August 5, 2026

# The 42nd (2026) International Prize for Biology Awarded to Dr. Sharon Rugel Long, Steere-Pfizer Professor of Biological Sciences – Stanford University, USA

On July 10, the Committee on the International Prize for Biology (chaired by Dr. FUJIYOSHI Yoshinori, Specially Appointed Professor, Institute of Science Tokyo) decided to award the 42nd (2026) International Prize for Biology to Dr. Sharon Rugel Long, Steere-Pfizer Professor of Biological Sciences, Department of Biology – Stanford University, USA.

## 1. International Prize for Biology

The International Prize for Biology was established in 1985 (Showa 60) to commemorate the 60th anniversary of the reign of Emperor Showa and his long-standing biological research, while also aiming to promote the biological sciences. The purpose of the Prize is to recognize researchers who have achieved outstanding accomplishments in biological research and made significant contributions to the advancement of science worldwide.

On the occasion of the Prize's 25th anniversary, its scope was expanded to honor His Majesty the Emperor Emeritus for his many years of research in fish taxonomy (gobioid fishes), in recognition of his contributions to the development of the Prize, while further promoting the advancement of the biological sciences.

The Prize, consisting of a certificate, a medal, and a purse of 10-million yen, is given to the recipient together with an Imperial Gift.

## 2. Recipient of the 42nd Prize

Dr. Sharon Rugel Long (born 1951, Steere-Pfizer Professor of Biological Sciences, Department of Biology, Stanford University)

Awarded the 42nd International Prize for Biology in the field of “Biology of Symbiosis (interspecific interactions).” Working within the context of root nodule symbiosis between rhizobia and leguminous plants, Dr. Long elucidated the mechanism by which the symbiotic partners recognize one another through chemical signaling and thereby establish their symbiotic relationship. This discovery established the theoretical basis for how chemical communication between different organisms enables symbiosis with the appropriate partner. The scholarly contribution of her discovery has been profound and is highly regarded as underpinning major advances in the biology of symbiosis.

## 3. Presentation Ceremony and Commemorative Symposium

The presentation ceremony in honor of the Prize recipient will be held around December at The Japan Academy. The date will be announced in due course. Their Imperial Highnesses Crown Prince and Crown Princess Akishino are expected to be present at the ceremony.

To celebrate the award to Dr. Sharon Rugel Long a commemorative symposium for the 42nd International Prize for Biology is planned to be held on December 19th (Sat) and 20th (Sun) in Nara.

# The recipient of the 42nd (2026) International Prize for Biology was announced.

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On July 10, the Committee on the International Prize for Biology (chaired by Dr. FUJIYOSHI Yoshinori, Specially Appointed Professor, Institute of Science Tokyo) decided to award the 42nd (2026) International Prize for Biology to Dr. Sharon Rugel Long, Steere-Pfizer Professor of Biological Sciences, Department of Biology – Stanford University, USA.

## 1. Report on the Process of Selection

The Selection Committee, chaired this year by Dr. TERAKITA Akihisa and composed of 19 members, including three overseas members, functioned under the auspices of the Committee on the International Prize for Biology. The Selection Committee reviewed all of the nominated candidates.

This year, the applicable area of the Prize was stipulated as "Biology of Symbiosis (interspecific interactions)." The committee distributed a total of 1,542 nomination forms to various Japanese and overseas universities and institutions engaged in the subject field of Biology. In response, the committee received a total of 56 recommendations. As there was some overlap, the actual number of individuals recommended was 37, residing in 17 countries and regions throughout the world.

The Selection Committee carefully reviewed all the candidates through a total of five times screening process. Ultimately, the members decided to recommend Dr. Sharon Rugel Long, as the recipient of the 2026 International Prize for Biology. Based on the recommendation of the Selection Committee, the Committee on the International Prize for Biology decided at its July 10 meeting to select Dr. Long as the recipient for the 2026 Prize.

## 2. Recipient of the 42nd Prize

Name: Dr. Sharon Rugel Long

Year of Birth: 1951

Nationality: United States of America

Position: Steere-Pfizer Professor of Biological Sciences,
Department of Biology – Stanford University

Education and Professional Positions:

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|---|---|
| 1973 | Graduated from California Institute of Technology (B.S. with Honors) |
| 1979 | Graduated from Yale University (Ph.D. in Cell and Developmental Biology) |
| 1979–1981 | Postdoctoral Fellow, Harvard University |
| 1982–1992 | Assistant Professor/Associate Professor, Department of Biology, Stanford University |

| | |
|---|---|
| 1992–present | Professor, Department of Biology, Stanford University |
| 1994–2001 | Investigator, Howard Hughes Medical Institute |
| 2000-present | Wm.C.Steere, Jr.-Pfizer, Inc. Professorship in Biological Sciences, Stanford University |
| 2001–2007 | Dean, School of Humanities and Sciences, Stanford University |
| 2018–present | Co-founder and Scientific Advisory Board Chair, ExoPolymer, Inc. |

Main Awards and Distinctions:

| | |
|---|---|
| 1984 | NSF Presidential Young Investigator Award |
| 1988, 1992 | Dean's Award for Teaching Excellence, Stanford University |
| 1992–1997 | MacArthur Fellowship, Ellen MacArthur Foundation |
| 1993–present | Member, National Academy of Sciences |
| 1994 | Fellow, American Academy of Arts and Sciences |
| 1997–2000 | Bing Teaching Fellow, Stanford University |
| 1998 | INRA George Morel Memorial Fellowship |
| 1998 | Distinguished Alumni Award, California Institute of Technology |
| 1999 | Fellow, Association for Women in Science |
| 2000 | Fellow, American Philosophical Society |
| 2002 | Wilbur Cross Medal, Yale University |
| 2007 | Fellow, American Society of Plant Biologists |
| 2016 | Lifetime Research Award, International Society for Molecular Plant-Microbe Interactions |
| 2019 | Selman A. Waksman Award in Microbiology, National Academy of Sciences |

## 3. Achievements Recognized by the Award

Dr. Sharon Rugel Long, Professor of Biology at Stanford University, USA, elucidated the mechanism by which rhizobia (a group of bacteria that live symbiotically in the roots of leguminous plants) and host plants recognize one another as appropriate partners and establish a relationship known as root nodule symbiosis. Leguminous plants are able to utilize atmospheric nitrogen gas as a nutrient source, even though most organisms cannot use it directly. This capability derives from their symbiotic association with rhizobia, which inhabit root nodules formed on the host plant's roots, fix molecular nitrogen, and supply the fixed nitrogen to the host plant as a source of nitrogen nutrition. This symbiotic relationship exhibits host specificity: Although alfalfa and pea are both leguminous plants, alfalfa rhizobia can establish a symbiotic relationship with alfalfa, whereas they are unable to form symbiosis with pea. When Dr. Long began her research, little was known about the molecular mechanisms by which rhizobia and leguminous plants recognize one another and establish root nodule symbiosis. Through molecular genetics, biochemical, and cell biological studies of both rhizobia and their host plants, Dr. Long elucidated the mechanisms underlying host specificity.

Dr. Long demonstrated that flavonoids secreted by host plant roots induce the expression of the rhizobial *nod* genes required for symbiosis. She also made major contributions to the study of Nod factors, the bacterial signal molecules synthesized by enzymes encoded by *nod* genes, and to the elucidation of their function. For example, luteolin, a flavonoid secreted by alfalfa, induces *nod* gene expression in alfalfa rhizobia, whereas flavonoids secreted by other plants lack this inducing activity. In other words, these findings demonstrated that flavonoids secreted by host plants trigger the synthesis of Nod factors in their rhizobial partners.

Dr. Long also made major contributions to elucidating the effects of Nod factors on host plants. The structure of Nod factors differs among rhizobial species. She discovered that the Nod factors produced by alfalfa rhizobia trigger periodic fluctuations in intracellular calcium ion concentrations (calcium spiking) in the cells of alfalfa roots. By contrast, Nod factors produced by other rhizobial species failed to elicit the same response in alfalfa. These findings demonstrated that the structural specificity of Nod factors governs host specificity by inducing calcium spiking, thereby initiating root nodule symbiosis only with compatible host plants.

Dr. Long demonstrated that the "molecular dialogue" between host plants and rhizobia, mediated by flavonoids and Nod factors, is transduced into calcium spiking within host cells, thereby initiating root nodule symbiosis. Her scholarly contributions are of exceptional significance. In recognition of these achievements, the Selection Committee concluded that Dr. Long is the most deserving recipient in the award field of "Biology of Symbiosis (interspecific interactions)" for the 42nd International Prize for Biology, and decided to confer the Prize upon her.

In addition, Dr. Long has published 158 scientific papers, which have been cited more than 17,000 times (Scopus, as of July 2026). Not only is she an outstanding researcher, but she is also highly esteemed as an educator.

## 4. Presentation Ceremony

The presentation ceremony in honor of the Prize recipient will be held around December at The Japan Academy. The date will be announced in due course. Their Imperial Highnesses Crown Prince and Crown Princess Akishino are expected to be present at the ceremony.

## 5. Commemorative Symposium

To celebrate the award to Dr. Long, a commemorative symposium will be held December 19–20, 2026 in Nara, co-organized by the Nara Institute of Science and Technology and the Japan Society for the Promotion of Science. Presentations on the latest research findings will be given by Dr. Long and other Japanese and international researchers pursuing pioneering work in the field of the biology of symbiosis.

### 6. Dr. Long's Research Achievements and Major Publications

**Research Achievements:**

In the early 1980s, root nodule symbiosis between rhizobia and leguminous plants was known to exhibit strict host specificity, and it had been suggested that its establishment involved a multistage process of genetic regulation; however, the underlying molecular mechanisms remained unclear. Through molecular genetics, biochemical, and cell biological analyses of both rhizobia and host plants, Dr. Sharon Rugel Long focused on the "molecular dialogue" conveyed through chemical signals exchanged between the two and made major contributions to elucidating the mechanisms underlying host specificity and the subsequent molecular mechanisms of root nodule symbiosis.

In 1982, Dr. Long identified the genetic region in rhizobia required for the establishment of root nodule symbiosis and was the first in the world to report the *nod* genes located within this region (Ref. 1). This discovery led to the subsequent identification, by her lab and others, of both the common *nod* genes conserved among rhizobial species and also strain-specific *nod* genes, sparking a fierce race among researchers to elucidate their functions.

In 1985–1986, Dr. Long demonstrated that luteolin, a flavonoid secreted by alfalfa roots, induces the expression of the *nod* genes in alfalfa rhizobia, *Sinorhizobium meliloti* (Refs. 2, 3). This discovery demonstrated the existence of interspecies communication mediated by chemical signals from the host plant to the rhizobium and revealed that host plants actively regulate symbiosis with rhizobia through flavonoid signaling.

Subsequent studies led by Dr. Long demonstrated that the enzymes encoded by the *nod* genes induced by flavonoids synthesize the Nod factor (a rhizobial signaling molecule comprising a chitin-oligosaccharide backbone). In 1990, Dr. Long proposed that the products of the *nodP* and *nodQ* genes, which are involved in host specificity in *Sinorhizobium meliloti*, chemically modify the chitin-oligosaccharide backbone of the Nod factor to generate host-specific Nod factors (Ref. 4). The structural variation in Nod factors correlated with the observation that the Nod factor induces morphological changes, including deformation of root hairs (epidermal cells of roots protruding like hairs) and division of cortical cells that give rise to root nodules, as well as the expression of symbiosis-related genes, but only in compatible host plants.

In 1996, Dr. Long discovered that only host-specific Nod factors induce calcium spiking in the root hair cells of host plants (Ref. 7). She further demonstrated that calcium spiking is absent in certain symbiosis-defective mutant host plants, establishing that calcium spiking is required for the establishment of symbiosis and that the genes responsible for these mutant phenotypes are involved in the induction of calcium spiking. These findings indicated the existence of chemical communication from rhizobia to host plants and showed that this chemical signal is transduced into an intracellular signal in the host through calcium spiking. This discovery became one of the greatest turning points in the history of root nodule symbiosis research. Thereafter, genes regulating symbiosis in host plants came to be classified according to their roles in calcium spiking—either as genes involved in its induction or as downstream components of the calcium signaling pathway—and their identification and functional characterization advanced rapidly.

In addition to the achievements described above, from the late 1990s onward Dr. Long's research group accelerated molecular genetic studies of host plants by developing and making publicly available an expressed gene database for the host plant *Medicago truncatula* (Ref. 8). In 2001, the group also decoded the complete genome sequence of *Sinorhizobium meliloti* (Refs. 10, 11). Building on these genomic resources, Dr. Long developed the world's first GeneChip (a high-density microarray platform for gene expression analysis) incorporating genes from both the host plant and the rhizobium. Analyses using this platform led her to propose that root nodule symbiosis is a developmental program involving extensive reprogramming of gene expression in both symbiotic partners (Ref. 15). Dr. Long subsequently combined the GeneChip platform with symbiosis-defective host plant mutants to identify genes whose DNA was deleted in these mutants, leading to the discovery of the *DMI3* gene, which is essential for root nodule symbiosis (Ref. 14). DMI3 encodes a calcium/calmodulin-dependent protein kinase that is activated by calcium and calmodulin (a calcium-binding protein) and phosphorylates target proteins. Subsequent studies established that DMI3, activated by calcium spiking, functions as a central regulator that activates the downstream signaling pathway required for the establishment of symbiosis.

Root hair cells deformed through rhizobial infection form an infection thread, through which the rhizobia enter and establish residence inside the developing root nodule. In the 2010s, Dr. Long's research group showed that plasma membrane domains containing Nod factor receptors are dispersed across the surface of root hair cells in the absence of rhizobial infection. On the other hand, upon rhizobial infection, these membrane domains reorganize toward the future site of infection thread formation, initiating its formation and thereby promoting the rhizobial infection (Ref. 18).

Dr. Long's research elucidated the initial stages of the process underlying the establishment of root nodule symbiosis. Rhizobia perceive flavonoids released by the host plant and respond by synthesizing host-specific Nod factors, which initiate symbiosis by inducing calcium spiking in the host. In host cells that have received Nod factors, the resulting calcium spiking is transmitted through DMI3 to downstream pathways that regulate symbiosis. In root hair cells, Nod factor-dependent reorganization of plasma membrane domains gives rise to infection thread formation, thereby promoting rhizobial infection. These dynamic mechanisms underlying root nodule symbiosis are now described in numerous textbooks and review articles as the fundamental principles of its establishment.

Dr. Long elucidated the mechanism by which the bidirectional "molecular dialogue" between host plants and rhizobia, mediated by flavonoids and Nod factors, governs the establishment of host-specific root nodule symbiosis. Furthermore, through her discovery of calcium spiking, she revealed a fundamental principle by which chemical communication between different organisms is transduced into intracellular signal transduction, thereby laying the theoretical foundation for root nodule symbiosis research. Her findings have driven progress in the field for several decades and continue to shape the direction of research on plant-microbe interactions today.

**Representative Publications:**

1. S. R. Long, W. J. Buikema and F. M. Ausubel. (1982) Cloning of *Rhizobium meliloti* nodulation genes by direct complementation of Nod-minus mutants. Nature 298:485-488.
2. J. T. Mulligan and S. R. Long. (1985) Induction of *Rhizobium meliloti nodC* expression by plant exudate requires *nodD*. Proc. Natl. Acad. Sci. USA 82:6609-6613.
3. N. K. Peters, J. W. Frost and S. R. Long. (1986) A plant flavone, luteolin, induces expression of *Rhizobium meliloti* nodulation genes. Science 233:977-980.
4. J. Schwedock and S. R. Long. (1990) ATP sulfurylase activity of the *nodP* and *nodQ* gene products of *Rhizobium meliloti*. Nature 348:644-647.
5. D.W. Ehrhardt, E.M. Atkinson and S.R. Long. (1992) Depolarization of alfalfa root hair membrane potential by *Rhizobium meliloti* Nod factors. Science 256: 998-1000. DOI: 10.1126/science.10744524
6. R. F. Fisher and S. R. Long. (1993) Interactions of NodD at the *nod* box: NodD binds to two distinct sites on the same face of the helix and induces a bend in the DNA. J. Mol. Biol. 233:336-348. PMID: 8411148
7. D. W. Ehrhardt, R. Wais, and S. R. Long. (1996) Calcium spiking in plant root hairs responding to *Rhizobium* nodulation signals. Cell 85:673-681.
8. P. A. Covitz, L. S. Smith and S. R. Long. (1998) Expressed sequence tags from a root-hair-enriched *Medicago truncatula* cDNA library. Plant Physiol. 117:1325-1332.
9. V. Oke and S. R. Long. (1999) Bacterial genes induced within the nodule during the *Rhizobium*-legume symbiosis. Molecular Microbiology 32 (4):837-849.
10. F. Galibert, T.M. Finan, S.R. Long, A. Pühler, P. Abola, F. Ampe, F. Barloy-Hubler, M. J. Barnett, A. Becker, P. Boistard, G. Bothe, M. Boutry, L. Bowser, J. Buhrmester, E. Cadieu, D. Capela, P. Chain, A. Cowie, R. W. Davis, S. Dréano, N.A. Federspiel, R.F. Fisher, S. Gloux, T. Godrie, A. Goffeau, B. Golding, J. Gouzy, M. Gurjal, I. Hernandez-Lucas, A. Hong, L. Huizar, R.W. Hyman, T. Jones, D. Kahn, M.L. Kahn, S. Kalman, D.H. Keating, E Kiss, C. Komp, V. Lelaure, D. Masuy, C. Palm, M.C. Peck, T.M Pohl, D. Portetelle, B. Purnelle, U. Ramsperger, R. Surzycki, P. Thébault, M. Vandenbol, F.-J. Vorhölter, S. Weidner, D. H. Wells, K.Wong, K.-C. Yeh, J. Batut. (2001) The composite genome of the legume symbiont *Sinorhizobium meliloti*. Science 293: 668-672. DOI: 10.1126/science.1060966
11. M.J. Barnett, R.F. Fisher, T. Jones, C. Komp, A.P. Abola, F. Barloy-Hubler, L. Bowser, D. Capela, F. Galibert J. Gouzy, M. Gurjal, A. Hong, L. Huizar, R.W. Hyman, D. Kahn, M.L. Kahn, S. Kalman, D.H. Keating, C. Palm, M.C. Peck, R. Surzycki, D.H. Wells, K.-C. Yeh, R.W. Davis, N.A. Federspiel, and S.R. Long. (2001). Nucleotide sequence and predicted functions of the entire *Sinorhizobium meliloti*. pSymA megaplasmid. Proc. Natl. Acad. Sci. USA 98 (17): 9883-9888. doi: 10.1073/pnas.161294798
12. G. E. D. Oldroyd and S. R. Long. (2003) Identification and characterization of NSP2, a gene of

*Medicago truncatula* involved in Nod factor signaling. Plant Physiology 131: 1027-1032.

13. S. L. Shaw, and S. R. Long. (2003) Nod factor elicits two separable calcium responses in *Medicago truncatula* root hair cells. Plant Physiology 131:976-984.
14. R.M. Mitra, C.A.Gleason, A. Edwards, J. Hadfield, J.A.Downie, G.E.D. Oldroyd and S.R. Long (2004). A Ca2+/calmodulin-dependent protein kinase required for symbiotic nodule development: gene identification by transcript-based cloning. Proc. Natl. Acad. Sci. USA 101 (13): 4701-4705.
15. M. J. Barnett, C.J. Toman, R.F. Fisher and S. R. Long. (2004). A dual-genome symbiosis chip for coordinate study of signal exchange and development in a prokaryote-host interaction. Proc. Natl. Acad. Sci. USA 101 (47): 16636-16641.
16. C.G. Starker, A.L. Para-Colmenares, L.S. Smith, R.M. Mitra, and S.R. Long (2006). Nitrogen fixation mutants of *Medicago truncatula* fail to support plant and bacterial symbiotic gene expression. Plant Physiology, 140: 671-680.
17. D. Wang, J. Griffitts, C. Starker, E. Fedorova, E. Limpens, S. Ivanov, T. Bisseling and S. R. Long (2010) A nodule-specific protein secretory pathway required for nitrogen-fixing symbiosis. Science 327: 1126-1129.
18. C.H Haney, B. Riely, D. Tricoli, D.R. Cook, D.W. Ehrhardt and S.R. Long (2011) Symbiotic rhizobia bacteria trigger a change in localization and dynamics of the *Medicago truncatula* receptor kinase LYK3. Plant Cell 23:2774-2787. Online / June 2011/tpc.111.086389.
19. C. Lang and S.R. Long (2015). Transcriptomic and genetic analysis of differentiation in *Sinorhizobium meliloti-Medicago truncatula* nodulation. Molec. Plant-Microbe Interactions 28:856-868 http://dx.doi.org/10.1094/MPMI-12-14-0407-R
20. M.J. Barnett, D. Solow-Cordero, S.R. Long (2019) A high-throughput system to identify inhibitors of *Candidatus* Liberibacter asiaticus transcription regulators. Proc.Nat.Acad.Sci. doi:10.1073/pnas.1905149116