Annual Reviews Conversations Presents

An Interview with Govindjee

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Don Ort: Hello. My name is Don Ort. I'm an associate editor of the *Annual Review of Plant Biology*, and I make my living here at University of Illinois, with USDA Photosynthesis Research Service, as well as a faculty member of plant biology. It's really my huge pleasure to be here with my close colleague, and friend for a long time, Professor Govindjee. Govindjee is an emeritus professor in the departments of biochemistry and plant biology, and by any account he's an icon of photosynthesis on this campus and internationally throughout the world.

What I hope, Gov, is that we can spend the next 30 minutes talking about your career. I think that you have lived through some of the really exciting discoveries in photosynthesis and you have participated in them, and a number of them have occurred right here on this University of Illinois campus. Maybe the way that we can start out is: Just talk a little bit about how you got into photosynthesis research. Did you come to graduate school at the University of Illinois with the intent of doing photosynthesis research, or did you get involved once you were here?

Prof. Govindjee: Okay, I will answer you. Well, I became interested in photosynthesis when I was an undergraduate student—undergraduate at the University of Allahabad, India, and there was a botany society, a botanical society as they call it, and I ran a mock symposium on discoveries in photosynthesis, and in that we had Joseph Priestley. We discovered important things—

Don Ort: In the mock symposium.

Prof. Govindjee: —in the mock symposium. There was Otto Warburg, and there was Jan Ingenhousz and even Robert Emerson from the University of Illinois at Urbana-Champaign. So we decided all the kids—and we were students and it was run by the students, for the students—we decided each one of us will take part and somebody would become Emerson. We guessed what they would wear, we guessed how they looked like, and we did a mock symposium and we talked about their discoveries.

Don Ort: So who were you?

Prof. Govindjee: I think I was Robert Emerson; in fact, I kind of forget whether I was Warburg or Emerson—I think I was Emerson. And that went on very well and the kids liked it; well, that was the end of it and we had fun. Then I became a student of a man named Shri Ranjan, who had come from England, studying under Felix Frost Blackman, known for the Blackman reaction in photosynthesis—the dark reaction. So he had come and he said, "You boys"—that's the way he speaks—"You boys, you go to the library and study and tell me what you've found." So I went to the library, and I decided to write a paper, "A Role of Chlorophyll in Photosynthesis." And in that, I studied [Richard M.] Willstätter and many other top people, and I discovered a paper by a man named Robert Emerson: Emerson and [Charlton M.] Lewis's 1943 paper. I was fascinated by that paper because he had discovered a phenomenon called the red drop, and I was just puzzled. And so I wrote to Robert Emerson and said, "Dear Professor Emerson, I would like to work with you to find out about this red drop in photosynthesis." And he wrote back and he said, "Well, Illinois is a flat land; there are no mountains, and you are coming from India"—he thought that I'm from the hills of the Himalayas—"and therefore you may not like it here. However, if you really want to come here, I'll be delighted to help you get admission."

Don Ort: And so what year was that, that you came here?

Prof. Govindjee: 1956. I came here in September in 1956, and I came by train from New York to Urbana.

Don Ort: And so Robert Emerson was here? Who else was here that was involved in photosynthesis research?

Prof. Govindjee: There was Eugene Rabinowitch, a great man, and the two together ran the photosynthesis lab—photosynthesis project, that was called, directly under the graduate college. So that's how I came.

Don Ort: Well I know there's a lot of people fascinated by the fact that you go by just a single name, and in fact Sabeeha Merchant at the university at—UCLA told me just very recently that one of her graduate students got a signed Z-Scheme poster from you. And she saw your single name and said, "Oh, he has only one name. He's like Madonna."

Prof. Govindjee: Yeah, I have. That's happened to me. People have said that.

Don Ort: So I suspect that the reason that you have a single-word moniker is probably somewhat different from the reason that Madonna has.

Prof. Govindjee: Of course.

Don Ort: Can you tell us why yours is just a single—?

Prof. Govindjee: Sure, sure. Well, you see, in India, for some reason there were distinctions between different people. There were four castes; Brahmins were the higher caste. They were the only ones to learn things from books, education; they are the priests to us. So my father, whose name was a very long name, Visheshwar Prashad Asthana. So Asthana was—I don't know how to say it, even, because it was so long ago—was his family name. They, along with many other people, who were mainly educationists, decided, "This is all not good and we must do something about it." So they had a group of—reformist Hindu group who decided, "Let us drop our family names because that indicates our family heritage and therefore the caste we'd come from." So he dropped his family name, Asthana.

Don Ort: Was that before you were born?

Prof. Govindjee: I think so. I never knew that. So what happened: He had Prashad as his middle name, so no problem with him. But the children were not given the middle name. I was given the name Govindjee. So I was left with one name, but nobody bothered until I come here and go to the University of Illinois administration building, and I said, "I have a fellowship. I came on a fellowship, a University of Illinois fellowship and a Fulbright travel grant."

So he says, "What is your name?" I said, "Govindjee." And he says, "Starts with what, G?" I said yes. So he looks; he says, "You have no fellowship." I said, "What do you mean, no fellowship? Here is my paper." And he looks at it: "Oh, Mr. Jee, you are with a J, not with a G!" Because the Govindjee was split in two parts, and so I said, "Sir, I have one name only. That's a mistake; put it together." So [from] that day on, when I arrived here, it became a single name, with Jee part of Govind: so, Govindjee.

Don Ort: And so I suspect this is not the only trouble that you've had having a single name throughout your career.

Prof. Govindjee: Every day I now travel as Govindjee, first-name-unknown Govindjee. I travel as Alana Govindjee. I travel as Govindjee Govindjee, Professor Govindjee, Mister—and I'm in trouble because at the airports these days, your passport must match your ticket, and my passport is Govindjee alone.

Don Ort: And so for the rest of your family, Govindjee has become the family name?

Prof. Govindjee: Yes, and my son, who is a professor at Berkeley, he writes Sanjay Govindjee. My daughter, who works at IBM, writes Anita Govindjee.

Don Ort: So, back to the science. It seems to me that one of the really exciting discoveries that you were involved with you've already brought up, and that is the discovery of two light reactions that—that is, that there are two light reactions in photosynthesis that partner together to oxidize water, work in series, and to reduce NADP and CO_2, and so you lived through all that. And a lot of that happened here at the University of Illinois. You've already brought up one thing, and maybe this is the place to start: the red drop phenomenon.

Prof. Govindjee: Okay.

Don Ort: Is this the place to start?

Prof. Govindjee: Yeah. Sure.

Don Ort: So, tell us what the red drop is and what it meant and what it didn't mean, and when it happened.

Prof. Govindjee: Okay, well, the experiment was done on a green alga, *Chlorella*.

Don Ort: It was done by Emerson?

Prof. Govindjee: By Emerson and Lewis. Lewis was a physicist and Emerson was a biologist, and they did it together—did the work at Stanford [University], Carnegie Institution of Washington. And they started studying the effect of different colors of light on photosynthesis. So, let's say chlorophyll absorbs red light and blue light, so the expectation was that your photosynthesis—rate of photosynthesis is parallel to the absorption of chlorophyll. And so if you divide the oxygen involved by the number of photons of SOD, or intensity as you like to call it, then you should get a flat line because if anything absorbs light it does photosynthesis; therefore, you divide one by the other and should have a flat line.

And that should equal to what we call quantum yield: If you divide the number of oxygen [atoms] by number of photons of SOD, it's the quantum yield, and Emerson and Lewis found—"Oh no! It stops where exactly the peak of absorption in the red of chlorophyll is." It starts dropping.

Don Ort: So the amount of oxygen that you were getting with red light was less than what was expected?

Prof. Govindjee: Beyond 685—-let's say 500 light, 700-nanometer light.

Don Ort: —and so it was called the red drop condition.

Prof. Govindjee: It was called—they didn't understand it at all, and that's why I was puzzled about it. What is it? Why is it? So I asked Emerson. Emerson was puzzled too. But while I was here in Urbana as a student taking courses in physics, chemistry, and math, Emerson was in the darkroom, doing these experiments to find out.

Don Ort: And so that led to Emerson enhancement?

Prof. Govindjee: Exactly.

Don Ort: And so what was that?

Prof. Govindjee: Oh, that was a simple experiment that he did. He said, "Well, if the efficiency is low, can I increase the efficiency by adding another color of light?" So in the green alga *Chlorella*, he had this far-red light, 700-nanometer light, and he measured the rate of oxygen evolution in that light. And then he had 650-nanometer light—which is sort of reddish-orange light, more red—and he measured the rate of oxygen evolution and he got, let's say, two in one and ten in the other. Then he decided to add the two lights together, and instead of 12 he had 15 or 20. Whatever the number was—I don't remember, I just say—

Don Ort: So the two colors of light were more than added together, so it enhances photosynthesis.

Prof. Govindjee: Exactly. So that was the synergistic effect of light, and it was discovered while I was actually totally unaware of the discovery because I was taking all these courses from all these professors at this university here.

Don Ort: And so how did Emerson enhancement and the explanation of the red drop lead to the discovery of these two photo systems operating in series?

Prof. Govindjee: Okay, so what he did is he decided to vary the wavelength of one of the lights. And so he kept the far-red light, the 700-nanometer light, fixed, and let's say the rate was two, and he varied the wavelength of the other light, and then he measured what is called the action spectrum of the effect. And so he found that that spectrum matched that of chlorophyll B in *Chlorella*; it matched that of [unintelligible], another pigment in the diatom—because they're all brown pigments, and like that in the red alga, it matched another pigment, a red pigment called phycoerythrin.

I said, "Aha! What it means is that one reaction is being run by chlorophyll A and another reaction is run by another pigment, and when both are excited you have full photosynthesis." So he got this idea and he presented it in 1958 at a conference which I attended—I was not still doing anything much. So he said, "Two pigment systems, two light reactions must be the reason for this phenomenon."

Don Ort: And so at the same time, as I understand it, there was this controversy going on about the so-called quantum yield of photosynthesis, with some very famous people saying there were four quantum requirements and some very famous people, Emerson, saying it was eight or more. And so the eight would favor two photosystems and the four just a single photosynthesis.

Prof. Govindjee: Absolutely. So the other famous person was Otto Warburg, the Nobel Laureate in 1931 in physiology of medicine, and he was the professor of Robert Emerson in the sense that Emerson got his PhD under Warburg in Berlin. So there was this connection of—student-professor connection, and he has the student finding eight to twelve photons of light needed to get an oxygen and Warburg finding three to four photons. So this was a big controversy in the rate, across the whole world essentially, but the major people who were favoring Warburg was an American named Dean Burk at NIH [National Institutes of Health], and the people who measured what Emerson was measuring was people in Wisconsin.

And so therefore there was this controversy raging, and it was a question: Who was right or wrong? And it is very clear to me that in my PhD thesis—and my wife, who also had her PhD in the same department—was eight to twelve. But then Warburg, when Emerson died, which—we have not discussed that—Warburg started telling people around the world. "Problem is solved," he said. And so Rajni and I—Rajni is my wife—then we made measurements in exactly the identical conditions of Warburg, and Warburg was wrong.

Don Ort: Though Warburg never accepted that, is that correct?

Prof. Govindjee: And Warburg never accepted that. In fact, in 1969 he wrote a paper saying he measured 12 photons per oxygen, but he said it is wrong to calculate it this way. And he invented very complicated means to say that, yes, you see 12, but it is really four."

Don Ort: So something about the eight was the right answer, as it turned out?

Prof. Govindjee: Absolutely.

Don Ort: So I guess the big change in your career was when Emerson died in 1959, and so maybe you could say a little bit about his death and how it changed your career.

Prof. Govindjee: Yeah, well Emerson was a wonderful scientist and wonderful person.

Don Ort: I've seen pictures of him. He was a very tall, big man.

Prof. Govindjee: He was very tall. He was very athletic; he was in the ski club here—not the ski club, the ice skating rink—he was a master there. And he was just—from New England, an easterner for us and the Midwest people—but he was a wonderful person. He took care of us—he even sidetracked it—he even made breakfast on my birthday in the laboratory. This is the kind of person he was. So we were shattered. He died on February 4, 1959, in a plane crash, which went into the East River; he was going to Harvard for a meeting. So we were shattered, and Eugene Rabinowitch, who was a physicist—a physical chemist, really—was the other professor, as we mentioned his name before, and we thought, "We'll go back to India" (we came from India, from Allahabad, as I mentioned before), and he put his hand on my shoulder and said, "Govindjee, Rajni, would you like to be my students?"

And this was surprising because we were biologists, and we didn't accept it instantly and he knew why, so he immediately said, "You don't have to change your thesis topic. You do whatever you wish to do and that will be fine with me." And that's the day when we started asking important questions. That was—Emerson had said chlorophyll B does one reaction; chlorophyll A does the other reaction. Now this ran into total—it was contrary to the work of [L.W.M.] Doysens in the Netherlands, who said every photon going chlorophyll B and sub-100% chlorophyll A, and therefore Emerson could not be right in his explanation of this.

Don Ort: So when chlorophyll B absorbs light it transfers it to A before it does photochemistry?

Prof. Govindjee: Right, that was Doysens' PhD thesis in 1952. And so Emerson's idea ran contrary to it, and I used to discuss this with Emerson going—because we used to walk together, because I lived on Green Street and it was on the way to his house on Main Street. And whenever I said anything, he said, "Govindjee, experiments dictate what I conclude." And I'm listening. So I did the experiment. The experiment was: I ran the action spectrum—the Emerson effect—with 10-nanometer-apart wavelengths. And I discovered that chlorophyll A was in the same system that chlorophyll B was, and so we published the paper in Science. That was my—part of my PhD thesis.

Don Ort: But you didn't publish that with Emerson?

Prof. Govindjee: No! We couldn't. I wanted to put his name—actually, that's the truth—and what happened was: Emerson was so careful, he would not let any paper go out of here unless he had checked every word of it, which means people said, "He will rise from his grave if there's something wrong in your sentences." So we were advised not to put Emerson's name on the paper. It's unfortunate, but that's the way it was. Rabinowitch's name is on the paper.

Don Ort: Very interesting. Very interesting. So let's jump forward a few decades into—another thing that you've spent a fair amount on your career on is the water oxidation process, water being the primary electron donor for photosynthesis. Maybe you can tell us a bit about that. I mean, you got into it a little bit of an odd way?

Prof. Govindjee: Yeah. Well, oxygen evolution, as you just said, is the most important thing. I mean, we are alive because of photosynthesis: oxygen and photosynthesis. So my first interest right away—after everything was solved in the two-pigment system hypothesis, and we did a lot more work than we have more time to speak [about] here, and we discovered light effects in chlorophyll first, and so on and so forth. So I said, "Let us look at [the] oxygen side," and we did many things. We tried to invent a new method, nuclear magnetic resonance [NMR], proton NMR, to look at manganese. We tried to made antibodies against the oxygen evolving. We did so many—we looked at the chloride at work there, with the new method of NMR, again. But none of this seemed to lead us to anywhere except to say, "Okay, yes, there is oxygen evolution, and manganese is changing," and so on and so forth.

Don Ort: And so why was manganese important?

Prof. Govindjee: Well, manganese clearly was shown to be—without manganese, oxygen evolution doesn't take place, and only when you have manganese, then oxygen evolution takes place. So that's why we were interested in manganese. But now what happens is: Again Warburg comes into the picture. Warburg said, "Aha! Oxygen doesn't come from water, but oxygen comes from bicarbonate, from CO_2," so I said, "Oh, that's interesting. That's another way to get into it." Alan Stemler was my PhD student, and so it was decided—actually, he was—

Don Ort: And so this was in the '70s, the 1970s?

Prof. Govindjee: This was in the '70s, yeah, because we have jumped many years. So we decided to look for oxygen evolution through bicarbonate, see if bicarbonate—if Warburg was right here; he was wrong on the quantum yield we just discussed. So we discovered that when bicarbonate is absent—see, the oxygen evolution goes through a clock period, four clock—when the manganese changes, and Bessel Kok had invented some names: S states. It goes through four states. It's like a clock with four periods. So we decided to look at that. We had no machines, so we went to Berkeley—Alan Stemler actually went to Berkeley—and we made the experiment. Lo and behold, there was a big effect on what we call the S states.

Don Ort: So removing bicarbonate stalled the S states?

Prof. Govindjee: It actually made it very slow. So I said, "Oh, that may be." But it turns out that process includes not only the water side but also includes what is called the reducing side of what we called the photo system to—the system that is involved in oxygen evolution. Bessel Kok was the—we sent to the *Proceedings of the National Academy of Sciences* our paper, and Kok was the communicator. And he said, and I agreed with him, "You cannot talk." Then came another student—I will not mention the names of the students because it would take too much time, but they're all there; they're the ones who did all the work. So the other student showed: "Oh, clearly it is like the herbicide. A herbicide like diuron kills the plant by blocking the reducing side of photosynthesis."

Don Ort: And so when you move bicarbonate it mimics the effect of diuron.

Prof. Govindjee: It mimicked the effect of diuron. We said, "Oh, the effect is—" From that day on—it was 1975. Twenty-five years of my life with eight PhD students: We have worked on this process and we have convincingly shown that bicarbonate definitely is needed for the reduction of plastoquinone to plastoquinol. And many experiments—biochemistry, biophysics, molecular biology using site-directed mutagenesis—herbicides, everything clearly puts—and what is now very exciting to me [is] that in Beijing (they were there last summer), at the last photosynthesis congress, Professor [Jian-Ren] Shen from Japan came and presented his new photosystem II structure at 1.9× resolution, and there is clearly a bicarbonate ion sitting on—between these two quinones called QA and QB and there's a nonheme ion in the middle—it's sitting right on the nonheme ion. Therefore—it now makes me very happy that our results are confirmed in a way. And now a new set of experiments certainly are open and I wish I were an assistant professor writing grants and getting on to the [unintelligible] that are near there to mutate them and to study the process. So that's where we are.

Don Ort: So now we know where it is. Do we understand the mechanism by which it interferes or it facilitates electron transfer between QA and QB?

Prof. Govindjee: Yeah, absolutely. Actually, those are my experiments with my PhD students and I didn't describe [them] to you. First of all, it is clear that when you remove the bicarbonate—the protonation means proton movement in the site of the quinone, which is called QB; the second quinone is not there. It disappears. And we did this work in Germany with a friend, Wolfgang Junge, and then we have studied the entire process: what happens with one flash of light, one electron moves, and it gives a second flash of light, second electron moves. This is called two-electron gate, and in 1976 already I discovered that its effect is on the two-electron gate where protons come in. So then there were other students who did very thorough investigations on this, and it's clear that one of the functions is somehow to aid in the protonation of the plastoquinol.

Don Ort: I see.

Prof. Govindjee: But it's still not a proven mechanism, and that's why we need to do more work.

Don Ort: Yeah. Then, well I guess it's for them—for your students in the next generation to do it then, huh?

Prof. Govindjee: Yeah.

Don Ort: Well before we run out of time this afternoon, I'm dying to ask the question: What's the most exciting thing that you've done in photosynthesis research in your career?

Prof. Govindjee: Well, this is a very difficult question to answer.

Don Ort: Well, pick one then.

Prof. Govindjee: Yeah, I will. I tell you—I'll say something here. I say that what really has made me feel—made me play, so to say, with plants is the light that comes out of the plant. I will not talk about much about that, but the light—the plants give off light, they give off what we call fluorescence, and there are many, many things that they do which makes them give off light.

Don Ort: But they give off light—they've absorbed light and they give off some of that light.

Prof. Govindjee: They give some of that light back and there are varied types of light they give back, and I studied that, so my main love with plants is to play with the light that the plants are giving out. But I won't talk about that. I will just tell you one thing that really fascinated me and that is: What is the first step of photosynthesis? See, light is absorbed, as we discussed, and then it is transferred to the various chlorophyll pigments, and then the chemistry takes place. So that is the area that really fascinated me most.

Don Ort: So there's these two kinds of pigments, the antenna pigments, and there's a lot of those, right, and they're funneling—

Prof. Govindjee: —funneling that energy to the reaction center where the actual photochemistry takes place. So the one of the first things I played with was what the mechanism of the energy movement is, and I won't talk about it. We went down to liquid helium temperatures, so room temperature to liquid helium temperature, and we found the mechanism. And then—

Don Ort: And so that was the discovery of Förster energy transfer.

Prof. Govindjee: Förster energy transfer, and we believe that our experiment isn't consistent with that. But that doesn't mean that that's the only mechanism. That's one of the mechanisms. Then the question was where the chemistry starts. That was the first step; that was the most exciting—what's the first step? Is it an excited state of a molecule going to singlet state, what is called the singlet state, or going to the triplet state? Because people used to think that triplet lives long before chemistry starts, but if the process goes to the singlet state, it will be very fast, and if it goes to the triplet state, it will be very slow. So we went to Argonne National Laboratory—

Don Ort: And so what years are we talking about?

Prof. Govindjee: Well now, we started in the '70s. But the actual final result on the oxygen system—because you mentioned the oxidized state with that—was done in the '80s. There we discovered that the—it was 1 to 3 ps—I mean 10^{-12} s—was the charge separation, the chlorophyll—

Don Ort: So after the absorption of light—you got charge separation in 1 to 3 ps after the absorption of light.

Prof. Govindjee: Yeah, actually we're now using the reaction center itself in these experiments, because you see the transferred time of the system is avoided by using the—

Don Ort: Again, you excite right into the chlorophyll—right into the reaction center.

Prof. Govindjee: So 1 to 3 ps was our result. The reason it was so exciting was because another Nobel laureate, George Porter in England, published papers: 20 ps and not 3 ps. And we just had to sit in the meetings and look as if we don't know anything, you know. We are the slow people. But it's proven that 1 to 3 ps is the correct number and that 20 ps was the charge transfer because even in the reaction center there's a charge to it. I mean, not charge-energy transfer, excitation-energy transfer. So they had been measuring the energy-transfer time, and we were measuring the charge. And we could measure the few [unintelligible] is the acceptor of the electron and chlorophyll B at 680 [nm] is the donor. So we measured that and we are very happy and [unintelligible] had a sixtieth birthday, and we went out and celebrated it.

Don Ort: And so by showing it—it was this rapid, you proved. It had to be from a singlet state, not from the longer, triplet state.

Prof. Govindjee: Yeah, but you know it was not even said in the paper, it was so obvious. That was the question that was in my mind, and I felt satisfied. Everybody already believed that it was from the singlet state for many other reasons, but to me this was—personally, to me it was—

Don Ort: So it sounds you've made a bit of your career arguing with the Nobel laureate in photosynthesis. I mean—I think there've been three, right? And so you've argued with two of them. What about [Melvin] Calvin? Did you argue with him?

Prof. Govindjee: No, I argued with Warburg. I argued with Porter. Porter was a very nice person, by the way, wonderful—really a gentleman. No, I'd never argued with Calvin, but I argued with him after his death. He is gone, but another man named Andrew Benson worked with him, and I'm trying to see what Benson did that Calvin didn't recognize.

Don Ort: So you've spent probably the last 10 years dedicating most of your scholarship to the history of photosynthesis, and I think it's fair to say you're the renowned expert in that area in the world right now and probably forever. What kinds of activities do you—have you been doing, do you foresee doing in this arena?

Prof. Govindjee: Well, there are two things I'm doing. One is trying to make sure that people who pass away while I'm alive, they get recognized for their discoveries and their discoveries are put in perspective of the field. That's one thing: doing tributes to people and helping. The other, of course, is photosynthesis education. We're doing that by producing what we call the Z-Scheme of the—two-electron transfer scheme that we talked about, and distributing it free around the world. Even in China we distributed many hundreds of copies, and in India, and we're thinking of sending it to Africa. So that's—I'm helped by a dentist, Dr. [Wilbert] Veit in this—in that game.

But also we're doing books. *Advances in Photosynthesis and Respiration* is now in volume 34, and it's going well. And just one volume is being uploaded: the molecular biologist side of it this month. And another one will be in the overall process next month. So that keeps me—I feel involved, and I feel that I'm doing some service.

Don Ort: Well, Govindjee, you must then also be grateful to Annual Reviews because they're kind of doing the same sort of thing across the whole area of the scholarship that they represent. They're doing these kinds of interviews.

Prof. Govindjee: Absolutely, in fact I feel honored to be asked by Annual Reviews to do this with you because I always looked upon it as something very high up that you perhaps never reach—the stage where you're maybe ask to do this. So I feel really honored that I've been asked by this wonderful, most exciting—I read every one of them, especially the photosynthesis [reviews].

Don Ort: The *Annual Review of Plant Biology*.

Prof. Govindjee: Yes.

Don Ort: Well on behalf of Annual Reviews, I really want to thank you for giving your time and reliving at least this glimpse of your career with us. I hope that people who view this video feel that they've gotten to know you a little bit and have some sense of the evolution of the discovery of the photosynthetic process, and so I thank you very much.

Prof. Govindjee: Oh, thank you, Don.