

From Chemistry to Plant-Microbe Interactions: A Fifty-Year Journey Through Science

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Abstract: This manuscript presents a brief overview of some of the scientific work that I have been involved in during the past 50 or so years. In this period of time, I have moved from the study of Chemistry to Biochemistry to Molecular Biology and Biotechnology to Soil Microbiology to Plant-Microbe Interactions. I have followed a variety of research topics in what may seem to some to be a haphazard fashion. Nevertheless, I have endeavored to mention a number of significant turning points and manuscripts in my career. However, given that my career has been long and focused on a variety of different topics, I am sure that I have omitted some important events and manuscripts.

Keywords: Plant growth-promoting bacteria, Plant-microbe interaction, Scientist' career, Scientist' life

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The Path of a Scientist and the Role of Mentorship

Anyone who studies science and endeavors to be a professional scientist might ask themselves the question, how does one become an effective and successful scientist? To someone just starting out in their career this question may seem a daunting task. Moreover, there is no simple and unique answer to this question. Everyone has to find their own approach to becoming a scientist and answering this question. Nevertheless, it may be fair to say that many, if not most, successful scientists and scholars have trained or interacted with other successful scientists and/or scholars, like scholars of olden times, learning at the feet of their masters. As a consequence of those interactions, the student mentees learn techniques and ways of thinking and problem solving that, when paired with lots of hard work, generally results in a modicum of success for the younger developing scientist. Unfortunately, all too often, many young scientists develop into de facto scientific clones of their mentors; asking the same questions and using the same approaches as their mentors. On the other hand, for young scientists to develop into truly

innovative and creative thinkers whose scientific impacts will last for a long time and open up new ways of thinking and doing things, it is necessary for them to generate their own unique ideas and approaches despite the fact that they might fail from time to time. In this regard, I have always endeavored to be an innovative and creative thinker, however, as described below, my work often hit dead ends and forced me to completely shift gears. While my supervisors/mentors were all good scientists, sometimes the best thing that they did for me was to leave me to figure things out for myself.

Beginnings as a Novice Researcher Without Clear Direction

Following a rather poor undergraduate career plagued by immaturity and a lack of ambition on my part, I eventually obtained a B.Sc. in Chemistry from the City College of New York. I was subsequently pleasantly surprised to be accepted to do graduate work in Chemistry at the relatively new University of Waterloo in 1969. At the time, I had absolutely no experience as an independent researcher, notwithstanding the fact that I had worked previously as a research technician in a hospital laboratory and knew almost nothing about enzyme kinetics and mechanisms (my M.Sc. and Ph.D. thesis topics). I spent the first two years of my graduate studies following an approach that was more or less what my M.Sc. supervisor suggested. In writing my M.Sc. thesis, which took 6 (painful) drafts, prior to the existence of personal computers and word processors, I began to understand how all of the kinetic data that I had collected in the previous two years could be used to better understand how enzymes interacted with various chemical substrates and inhibitors [1,2]. At that time, I developed the idea that the proteolytic enzyme papain (the source of my studies) could bind substrates and inhibitors to their active site in non-conventional ways (i.e., non-productively) [2]. This early work subsequently played an important role many years later helping me to understand the functioning of the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase, a key enzyme used by plant growth-promoting bacteria in facilitating the growth and development of plants. My M.Sc. studies were also important to my thinking regarding designing my Ph.D. studies which included modifying tryptophan residues within the active site of papain that might be involved in the binding of various substrates to the enzyme [3].

Following the completion of my graduate studies and upon my arrival at the University of Toronto in September of 1974 as a naive post-doctoral fellow I was given the task of characterizing the components within a crude *E. coli* cell extract that catalyzed the synthetic reaction between radiolabeled fMet-tRNA and the antibiotic puromycin, with this reaction being a model for peptide bond formation within *E. coli* ribosomes [4]. I spent a few months varying all of the parameters of this reaction with no apparent success until I realized that the key to understanding this ribosome-catalyzed reaction was lowering the concentration of puromycin that was used from 354 μM to 1.2 μM . My graduate training enabled me to understand that this reaction was behaving like a typical enzyme catalyzed reaction so that the lower level of puromycin yielded a much greater effect on the formation of fMet-puromycin, i.e., an enhancement of 18-fold versus an enhancement of 1- to 2-fold in the presence and absence of EF-P (elongation factor P from *E. coli* cell extracts), respectively [4]. Using a double reciprocal plot of the data, it was calculated that the affinity of the ribosomes for puromycin without EF-P was 2.4×10^{-5} M without EF-P and 2.0×10^{-6} M with EF-P. That is, puromycin bound to ribosomes with an affinity approximately 10-times greater in the presence than in the absence of EF-P. I subsequently purified and characterized this new protein synthesis factor



[5,6]. To better understand the role of this new protein synthesis factor, I collaborated with a scientist at the Michigan Cancer Foundation in Detroit and discovered that when different aminoacyl-tRNAs were used instead of puromycin, they responded differently from one another in their rate of forming a peptide bond with fMet-tRNA [7]. Notwithstanding the innovative nature and reproducibility of this work, at the time, scientists working in this field were reluctant to accept that EF-P was separate and distinct from all of the other known protein synthesis factors. However, the data within these manuscripts as well as later studies by others [8] strongly suggested that EF-P probably functions by altering the affinity of the ribosome for various aminoacyl-tRNAs, thus increasing their reactivity as acceptors for the ribosomal peptidyl transferase activity.

Transitions in Scientific Career and Research Focus

Following four years as a post-doctoral fellow at the University of Toronto, I accepted a three-year Research Associate position at the National Research Council of Canada (NRCC) in Ottawa (although I stayed there only one year). At NRCC, I worked in a small lab (just me, a research technician, and the lab director) on bacterial hydrogen production. The assay that we used included an oxygen electrode to monitor hydrogen production from crude extracts of some anaerobic bacteria together with methyl viologen under strongly reducing conditions. We then substituted various polymeric viologens instead of methyl viologen into this reaction and assessed how well they worked [9]. In an effort to better understand the role played by bacterial hydrogenases and to develop an expression vector for other bacterial hydrogenases, I generated a mutant (using traditional chemical mutagenesis) in the *E. coli* outer membrane hydrogenase [10]. At the same time, I purified and characterized the periplasmic hydrogenase from the anaerobic and difficult to grow bacterium *Desulfovibrio desulfuricans* [11]. Leaving NRCC earlier than I had originally anticipated, I subsequently isolated the gene for the *E. coli* membrane-associated hydrogenase [12]. However, in my next position it was impossible to continue working on bacterial hydrogen production.

I spent the next few years working for Canada's first biotechnology company. There I led a small group that developed methods for recombinant DNA technology (then still in its relative infancy), sequencing short chemically synthesized DNA oligomers that were prepared by another group within our company, and using the short DNA oligomers to synthesize whole genes [13-16]. At the time, the key to the technique for the rapid and reliable sequencing of short DNA oligomers lay in the use of DEAE-cellulose filters which were used to remove the excess of radiolabeled ATP, that was used to end label the DNA oligomer, from the labelled oligomer. The labelled DNA oligomer stuck to the filter while the ATP did not. Then the labelled DNA oligomer was eluted from the filter using ammonium bicarbonate. The ammonium bicarbonate was removed from the mixture by diluting the mixture with water prior to lyophilization where both the water and the ammonium bicarbonate were removed [14]. While none of these areas of research were continued when I left the company to take up a faculty position with the University of Waterloo, many of the skills that I learned at this time became the building blocks of my future university research.

In the fall of 1982, a position for someone with experience in recombinant DNA technology, some knowledge of microbiology and the ability to teach modern biotechnology became available within the Department of Biology at the University of Waterloo. Having much of the necessary experience in recombinant DNA technology (skills which were relatively unique at that time) and despite never having formally studied microbiology, following the interview process, I was hired at the rank of Associate Professor. Most new university faculty members, once in their new labs, usually begin their independent research careers following up on the work that they have done as either a graduate student or a postdoctoral fellow. However, given the fact that I had been involved in a range of different projects in several seemingly unrelated fields since completing my Ph.D. I decided to initially focus on two completely new projects, both of which I knew nearly nothing about at the time. However, both projects were based on interesting ideas that I had come across over the years. The first project involved studying C4 plants, where the C4 pathway in plants uses a relatively minor photosynthetic pathway to fix carbon dioxide. This pathway allows C4 plants

to thrive in hot, dry environments with high light intensity because C4 plants are more efficient at photosynthesis than the much more common C3 plants that photosynthesize using a quite different mechanism. These studies focused on the enzyme phosphoenolpyruvate (PEP) carboxylase which binds directly to carbon dioxide (actually bicarbonate) and produces oxaloacetate [17] and were directed toward trying to understand why these plants were photosynthetically more efficient than C3 plants [18-24]. Notwithstanding, a modicum of success achieved by our lab in this endeavor, after some time it became clear to me at the time that I did not have sufficient knowledge of plant physiology and biochemistry to make any real impact on this field.

The second project that I undertook upon joining the Department of Biology at the University of Waterloo was an effort to genetically modify strains of the nitrogen-fixing bacteria *Azotobacter* spp. [25-28] by genetically engineering these strains to express bacterial cellulase genes. This project was predicated on the notion that nitrogen fixation, which is a highly energy intensive process (with ATP as the energy source), might be facilitated if the diazotrophic *Azotobacter* was able to utilize soil cellulose (which is often in plentiful supply) as a carbon and energy source. Unfortunately, in our experience the introduction of foreign DNA into *Azotobacter vinelandii* created a noticeable metabolic load [29,30] in the bacterium which was deleterious to its functioning and ecological competitiveness. On the other hand, this work led to me recognizing that the generation of a metabolic load was a common consequence of introducing foreign DNA into almost any organism, a key factor to bear in mind when utilizing any host organism to produce a target protein [29].

The other component of the *Azotobacter* project was the isolation and characterization of cellulase proteins and genes [31-33]. When this project was initiated relatively little was known about cellulases and their genes, however, over time it became clear that in nature there were a multiplicity of cellulases, functioning in various steps of cellulose breakdown. Some organisms have been found to have several different cellulases, each often with multiple components. However, since it was not our objective to become experts in cellulose degradation and given the abovementioned problem with introducing foreign DNA into *Azotobacter*, it was decided to abandon this line of research.

Concurrent with these projects, I collaborated with chemical engineers at the University of Waterloo on the scale-up of the growth of recombinant microorganisms. These studies included work on the use of mechanical devices to disrupt the cell walls of recombinant bacterial cells [34]; regulation of the expression of cloned genes in *E. coli* [35]; studies of the cross-flow ultrafiltration purification of proteins [36,37]; pulsed-electric-field cross-flow ultrafiltration of proteins [38]; and bioreactor design [39]; and the growth of recombinant organisms [40,41]. Together with my engineering colleagues, a range of unique approaches for the practical growth and harvesting of recombinant *E. coli* cells was developed. In addition, at more or less the same time, I collaborated with a colleague in the Department of Biology in an effort to ascertain whether bacteria, like certain fish and plants, also produced antifreeze proteins as a means of surviving freezing and cold temperatures. Once this was shown to be the case, we then characterized the identified bacterial antifreeze proteins [42-45]. Moreover, during this time, together with my departmental colleague Jack Pasternak, we produced the first edition (and then several subsequent editions) of the textbook "Molecular Biotechnology" published by the American Society for Microbiology [46]. The 6th edition of this, now ~1000-page textbook, was published in 2022. Over the years, this book has been translated into eight other languages; the 7th edition is currently in preparation with a different co-author with the expected publication date of this edition estimated to be mid-2027.

Shift Toward Plant-Microbe Interaction Studies and Their Development

In the early 1990s two separate labs reported isolating bacterial genes for 1-aminocyclopropane-1-carboxylate (ACC) deaminase and then expressing the isolated gene in tomato plants [47,48]. The genetically engineered tomato plants ripened more slowly than non-transformed plants so that these tomatoes could be picked without fear that they would spoil either during shipping or while in the grocery store. I vividly recall hearing a colleague giving a journal club seminar about this exciting

new work (relatively few transgenic plants had been produced prior to that time). I immediately began to wonder why it was that some soil bacteria contained an enzyme that could lower ACC levels and hence ethylene levels, since ACC is the immediate precursor of ethylene in all higher plants but as far as I knew, ACC did not exist in bacteria. What could be the benefit of such an enzyme to the soil bacteria that possessed this activity? At the time our lab possessed several plant growth-promoting bacteria (PGPB), that had been provided to us by a company in western Canada. We had only just started to work with these bacterial strains with our focus being iron metabolism and siderophore production (where siderophores are molecules that bind extremely tightly to the low levels of iron found in many environments), I had hoped to create bacterial siderophore minus mutants of these strains and examine the effect of the siderophore mutants on plant growth and development. However, after hearing about bacterial ACC deaminase I asked one of my grad students to set up an assay for this enzyme and check to see whether any of our bacterial strains had ACC deaminase activity. Fortunately, we found that one of the strains in our possession produced this activity [49]. To prove there was a direct relationship between canola seedling root elongation (our biological assay) and ACC deaminase activity, we created bacterial mutant strains that that lacked ACC deaminase activity and found that these mutant strains could no longer promote plant growth [50,51]. Serendipitously, when the company that had originally provided many of our PGPB strains indicated to us that whatever work we did with those strains was entirely their property, we decided to develop a unique and simple procedure to isolate new PGPB that contain ACC deaminase activity from various soils [52]. Henceforth, any bacterial strains that we isolated and any ideas that we developed using those newly isolated bacterial strains, according to the official policy of the University of Waterloo, would be ours. According to Policy #73 at the University of Waterloo “ownership of intellectual property belongs to the creators”. The policy covers authorship, collaborative work, copyright, patents and data management. This far-reaching policy has resulted in the successful formation of hundreds of spin-off companies whose existence was based on work originally done on the University of Waterloo campus.

The idea of studying the role of ACC deaminase in soil bacteria intrigued us to the point where we completely abandoned trying to isolate bacterial siderophore mutants and focused all of our efforts on characterizing ACC deaminase biochemically, developing a model to better understand the role of this enzyme in soil bacteria [53] and then we began testing the model in various ways. This model, in its simplest terms, starts with soil bacteria binding to plant roots so that the bacteria can take up ACC that is exuded by plants. Synthesis of increased levels of ACC by plants occurs as a consequence of various environmental stresses. The uptake and cleavage of some of the exuded ACC results in the bacteria acting as a sink for plant ACC with the result that the ethylene concentration in plant roots (and eventually throughout the plant) is lowered from what it would have been in the absence of the ACC deaminase. At the same time, bacterially secreted IAA (a very large percentage of ACC deaminase-containing plant growth-promoting bacteria produce and secrete IAA) enters the plant, and together with endogenous plant IAA, increases plant cell elongation and proliferation. The elevated level of IAA within the plant concomitantly increases the transcription of the plant enzyme ACC synthase resulting in the synthesis of an increased amount of ACC and ethylene. The increased level of ethylene feedback inhibits the plant's auxin response factors therefore decreasing the positive growth impacts of the increased IAA. By lowering the ethylene level within the plant, bacterial ACC deaminase (from within the bacterial cytoplasm) relieves the ethylene repression of auxin/IAA response factor synthesis, and therefore indirectly increases plant growth. In this way, increasing ethylene may limit the amount of its own synthesis. Of course, ACC deaminase also lowers the level of ethylene which by itself directly can decrease plant growth (Fig. 1). In concert with the model proposed here, it has been reported that ethylene can inhibit the transport of IAA in various plants. This model, which is largely based on the known effects of ethylene and IAA on plant growth and development, makes some important predictions regarding the functioning of ACC deaminase under various environmental conditions.

Many abiotic and biotic stresses have been found to increase the production of ethylene in most plants and this increased level of ethylene inhibits plant growth and development in addition to the inhibitory effects of the stress per se [54]. Thus, together with other colleagues we began to examine whether ACC deaminase-containing bacteria could decrease some of the deleterious effects of various environmental stresses on the growth and development of plants. All of our initial studies utilized

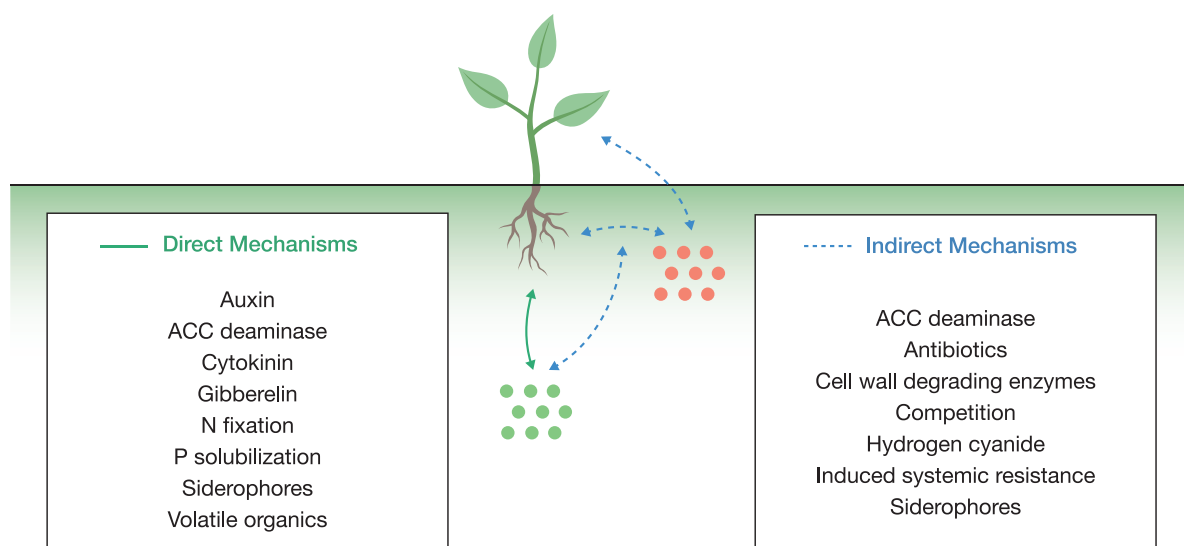


Fig. 1. A schematic of our model explaining the functioning of ACC deaminase.

either canola or tomato, plants that were relatively easy to grow in the laboratory, growth chamber and greenhouse. Most of the studies that we performed with other plants were done in collaboration with others. Since at the time we did not have access to a GC capable of accurately measuring plant ethylene levels, most of these experiments included comparing the behavior of plants treated with bacterial strains that contained ACC deaminase with those that has been genetically engineered to lack this activity [50,51]. We subsequently showed that strains that contained bacterial ACC deaminase could significantly decrease the toxicity of various environmental metals and organic compounds on plants [55-71]. While we did not develop the idea of phytoremediation, i.e. using plants to remove toxins from the environment, we were amongst the first labs to demonstrate that phytoremediation processes could be improved significantly by including ACC deaminase-containing plant growth-promoting bacteria. Moreover, we demonstrated that transgenic plants expressing bacterial ACC deaminase genes were also quite effective in proliferating in metal-contaminated soil in an open field [72,73]. Should phytoremediation eventually become a practical and common means of cleaning the environment, protocols are initially likely to be limited to removing and degrading toxic organic compounds, a process which is significantly facilitated by the presence of ACC deaminase-containing plant growth-promoting bacteria. At the present time, notwithstanding considerable laboratory success, the large-scale environmental cleanup of metals (which are not biodegradable) is beyond our ability to accomplish.

In various environments, a significant portion of the damage to crop plants is a consequence of fungal phytopathogens. Again, in collaboration with others, we were among the first to show that ACC deaminase-containing plant growth-promoting bacteria were able to suppress many of the deleterious effects of fungal and bacterial pathogens [74-78].

In an environment that includes increasing amounts of severe weather worldwide (likely a product of global climate change), several abiotic stresses have had a dramatic negative effect on crop growth and development. These include drought, high levels of salt in many soils, and flooding. Again, in collaboration with several others, we were the first to demonstrate that ACC deaminase-containing plant growth-promoting bacteria were able to confer plants with resistance to both drought and salt stress [79-96]. Of course, there is a limit to the extent that ACC deaminase-containing plant growth-promoting bacteria can improve plant growth under severe stresses of this sort, e.g., ultimately plants cannot grow in the absence of water. Moreover, flooding also significantly stresses plants [97]. Therefore, we have shown that the presence of ACC deaminase-containing plant growth-promoting bacteria or ACC deaminase-containing transgenic plants can help plants to overcome this growth inhibitory stress [76,98,99].

The nodulation of legumes by *Rhizobia* results in the synthesis of a low level of ethylene synthesis within plant roots and this small increase in root ethylene ultimately limits the extent of nodulation by these bacteria [100]. In addition, increased

levels of ethylene in plant roots increase the rate of nodule senescence, thereby limiting the extent of nitrogen fixation that occurs in the nodules [101]. Fortunately, we discovered that strains of *Rhizobia* that contain ACC deaminase activity or the addition of free-living bacteria that synthesize ACC deaminase along with *Rhizobia* strains lacking this enzyme, both increase the extent of legume nodulation by the *Rhizobia* strain and decrease the rate of *Rhizobia* nodule senescence [102-112].

In addition to the abovementioned roles of bacterial ACC deaminase, we observed that ACC deaminase increases the *Agrobacterium tumefaciens*-mediated transformation frequency of commercial canola cultivars [113]. ACC deaminase also facilitates the rooting of plant cuttings [114], increases plant growth and fitness [115-117], increases the rooting of flower cuttings and decreases the wilting of cut flowers [118,119].

Having demonstrated that ACC deaminase could protect plants from a wide variety of stresses and therefore improve plant performance, we became curious as to how ACC deaminase expression was regulated in free living bacteria [120-123]. Following several studies, we developed a detailed model of the regulation of this bacterial gene. This model may be explained as follows [124]. In the first instance, in most ACC deaminase-containing plant growth-promoting bacteria there is both an ACC deaminase structural gene (*acdS*) and an ACC deaminase regulatory gene (*acdR*) (Fig. 2). The *acdR* gene codes for an Lrp protein which in other bacterial systems functions as an octamer. The Lrp protein complex can bind to a short DNA sequence on the bacterial genome known as an LRP box which in this case overlaps the transcriptional promoter for the *acdR* gene thereby preventing further transcription of this gene. Alternatively, the Lrp protein complex can bind to a complex that includes both ACC and the AcdB protein where the AcdB protein is equivalent to glycerophosphoryl diester phosphodiesterase. Subsequently, the complex including Lrp, ACC and AcdB can bind to either of two short sequences on the bacterial genomic DNA i.e., an FNR or CRP box (both of which overlap transcriptional promoters for the *acdS* gene). The binding of the Lrp, ACC and AcdB complex to an FNR box on the DNA is favored under anerobic conditions while binding to a CRP box on the DNA is favored under aerobic conditions. [Keep in mind that many of the soil bacteria that interact with plant roots exist at the interface of aerobic and anaerobic soil.] Following the binding of the Lrp, ACC and AcdB complex to the *acdS* promoter, transcription of *acdS* by bacterial RNA polymerase may occur and ACC deaminase is synthesized. ACC deaminase can cleave ACC to form ammonia

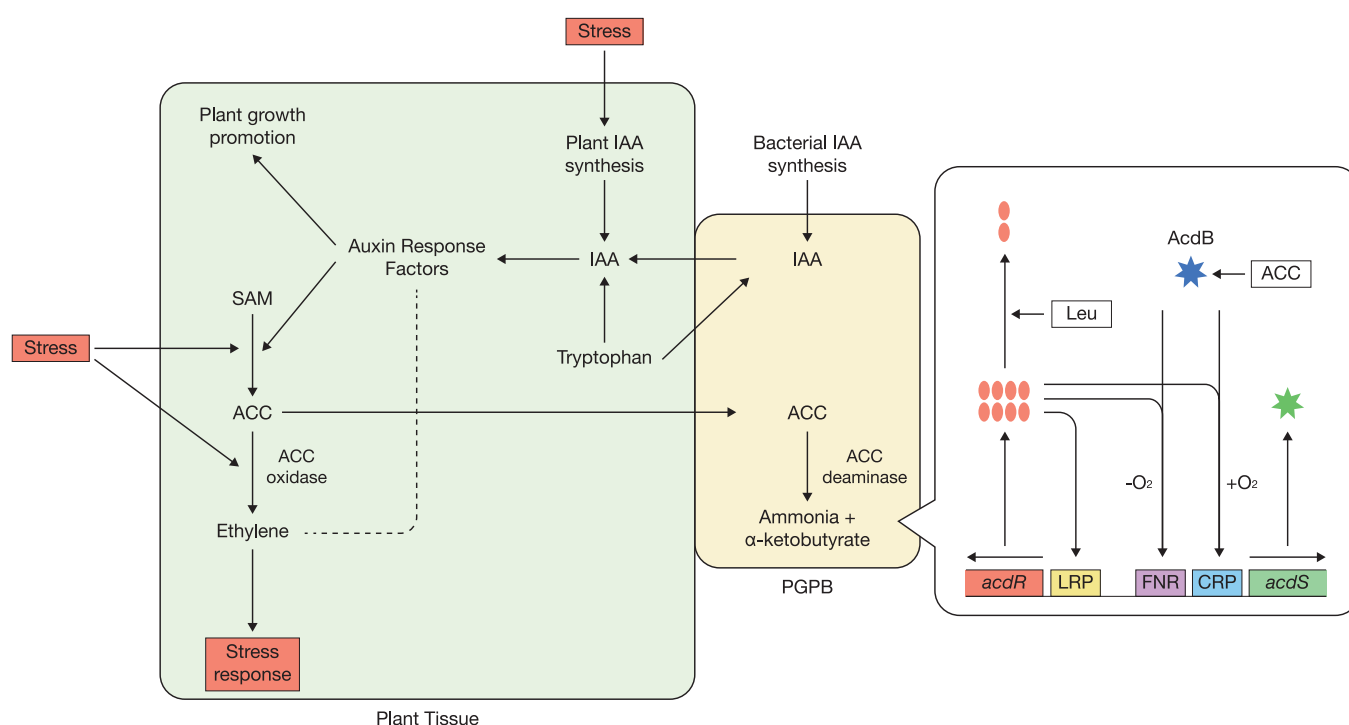


Fig. 2. A schematic of ACC deaminase regulation.

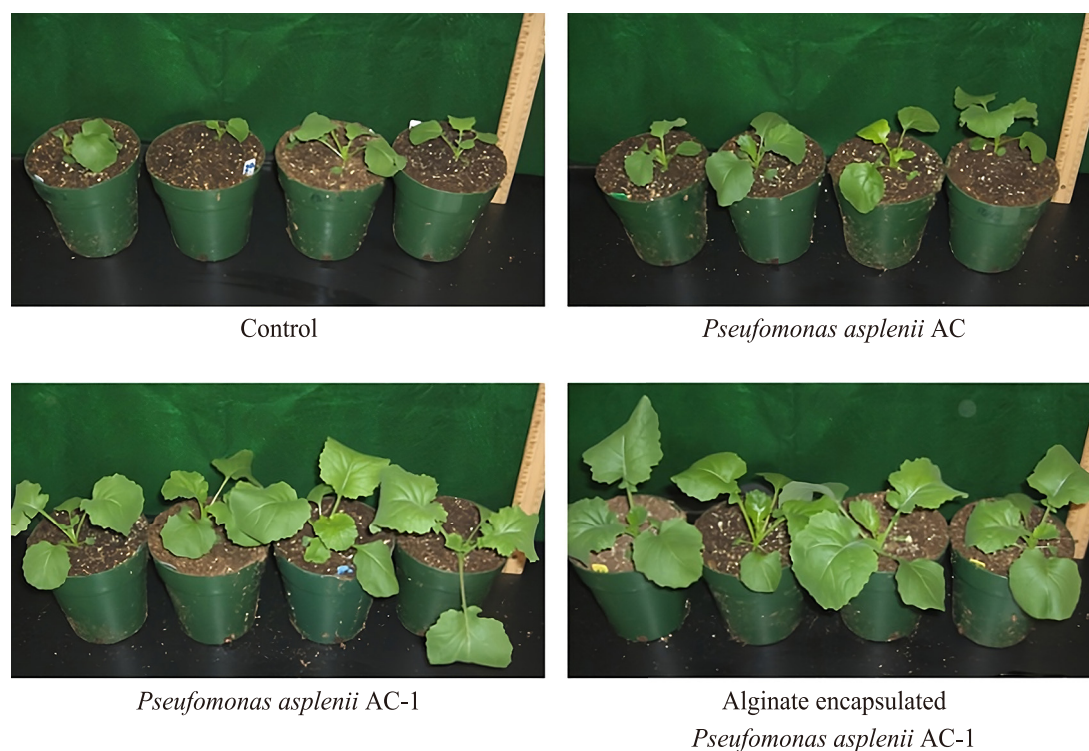


Fig. 3. Photos of the effectiveness of ACC deaminase.

and alpha-ketobutyrate with the alpha-ketobutyrate being a precursor of branched chain amino acids including leucine. In the presence of high levels of leucine within the bacterial cell, the Lrp octamer is dissociated into an inactive dimeric form thereby shutting down further transcription of *acdS*. While the regulatory model described above was worked out for one particular strain of *Pseudomonas* [125], subsequent isolation and characterization of other ACC deaminase-containing plant growth-promoting bacteria in several different laboratories have found that a large number of similarities to the mechanisms described here [126] (Fig. 3).

Prior to obtaining a GC where we could measure ethylene levels in plant tissues directly, our lab was able to gain access to an HPLC so that we could sensitively measure ACC levels in plants and plant tissues. To do this, we assumed since ACC had the structure of an alpha amino acid (albeit not one that could be inserted into proteins) that we could utilize variations of existing HPLC methods to derivatize, separate and then quantitate individual protein amino acids present within amino acid mixtures. In the procedure that we utilized, the amino acid mixture is derivatized using a commercially available fluorescent reagent and then the derivatized amino acids are separated and quantified by reverse phase HPLC. To measure ACC in plant tissues, the tissue was first frozen in liquid nitrogen and then ground by hand in a mortar and pestle, rinsed, centrifuged to remove cell debris and stored at -80°C prior to HPLC analysis (using a variant of the standard gradient so that the modified ACC was well separated from the other components of the mixture). With this system, it was possible to reproducibly measure between 1 and 25 pmol of ACC per 20 microL injection [127]. This technique was subsequently used by us to follow the increasing levels of ACC in canola seed extracts treated with various plant growth-promoting bacteria during seed imbibition [128].

Significance of Research Achievements on Plant–Microbe Interactions

Following some of our laboratory's success in the study of plant bacterial interactions, over the years, our lab began to

attract a large number of highly qualified and motivated graduate students, post-doctoral fellows and visitors with all of these individuals coming both from Canada and internationally. This wealth of bright and hard-working individuals coming to our lab enabled us to expand our focus and examine some side projects in detail. Some of these projects included the following. Since we had previously postulated the involvement of IAA in the promotion of plant growth and development by ACC deaminase-containing plant growth-promoting bacteria, it was clear that a more detailed examination of the role of IAA in plant-bacterial interactions was important to our overall understanding of the major mechanisms used by plant growth-promoting bacteria [129-137]. Briefly, the role of IAA, while consistent with our model, turned out to be rather complex in that many ACC deaminase-containing plant growth-promoting bacteria contained several (sometimes overlapping) biosynthetic pathways for the synthesis of IAA [125].

Based on discussions with various colleagues, we came to the realization that in nature plant roots interacted with a wide range of soil microbes including both bacteria and fungi. Among the beneficial fungi, researchers reported that the roots of the majority of plants interacted with mycorrhizae. Thus, it became clear that it was necessary for us to understand the mechanisms utilized by both plant growth-promoting bacteria and mycorrhizae and how the two types of organisms interact synergistically with one another. Given our lab's lack of knowledge of mycorrhizae, all of these experiments were done together with collaborators [138-142].

While it was not one of our major research objectives, we explored the possibility of commercializing plant growth-promoting bacteria. Following this brief foray into examining breadth of plant growth-promoting activities of various soil bacteria and the possibility of utilizing these bacterial strains instead of chemical fertilizers and soil conditioners, it became clear that notwithstanding the presence of several bacterial strains already in the marketplace, it would likely be many years before soil bacteria would be utilized on a large scale globally [143-146].

Using the then recently developed techniques of proteomics and transcriptomics, again in collaboration with others who had expertise with these techniques, we turned our attention to trying to understand precisely what changes ACC deaminase-containing plant growth-promoting bacteria caused in plants that were treated with microbes both in the absence and presence of several abiotic stresses such as the presence of high levels of salt [147-155].

Most of the thinking about plant growth-promoting bacteria included naively visualizing them as free-living soil bacteria that bound to the roots of plants and from that position effected plant growth. However, this simplistic approach ignored all of the bacteria that exist inside of plants, i.e. bacterial endophytes. Therefore, we began to explore the role those bacterial endophytes played in the life and functioning of plants [156-168]. We also tried to understand what bacterial genes and what plant genes enabled bacteria to live within plant tissues and not harm the plant [169]. Studying various bacterial endophytes, it became clear that these beneficial bacteria utilized more or less the same mechanisms that we and others had studied and elaborated in plant growth-promoting bacteria that bound to the outer surface of a plant's root. In retrospect, it is evident that our work (some of which has been highlighted here) merely scratched the surface of developing a deep understanding of how some soil bacteria facilitate the growth of plants. However, it is reassuring to believe that as we continue to increase our knowledge of precisely how plant growth-promoting bacteria function, the day when these naturally occurring bacteria replace the widespread and environmentally deleterious use of agricultural chemicals will be hastened.

Reflections on a Career as a Researcher

Throughout my career much of the success that our lab has had is attributable to the many bright and hard-working students, post-doctoral fellows and visiting scientists who have spent time working with us. Over the years, our laboratory has hosted 56 graduate students, 18 post-doctoral fellows and 36 visiting scientists plus a number of fourth year honors students as well as some summer students. In addition, throughout my career I have been fortunate to travel extensively, being a visiting professor

in 18 different universities in 14 different countries. I have also taught 11 courses (mostly on various aspects of Molecular Biotechnology) at 7 different universities in 5 different countries. In addition, I have given ~30-40 invited lectures at universities and scientific meetings all over the world. Throughout my travels, I have had an opportunity to meet a large number of students and more established scientists, many of whom have generously shared their thoughts and ideas with me. Moreover, following my official retirement from my faculty position at the University



of Waterloo 9 years ago, I have been fortunate to be able to continue to interact and collaborate with many individual scientists worldwide. My scientific interests have always been quite broad and throughout my career I have always enjoyed learning about the work of others. In addition to science, I enjoy reading novels, photography, attending live theatre productions, visiting museums, and learning about cultures other than my own.

Data Availability: All data are available in the main text or in the Supplementary Information.

Notes: The authors declare no conflict of interest.

Additional Information:

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