  
4  
5  
6 220 relatively stable, coercion will continue.  
7

8 221  
9  
10 222 **Elimination of coercion**  
11

12  
13 223 If the fitness of the receiver is negatively impacted by coercion, then Scott-Phillips et al.  
14  
15 224 (2012) predict that coercion will not continue indefinitely. Rather, evolutionary pressure will  
16  
17 225 favor mutations that change receiver behavior such that the receiver will stop responding to  
18  
19 226 coercive infochemicals. In the aforementioned example of a microbe releasing plant growth  
20  
21 227 promoting phytohormones, we suggested that plant carbon losses associated with increased  
22  
23 228 growth were ameliorated by the competitive advantages associated with increased stem height;  
24  
25 229 were this not the case, one would not expect coercion to last indefinitely. If the coercive  
26  
27 230 infochemical is not identical to the phytohormone that it mimics in the previous example, then  
28  
29 231 slight mutations in the active sites of proteins to which the phytohormone binds that allow the  
30  
31 232 plant to distinguish between the coercive infochemical and the phytohormone may be favored. If  
32  
33 233 the coercive infochemical is not chemically-distinct from the phytohormone it mimics, then the  
34  
35 234 mutations favored would be those that either change downstream responses to the production of  
36  
37 235 said phytohormone, or those that change the hormone itself. Since drastic changes in hormonal  
38  
39 236 pathways may not be possible in every case, coercion may be eliminated in some cases by the  
40  
41 237 extinction of the receiver.  
42  
43  
44  
45  
46  
47  
48  
49

50 238  
51 239 **Sensory manipulation**  
52

53 240 Sensory manipulation is an evolutionary process by which coercion becomes  
54  
55 241 communication (Figure 1). Scott-Phillips et al. (2012) constructed an evolutionary model to  
56  
57  
58  
59  
60

show that a coercive interaction turns communicative (i.e. a coercive infochemical becomes a signal) only if the receiver's response to coercion has a fitness benefit for the receiver; if the receiver's response has neutral or negative fitness effects, the coercive interaction will either stabilize or disappear over evolutionary time.

A possible example of this can be found in microbially-secreted phytohormones. The auxin, indole-3-acetic acid (IAA) is one of the most-studied microbially-derived phytohormones. Auxins are the primary regulators of plant growth and production of IAA has been shown to significantly increase root biomass in associated plants. Studies conducted on *Klebsiella planticola*, a representative plant growth promoting rhizobacterium, show that secretion of IAA in the presence of plants improves germination, root growth, and robustness to environmental factors (Binkov et al. 2013). The improvement of these traits specifically benefits the associated rhizobacteria. Additionally, the gall-forming plant pathogen, *Agrobacterium tumefaciens*, releases IAA during the infection process; this activity has been strongly correlated with increased virulence (Morris 1986). Research shows that IAA production by microbes is generally used to modulate plant growth. Pathogenic interactions should serve as reminders that this act is not altruistic on the side of the microbe and thus represents a coercive interaction. However, when additional information is considered, it is apparent that IAA biosynthesis by microbes represents only half of a communication system used by plants and microbes (Lambrecht et al. 2000). It has been shown that the root secretion of L-tryptophan results in greater production of IAA (Karnwal 2009). Extending this further, it is possible that the two organisms have developed a communication system as a byproduct of previously coercive acts. Thus, what began as coercion may have evolved into a signal and can be categorized as sensory manipulation.

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

264 Developing an improved framework to understand these complex associations will allow a  
265 greater understanding of the directionality of various communication mechanisms.

266 While Scott-Phillips et al. (2012) posit that ritualization, the evolution of signals from  
267 cues (Figure 1), is a more common pathway for the evolution of signaling than sensory  
268 manipulation, this theory is rooted in animal communication rather than plants and microbes.  
269 Since microbes have much faster evolutionary rates than plants, and can act as either sender or  
270 receiver of cues, we argue that sensory manipulation could play a major role in the evolution of  
271 plant-microbe communication. As our previous examples demonstrate, interspecific interactions  
272 are complex and many of their evolutionary histories and trajectories are unknown. We presented  
273 the release of autoinducers by plants and the modulation of phytohormones by microbes as  
274 coercive acts in interspecific interactions between plants and microbes. Given the right  
275 evolutionary pressure, both of these interactions could evolve into signals via sensory  
276 manipulation. Though the aforementioned examples could be stable over evolutionary time,  
277 other forms of signaling may have evolved by similar means. The sensory manipulation process  
278 could provide a functional framework to understand the evolutionary fates of coercive  
279 interactions as well as the evolution of certain signaling mechanisms and defection within  
280 seemingly established relationships.

281  
282 **CONCLUSIONS**

283 Developing an understanding of coercion is critical to forming a complete framework for  
284 the study of plant-microbe interactions, including the evolution of signaling. Here, we show that  
285 two commonly studied plant-microbe interactions, plant manipulation of microbial quorum  
286 sensing and microbial manipulation of plant hormones, are properly categorized as coercive

interactions. Furthermore, currently-observable coercive interactions such as these may meet multiple evolutionary fates: stabilize and remain coercive, destabilize and disappear, or turn into signaling through the process of sensory manipulation. A complete understanding of coercion is required for a comprehensive view of the drivers of plant and microbe behaviors in natural systems, understanding future evolutionary trajectories of currently observable plant-microbe interactions, and past evolutionary histories of plant-microbe signaling. Finally, future investigations should consider sensory manipulation alongside ritualization, the evolution of signals from cues, when delving into the evolutionary history of plant-microbe signaling.

## ACKNOWLEDGEMENTS

Thank you to the members of the Friesen at Michigan State University for their helpful comments on this work. This research was supported by the National Science Foundation under Cooperative Agreement No. DBI-0939454, a fellowship from Michigan State University under the Training Program in Plant Biotechnology for Health and Sustainability (T32-GM110523), and a National Science Foundation grant (DEB 1547024).

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

**REFERENCES**

Adonizio, A. L., Downum, K., Bennett, B. C., and Mathee, K. 2006. Anti-quorum sensing activity of medicinal plants in southern Florida. *Journal of Ethnopharmacology*. 105:427-435.

Annapoorani, A., Umamageswaran, V., Parameswari, R., Pandian, S.K., and Ravi, A.V. 2012. Computational discovery of putative quorum sensing inhibitors against LasR and RhlR receptor proteins of *Pseudomonas aeruginosa*. *J. Comput. Aided Mol. Des.* 26:1067-1077.

Baker, B., Zambryski, P., Staskawicz, B., and Dinesh-Kumar, S.P. 1997. Signaling in Plant-Microbe Interactions. *Science*. 276:726-733

Barto, E.K., Hilker, M., Müller, F., Mohney, B.K., Weidenhamer, J.D., Rillig, M.C. 2012. Fungal superhighways: do common mycorrhizal networks enhance below ground communication? *Trends in Plant Sci.* 17:633-637.

Bassler, B.L. 1999. How bacteria talk to each other: regulation of gene expression by quorum sensing. *Current Opinion in Microbiology*. 2:592-587.

Binkov, E.A., Tsavkelova, E.A., and Selitskaya, O.V. 2013. Auxin Production by the *Klebsiella plenticola* Strain TSKhA-91 and Its Effect on Development of Cucumber (*Cucumis stivus* L.) Seeds. *Microbiology*. 83:531-538



- 327 Bleecker, A.B., Kende, H. 2000. Ethylene: A Gaseous Signal Molecule in Plants. Annual  
328 Review of Cell and Developmental Biology. 16:1-18  
329
- 330 Chancelud, E., and Morel, J.B. 2016. Plant hormones: a fungal point of view. Molc Plant Path.  
331 17:1289-1297.  
332
- 333 Chernin, L.S., Winson, M.K., Thompson, J.M., Haran, S., Bycroft, B.W., Chet, I., Williams, P.,  
334 and Stewart, G.S. Chitinolytic Activity in *Chromobacterium violaceum*: Substrate Analysis and  
335 Regulation by Quorum Sensing. Journal of Bacteriology. 180:4435–4441.  
336
- 337 Corral-Lugo, A., Daddaoua, A., Ortega, A., Espinosa-Urgel, M., and Krell, T. Rosmarinic acid is  
338 a homoserine lactone mimic produced by plants that activates a bacterial quorum-sensing  
339 regulator. Science Signaling. 9:409.  
340
- 341 Danhorn, T., and Fuqua, C. 2007. Biofilm formation by plant-associated bacteria. Annual  
342 Review of Microbiology. 61:401-422.  
343
- 344 Degrassi, G., Devescovi, G., Solis, R., Steindler, L., and Venturi, V. 2007. *Oryza sativa* rice  
345 plants contain molecules that activate different quorum-sensing *N*-acyl homoserine lactone  
346 biosensors and are sensitive to the specific AiiA lactonase. FEMS Microbiology Letters.  
347 269:213-220.  
348

1  
2  
3 349 Desjardins, A.E., Manandhar, G., Plattner, R.D., Maragos, C.M., Shrestha, K., and McCormick,  
4  
5 350 S.P. 2000. Occurrence of *Fusarium* species and mycotoxins in Nepalese maize and wheat and the  
6  
7 351 effect of traditional processing methods on mycotoxin levels. *J Agric Food Chem.* 48:1377–  
8  
9 352 1383.  
10  
11  
12 353  
13  
14 354 Engebrecht, J., and Silverman, M. 1987. Nucleotide sequence of the regulatory locus controlling  
15  
16 355 expression of bacterial genes for bioluminescence. *Nucleic acids research.* 15:10455-10467.  
17  
18 356  
19  
20 357 Gao, M., Teplitski, M., Robinson, J.B., and Bauer, W.D. 2003. Production of substances by  
21  
22 358 *Medicago truncatula* that affect bacterial quorum sensing. *Molecular Plant Microbe Interactions.*  
23  
24 359 16:827-834.  
25  
26 360  
27  
28 361 Glick BR. Modulating Phytohormone Levels. *In Beneficial Plant-Bacterial Interactions*, Edited  
29  
30 362 by Glick BR. Springer International Publishing; 2015:65-96.  
31  
32 363  
33  
34 364 Grandclément, C., Tannières, M., Moréra, S., Dessaux, Y., and Faure, D. 2016. Quorum  
35  
36 365 quenching: role in nature and applied developments. *FEMS Microbiology Reviews.* 40:86-116.  
37  
38 366  
39  
40 367 Hardoim, P.R., van Overbeek, L.S., van Elsas, J.D. 2008. Properties of bacterial endophytes and  
41  
42 368 their proposed role in plant growth. *Trends in Microbiology.* 16:463-471.  
43  
44 369  
45  
46 370 Karnwal, A. 2009. Production of indole acetic acid by fluorescent *Pseudomonas* in the presence  
47  
48 371 of L-tryptophan and rice root exudates. *Journal of Plant Pathology.* 91:61-63.  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

- 372
- 373 Köhler, T., Curty, L.K., Barja, F., van Delden, C., and Pechere, J.C. 2000. Swarming of
- 374 *Pseudomonas aeruginosa* is dependent on cell-to-cell signaling and requires flagella and pili.
- 375 Journal of Bacteriology. 182:5990-5996.
- 376
- 377 Kurosawa, E. 1926. Experimental studies on the nature of the substance excreted by the
- 378 “bakanae” fungus, in Japanese. Trans. Nat. Hist. Soc. Formosa. 16:213-227. [Quoted from
- 379 Phinney (1983)]
- 380
- 381 Lambrecht, M., Okon, Y., Vande Broek, A., Vanderleyden, J. 2000. Indole-3-acetic acid: a
- 382 reciprocal signaling molecule in bacteria-plant interactions. Trends in Microbiology. 8:298-300.
- 383
- 384 Mahmoudi, E., Tarzaban, S., and Khodaygan, P. 2014. Dual behaviour of plants against bacterial
- 385 quorum sensing inhibition or excitation. Journal of Plant Pathology. 96: 295-301.
- 386
- 387 Morris, R.O. 1986. Genes Specifying Auxin and Cytokinin Biosynthesis in Phytopathogens. Ann
- 388 Rev Plant Physio. 37:509-538.
- 389
- 390 Palmer, A.G., Senechal, A.C., Mukherjee, A., Ané, J.M., and Blackwell, H.E. 2014. Plant
- 391 Responses to Bacterial *N*-Acyl L-Homoserine Lactones are Dependent on Enzymatic
- 392 Degradation to L-Homoserine. ACS Chemical Biology. 9: 1834-1845.
- 393

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

394 Penmetsa, R.V., Cook, D.R. 1997. A Legume Ethylene-Insensitive Mutant Hyperinfected by Its  
395 Rhizobial Symbiont. *Science*. 275:527-530.  
396  
397 Perez-Montano, F., Jimenez-Guerrero, I., Contreras Sanchez-Matamoros, R., Lopez-Baena, F.J.,  
398 Ollero, F.J., Rodriguez-Carvajal, M.A., Bellogin, R.A., and Espuny, M.R. Rice and bean AHL-  
399 mimic quorum-sensing signals specifically interfere with the capacity to form biofilms by plant-  
400 associated bacteria. *Res. Microbiol.* 164:749-760.  
401  
402 Rasmussen, H.N., Dixon, K.W., Jersakova, J., Tesitelova, T. 2015. Germination and seedling  
403 establishment in orchids: a complex of requirements. *Ann Bot.* 116:391-402.  
404  
405 Rasmussen, T.B., Bjarnsholt, T., Skindersoe, M.E., Hentzer, M., Kristoffersen, P., K  te, M.,  
406 Nielsen, J., Eberl, L., and Givskov, M. 2005. Screening for Quorum-Sensing Inhibitors (QSI) by  
407 use of a Novel Genetic System, the QSI Selector. *Journal of Bacteriology* 187:1799-1814.  
408  
409 Rasmussen, T.B., and Givskov, M. 2006. Quorum sensing inhibitors: a bargain of effects.  
410 *Microbiology*. 152: 895-904.  
411  
412 Ratcliff, W.C., Denison, R.F. 2009. Rhizobitoxine producers gain more poly-3-hydroxybutyrate  
413 in symbiosis than do competing rhizobia, but reduce plant growth. *International Society for*  
414 *Microbial Ecology* 3:870-872  
415

- 1  
2  
3 416 Redfield, R.J. 2002. Is quorum sensing a side effect of diffusion sensing? Trends in  
4  
5  
6 417 Microbiology. 10:365-370  
7  
8 418  
9  
10 419 Scott-Phillips, T.C. 2008. Defining biological communication. J. Evol. Biol. 21:387-395.  
11  
12 420  
13  
14  
15 421 Scott-Phillips, T.C., Blythe, R.A., Gardner, A., and West, S.A. 2012. How do communication  
16  
17 422 systems emerge? Proc R Soc B. 279:1943-1949.  
18  
19 423  
20  
21  
22 424 Sun T. Gibberellin Signal Transduction in Stem Elongation and Leaf Growth *In Plant*  
23  
24 425 *Hormones: Biosynthesis, Signal Transduction, Action!* Edited by Davies PJ. Springer;  
25  
26 426 2010:308-324.  
27  
28 427  
29  
30  
31 428 Ta, C.A.K., and Arnason, J.T. 2015. Mini Review of Phytochemicals and Plant Taxa with  
32  
33 429 Activity as Biofilm and Quorum Sensing Inhibitors. Molecules. 21:29.  
34  
35 430  
36  
37  
38 431 Teplitski, M., Robinson, J.B., and Bauer, W.D. 2000. Plants Secrete Substances that Mimic  
39  
40 432 Bacterial N-Acyl Homoserine Lactone Signal Activities and Affect Population Density-  
41  
42 433 Dependent Behaviors in Associated Bacteria. Molecular Plant-Microbe Interactions. 13: 637-  
43  
44 434 646.  
45  
46 435  
47  
48  
49 436 Tolmacheva, A.A., Rogozhin, E.A., and Dryabin, D.G. 2014. Antibacterial and quorum sensing  
50  
51 437 regulatory activities of some traditional Eastern-European medicinal plants. Acta Pharm. 64:173-  
52  
53 438 186.  
54  
55  
56  
57  
58  
59  
60

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

439

440 Tsavkelova, E.A., Cherdyntseva, T.A., and Netrusov, A.I. 2005. Auxin Production by Bacteria

441 Associated with Orchid Roots. *Microbiology*. 74:55-62

442

443 van't Padje, A., Whiteside, M.D., and Kiers, E.T. 2016. Signals and cues in the evolution of

444 plant-microbe communication. *Curr Opin in Plant Bio*. 32:47-52.

445

446 Yasuta, T., Satoh, S., Minamisawa, K. 1999. New assay for rhizobitoxine based on inhibition of

447 1-aminocyclopropane-1-carboxylate synthase. *Applied Environmental Microbiology*. 65:849-

448 852

449

450 Yuhashi, K., Ichikawa, N., Ezura, H., Akao, S., Minakawa, Y., Nukui, N., Yasuta, T.,

451 Minamisawa, K. 2000. Rhizobitoxine production by *Bradyrhizobium elkanii* enhances

452 nodulation and competitiveness on *Macroptilium atropurpureum*. *Applied Environmental*

453 *Microbiology*. 66:2658-2663

454

## TABLES

**Table 1.** List of definitions specific to plant-microbe interactions dependent on chemical information. Definitions are largely adapted from Scott-Phillips (2008) and Scott-Phillips et al. (2012). The term “infochemical” was borrowed from Barto et al. (2011).

Term	Definition
<i>Information</i>	a reduction in uncertainty
<i>Infochemical</i>	a biologically-derived molecule that reduces uncertainty
<i>Sender</i>	organism that releases an infochemical
<i>Receiver</i>	organism that detects an infochemical
<i>Cue</i>	any infochemical that (i) affects the behavior of other organisms; (ii) which is effective because the effect (the response) has evolved to be affected by the infochemical; but which (iii) did not evolve because of those effects
<i>Coercive Infochemical</i>	any infochemical that (i) affects the behavior of other organisms; (ii) evolved because of those effects; but (iii) which is effective for some reason other than that the effect has evolved to be affected by the infochemical
<i>Signal</i>	any infochemical that (i) affects the behavior of other organisms; (ii) evolved because of those effects; and (iii) which is effective because the effect (the response) has evolved to be affected by the infochemical
<i>Ritualization</i>	the evolution of signals from preceding cues
<i>Sensory manipulation</i>	the evolution of signals from preceding coercers

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

**FIGURE CAPTIONS**

**Figure 1.** Evolution of signaling in plant-microbe interactions. The left side of the figure shows the process through which signals evolve from cues, known as ritualization. This process was discussed by van't Padje *et al.* [2]. The right side of the figure shows the process through which signals evolve from coercion, known as sensory manipulation. Coercion and sensory manipulation are the focus of this paper.

For Peer Review



