

Have You Heard of Bonnie Bassler?

A Historical Perspective on a Remarkable Career

Clay Fuqua^{*[a]}

Abstract: The area of chemical communication in bacteria has grown explosively since the end of the 20th century. Among a number of key individuals and seminal findings that broke open this area of microbiology, the contributions of Bonnie Bassler and her colleagues are immense and multi-layered. In this short and informal review, I provide

perspective on my own entry into this research field, my introduction to Dr. Bassler and her early findings, followed by the founding of the Bassler lab and the flood of brilliant experimentation and public outreach that has done so much to propel the field of bacterial chemical communication.

1. Introduction: My Entry Into the Field

In the early 1990s, I was a postdoctoral fellow in the laboratory of Stephen C. Winans at Cornell University in Ithaca NY, focused on the biology of the plant pathogenic bacterium *Agrobacterium tumefaciens*. Steve and I were interested in identifying genes required for the acclimation of *A. tumefaciens* to the crown gall tumors that it incites on plants via an interkingdom gene transfer event – we thought of these as “tumor colonization” genes. Little did I know at the time this project was initiated that our studies would lead us headlong into the area of bacterial cell-cell communication and that our work would dovetail with an amazing path of research on the bioluminescent marine vibrios, and through this into the orbit of Bonnie L. Bassler.

Crown gall tumors excrete compounds called opines, unusual metabolites consumed by the infecting bacteria as custom nutrients. Opine synthesis is driven in the infected plant tissues by genes carried on the DNA that is transferred to the plant and integrated into its genome, called the T-DNA.^[1] T-DNA genes also encode production of phytohormones that cause proliferation of the infected plant tissue. In *A. tumefaciens* the T-DNA is carried on the tumor-inducing (Ti) plasmid and much of the interkingdom gene transfer process is driven by virulence (*vir*) genes outside of the T-DNA and also encoded on this plasmid. Additionally, the Ti plasmid carries genes for opine utilization corresponding to the opines produced from the infected tissues. We hypothesized that *A. tumefaciens* would respond to opines, as signals that the tumor was successfully established, and hence initiate a new phase of the infection. Earlier work had shown that opines stimulated expression of their corresponding catabolic genes on the Ti plasmid.^[2] We hypothesized that there are other genes stimulated by opines that remained poorly defined and drove the “tumor colonization” functions we sought.

The most interesting findings from this project however, were related to horizontal transmission of the Ti plasmid itself, not to plants, but to other bacteria. It had been shown years earlier that specific “conjugal” opines stimulated conjugative

transfer of the Ti plasmid to other agrobacteria.^[3] More recent work had identified opine-responsive regulators responsible for control of opine catabolic gene expression.^[2a,4] However, we had also obtained transposon mutants that uncoupled Ti plasmid conjugative transfer from opine control (hyper-conjugative mutants) and the transposon insertions were within previously unrecognized genes, expression of which was stimulated by the presence of opines.^[5] At this time, studies from Alan Kerr and Lian-Hui Zhang at the University of Adelaide in Australia had identified a small metabolite they called “conjugation factor” from *A. tumefaciens* that was distinct from opines.^[6] Findings from multiple labs converged in the early 1990s to reveal that the Ti plasmid conjugation regulatory pathway was strikingly similar to bioluminescence control in *Vibrio fischeri*: (i) the Conjugation Factor was found to be an acylated homoserine lactone autoinducer (*N*-3-oxooctanoyl-L-homoserine lactone, 3-oxo-C8-HSL) chemically related to the *V. fischeri* autoinducer (*N*-3-oxohexanoyl-L-homoserine lactone, 3-oxo-C6-HSL), (ii) the Ti plasmid gene *tral* was found to encode an acylhomoserine lactone (AHL) synthase required for production of the *A. tumefaciens* signal and with sequence similarity to LuxI from *V. fischeri*, and (iii) distal from *tral* on the Ti plasmid was a AHL-responsive transcription factor called TraR with sequence similarity to LuxR from *V. fischeri*.^[5,7] Additionally, the

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hyperconjugative mutant we had identified was found to be in a small gene we called *traM*, that was eventually proven to encode an integral component of the *A. tumefaciens* system, functioning as an anti-activator of TraR.^[8]

2. Connecting to the *Vibrio* Community

The Section of Microbiology at Cornell University had been the home institution for Everett Peter (“Pete”) Greenberg, one of the major figures in *V. fischeri* bioluminescence (*lux*) gene regulation, who had run a productive research program for years at Cornell. Pete Greenberg eventually moved to the University of Iowa (and is now at the University of Washington, Seattle). Shortly after Pete relocated to Iowa, Steve Winans was hired by Cornell for his research on *A. tumefaciens* virulence gene regulation. While at Cornell, Pete Greenberg had maintained a collaborative relationship and strong friendship with another early pioneer of *Vibrio lux* gene regulation, organic chemist Anatol Eberhard. Anatol held a faculty position at Ithaca College, an excellent predominantly undergraduate institution located on the hill across from Cornell University. In addition to other work in the area of *lux* gene regulation, Anatol was best known for determining the chemical structure of the *V. fischeri* autoinducer as *N*-3-oxo-hexanoylhomoserine lactone (3-oxo-C6-HSL) in 1981.^[9] As with any good organic chemist, once Anatol figured out a synthetic scheme for 3-oxo-C6-HSL, he generated a series of analogues, with short and longer acyl chains.^[10] We soon recognized that the *A. tumefaciens* Conjugation Factor was in fact 3-oxo-C8-HSL from the work of Zhang et al.^[7c] With encouragement from Pete, we reached out to Anatol and he kindly provided us concentrated stocks of synthetic 3-oxo-C8-HSL and several other analogues, dissolved in ethyl acetate, that were stored on the shelf in his lab refrigerator. Access to the AHL synthetic stocks greatly accelerated and improved our studies which had prior to this been using crude culture supernatants. In addition, Anatol graciously invited me to spend time in his lab at Ithaca College, performing extractions and learning the basics of AHL synthesis. One of the best parts of spending time in Anatol’s lab was the chance to talk with him informally and to hear his personal insights and perspectives.

3. Have You Heard of Bonnie Bassler?

During this time, I was learning as much about the *Vibrio* systems as I could, and a series of impactful papers were published from Michael Silverman’s lab at the Agouron Institute with a postdoctoral scientist who I did not know at that time named Bonnie Bassler. Silverman had been another major contributor to understanding the molecular genetics of autoinduction in *Vibrio* species, including the identification of the AHL-responsive LuxR transcription factor from *V. fischeri* with Joanne Engebrecht.^[11] The new papers reported elegant molecular genetic analysis of bioluminescence control in *Vibrio harveyi*, an enteric bacterial species of certain fish and a pathogen of shrimp. It was known that *V. harveyi* produced and responded to *N*-3-hydroxy-butanoylhomoserine lactone (3-OH-C4-HSL) but the details were unclear about what enabled this response, and the AHL synthase was unidentified.^[12] It confused me (as well as others) for some time that the LuxR protein identified from *V. harveyi* was not homologous to the LuxR transcriptional activator protein from *V. fischeri* and in fact was thought to be a repressor homologous to TetR.^[13] The Bassler and Silverman studies revealed that there were in fact two parallel systems that regulated bioluminescence in *V. harveyi* in response to two diffusible signals, one was 3-OH-C4-HSL, and there was a second diffusible signal, that remained undefined.^[14] In contrast to the LuxI-LuxR type AHL synthase and cytoplasmic transcription factor pair, LuxL and LuxM (adjacent coding sequences now known to encode a single polypeptide) were required for 3-OH-C4-HSL synthesis and neither sequence was homologous to *V. fischeri* LuxI. Even more surprisingly, the gene required for response to 3-OH-C4-HSL encoded a predicted membrane-associated, two-component sensor kinase, designated LuxN, clearly not homologous to LuxR from *V. fischeri*.^[14] Through further clever genetic detective work Bassler et al. identified the *luxQ* and *luxP* genes as encoding a second transmembrane sensor kinase and a periplasmic binding protein, respectively, required for response to the unidentified signal,^[15] and the *luxO* gene, as a response regulator homologue required for both branches of the pathway to be transduced to bioluminescence control.^[16]

Contemporaneously to these studies by Bassler, Silverman and colleagues, in 1993 Anatol Eberhard attended a Bioluminescence Symposium hosted in Hawaii where Bonnie presented her recent findings on bioluminescence control in *V.*



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harveyi up to that point. Anatol returned back to Ithaca College completely enthused by these results. He asked me, “Have you heard of Bonnie Bassler?”. I had to admit at that point that I did not automatically relate the Bassler name to the work I was reading about in *V. harveyi*. Anatol remained effusive; “She is turning the whole autoinduction field on its head with her work on *V. harveyi* and re-writing the book on how these systems work!”. Anatol described how Bonnie had so cleverly dissected the control pathway and had presented this work so clearly and enthusiastically that she had completely convinced him and everyone else at the conference that these findings were legitimate. “She is brilliant! That young woman is going places!”. In hindsight, I am convinced that Anatol, long-suffering as a researcher focused on the immensely complicated control of bioluminescence in multiple *Vibrio* species, was just delighted to see the puzzle begin to be solved. It helped that Bonnie was also such a compelling, engaging and energetic scientist. I can remember wondering to myself why he was not as enthusiastic about the fascinating system we were defining in *A. tumefaciens*? – but it now seems so obvious. Anatol had seen the future of chemical communication, and its name was Bonnie Bassler (to borrow a phrase from rock critic Jon Landau’s statement after seeing Bruce Springsteen perform). In relatively short order Bonnie moved to set up her own laboratory as an Assistant Professor at Princeton University, the institution where she has remained to the present day.

4. The Concept of Quorum Sensing

Around this same time period, after Pete Greenberg informally learned of our studies in *A. tumefaciens*, he invited Steve Winans to co-author a mini-review in the Journal of Bacteriology on the small number of LuxR-type proteins and their AHL ligands characterized up to that point. As my work in the Winans lab had revealed the LuxR-AHL-type system, Steve and Pete generously invited me to join them as a co-author. In this review we briefly described the understanding at that time of the *V. fischeri* LuxRI system, also alluding to the mysterious differences between it and the *V. harveyi* system.^[17] In describing the other bacteria with possible AHL-based regulatory systems that had been identified including *A. tumefaciens*, *Pseudomonas aeruginosa*, *Erwinia carotovora*, *Rhizobium leguminosarum* and even *Escherichia coli* (all regulating different target functions), we introduced the term “quorum sensing” to describe a general role for these systems in population density-responsive gene regulation. My recollection is that Steve Winans particularly relished this term because the signals that mediated quorum sensing could be described as “quormones”. Publication of this review presaged an explosion of research on bacterial chemical communication, and the term quorum sensing has gained wide adoption, although description of the signals as quormones never quite caught on the same way. It is also now clear that not all of the AHL systems simply impart population density but rather can

reflect a variety of environmental attributes. Even so the term quorum sensing has retained its resonance in the vernacular, even if sometimes its usage may be oversimplified.

5. The Early Bassler Lab and AI-2

The barrage of quorum sensing research that accelerated in the early 1990s has continued for decades and is arguably still underway with many more discoveries and innovations, and many fascinating variations on the basic theme of quorum sensing. A variety of signals are recognized including the AHLs, oligopeptides, gamma-butyrolactones, quinolones, and others. Bonnie Bassler has been at the lead of this wave of research and has become arguably the most prolific and visible spokesperson for this field. This is despite the fact that for years following the recognition that LuxR-LuxI-AHL systems are widespread among Proteobacteria, the two-component based *V. harveyi* quorum sensing system that she so elegantly dissected seemed like an anomaly. However, building on findings that multiple marine *Vibrio* isolates could induce the *V. harveyi* system,^[18] Bassler and colleagues showed that many bacteria, including the major model organisms *Escherichia coli* and *Salmonella typhimurium*, produced a signal that could induce the second *V. harveyi* LuxPQ system, and they designated this signal as autoinducer-2 (AI-2).^[19] The AI-2 signal was less stable than AHLs and resisted chemical identification for some time. Eventually, in a brilliant study in which the LuxP periplasmic binding protein bound to AI-2 was structurally and chemically interrogated, Bassler and colleagues identified the signal as furanosyl borate diester related to ribose and spontaneously derived from 4,5 dihydroxy-2,3 pentanedione (DPD), an excreted intermediate of the methionine salvage pathway driven by utilization of *S*-adenosylmethionine (SAM) as a methyl donor.^[20] Synthesis of the AI-2 signal required a gene that Bassler *et al.* designated *luxS* encoding an enzyme that cleaved ribosylhomocysteine to release homocysteine and DPD.^[20b,21] Different LuxS-harboring AI-2 producing bacteria can produce various DPD derivatives that still function as the AI-2 signal, such as the non-boronated (2*R*,4*S*)-2-methyl-2,3,3,4-tetrahydroxytetrahydrofuran produced in cultures of *S. typhimurium*, spontaneously formed from DPD in the absence of boron.^[22] Strikingly, SAM also serves as a precursor for AHLs.^[23] The observation that many bacteria release AI-2-type signals, prompted Bassler to propose that AI-2 could be considered as a universal bacterial language, or “Bacterial Esperanto”. While the breadth of this conclusion has been questioned (for example, LuxS is absent and AI-2 is not produced by the large Alphaproteobacteria group of which *A. tumefaciens* is a member^[21]) there is no remaining doubt that AI-2 signaling is quite common in the bacterial world.^[24] Thus, the *V. harveyi* quorum sensing “anomaly” is now recognized to be widely conserved and may be more broadly distributed than other forms of quorum sensing. In addition it has become clear that the multiple

signals and complex converging pathway architecture of *V. harveyi* is common among *Vibrio* spp., including *V. fischeri*.^[25]

6. Bassler and Colleagues Switch into High Gear

Bassler and co-workers spent years to lay the groundwork and painstakingly define the quorum sensing regulatory mechanisms in *V. harveyi*, and then extended this work into other vibrios such as the water-borne human pathogen *Vibrio cholerae*. This work generated multiple noteworthy and impactful findings, including a detailed understanding of the multi-pronged quorum sensing phosphorelay systems and the involvement of small regulatory RNAs in *Vibrio* quorum sensing.^[26] It was roughly at this time that the Bassler research program went into high gear, collectively producing a wide range of impactful studies on quorum sensing, and chemical signaling more broadly, in multiple different systems. The Bassler lab has identified several other diffusible signaling systems in the *Vibrio* spp.,^[25] including the *V. cholerae* autoinducer CAI-1, that defined a whole new group of signals categorized as the α -hydroxyketones also found in several other bacteria.^[22,25,27] Collaborations between the Bassler lab and structural biologists, synthetic chemists, microscopists, biophysicists and computational modelers have yielded a wide range of findings with major impacts in multiple areas of the life sciences. Recent work on biofilm formation, including but not limited to its integration with quorum sensing, has set a very high bar for the field.^[28] It would be impossible to summarize the wide range of research productivity from the Bassler lab alone in a single short review, and this is not to mention the many other researchers who have spurred their own research programs from these findings. The number of excellent scientists who have trained in the Bassler lab, contributing to its success, and who have now gone on to populate top positions in academia and industry is truly impressive. It is clear that the legacy of Bonnie Bassler is one of brilliant scientific research, but also of developing some of the best young scientific talent spanning multiple generations.

7. Wider Impacts and Recognition

Bonnie has served the wider science community in multiple capacities including being elected President of the American Society for Microbiology and serving as editor for multiple journals and compendiums on chemical communication. She has also been well recognized by the community through election to most of the major honorific societies for which she is eligible, and garnering multiple prestigious awards, most recently the Wolf Prize in Chemistry. However, one would be quite remiss not to acknowledge Bonnie Bassler's role as an ambassador to the general public for the chemical signaling community, as well as microbiology writ large. Her informative and engaging 2009 TED talk (https://www.ted.com/talks/bonnie_bassler_how_bacteria_talk) has garnered over 3 mil-

lion views, and her many other lectures, appearances and written pieces have added to the exposure for this area of the microbial sciences. The number of students who have been drawn into the field from the TED talk alone is a legion of individuals who might otherwise not appreciate microbiology at all. In addition to the ground-breaking science that Bonnie and her lab members have generated and continue to produce, she is clearly the public face of quorum sensing and related areas and is one of the most recognized microbiologists in general.

So today, when someone asks the question, "Have you heard of Bonnie Bassler?", the answer among most people familiar with science, is almost always "yes". I count myself fortunate to have not only heard of Bonnie Bassler, but to have operated close to her orbit, to have interacted with her multiple times over the years, and to have born witness to so much tremendous science. There are multiple important and influential figures who have contributed to the area of chemical signaling in bacteria, several who are mentioned above, but Bonnie Bassler uniquely stands out for her earthshaking impact on the field even amongst this group of amazing scientists.

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Data Availability Statement

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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REVIEW

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