

## Ruth Allen Award

The Ruth Allen Memorial Fund was established in 1965 by means of gifts from the estate of Dr. Ruth Allen through the generosity of her heirs: Sam Emsweller, Mabel Nebel, Hally Sax, and Evangaline Yarwood. The award, consisting of a certificate and income from the invested fund, is given for outstanding contributions to the science of plant pathology.

### Wen-Hsiung Ko



**Dr. W. H. Ko** was born in Chao Chow, Taiwan, in 1939, where he received his B.S. degree at National Taiwan University in 1962. His Ph.D. degree was earned in 1966 from Michigan State University, under the tutelage of Dr. John L. Lockwood. In 1969 Dr. Ko was appointed to the Department of Plant Pathology, University of Hawaii, Beaumont Agricultural Research Center, Hilo, Hawaii, where he currently is a professor. His work has focused on both basic and applied aspects of

*Phytophthora* diseases and species. Dr. Ko has been active in the American Phytopathological Society as associate editor of *PHYTOPATHOLOGY* and as a member of the Biological Control Committee and Soil Microbiology Committee. He is a member of the working group on *Phytophthora* of the ISPP.

Some members of the genus *Phytophthora* are homothallic and are capable of producing oospores by single isolates, where others are heterothallic and require the presence of opposite mating types known as A<sup>1</sup> and A<sup>2</sup> for formation of oospores. Heterothallic

*Phytophthora* are unique in that sexual reproduction occurs in matings between two completely different species, such as *P. infestans* and *P. cinnamomi*. *Trichoderma* and avocado root extract can also induce sexual reproduction in A<sup>2</sup>, but not A<sup>1</sup> isolates of some *Phytophthora* species. These observations suggested the possibility that chemical stimulation rather than hybridization is involved in oospore formation during mating. Since the original suggestion of chemical stimulation by Ashby in 1929, many researchers have attempted, but failed, to detect the presence of stimulatory substances in filtrates of both single and paired cultures.

Dr. Ko has developed a simple but elegant method to demonstrate hormonal regulation of sexual reproduction in three species of heterothallic *Phytophthora*. Both A<sup>1</sup> and A<sup>2</sup> mating types of *P. parasitica*, *P. palmivora*, and *P. cinnamomi* formed oospores by selfing when they were paired with different mating types on opposite sides of polycarbonate membranes. The test organisms did not reach the edge of the membrane, nor did they penetrate the membrane during incubation. This method unequivocally demonstrates the control of sexual reproduction in *Phytophthora* by substances originating in one mating type and reaching the site of activity in the opposite mating type by diffusion through the membrane. The results have since been confirmed with other species of *Phytophthora* using the same polycarbonate membrane method by other researchers in the U.S.A., England,

France, and Australia. The method has broad applicability. It has already been applied to the study of chemical regulation of sexual reproduction in species of *Pythium* and *Choanephora*, and to obtaining oospores of heterothallic isolates of *Phytophthora* for identification.

The sex hormone produced by the  $A^1$  mating type of *Phytophthora*, designated hormone  $\alpha^1$ , can induce sexual reproduction in the  $A^2$  but not the  $A^1$  mating type. On the other hand, sexual reproduction in the  $A^1$  mating type can only be induced by hormone  $\alpha^2$  produced by the  $A^2$  mating type. Both hormones  $\alpha^1$  and  $\alpha^2$  have recently been isolated and partially characterized by Dr. Ko. Sexual reproduction in homothallic *Phytophthora* was also found to be regulated by  $\alpha$  hormones. Dr. Ko's discovery casts doubt on the validity of the concept of heterothallism in *Phytophthora* and reveals a new phenomenon of sexuality in microorganisms.

Based on hormone production and responsiveness to hormones, 16 possible types divided into three groups of chemically regulated sexuality among members of *Phytophthora* are postulated by Dr. Ko. Members of group I (cross-induction = heterothallic) do not produce oospores in single culture. They can either stimulate others to produce oospores or produce oospores themselves when stimulated by the opposite mating type. Members of group II (self-induction = homothallic) are capable of producing oospores in single culture. The fungi belonging to group III (neuter) cannot stimulate others, nor can they be stimulated by others to produce oospores. Five of the 16 predicted sexuality types have been found in various species of *Phytophthora* isolated from nature by Dr. Ko and his associate.

Dr. Ko also discovered that the  $A^1$  and  $A^2$  mating types of *P.*

*parasitica* can be converted to  $A^2$  and  $A^1$ , respectively, during long-term storage and that the  $A^2$  mating type of *P. parasitica* can be converted to the  $A^1$  mating type by the fungicide chloroneb. The mating type changes were found to be reversible. Dr. Ko's discovery casts doubt on the previous interpretation that the  $A^1$  mating type is the homozygous recessive  $aa$  and  $A^2$  is the heterozygous  $Aa$ , because the homozygous recessive character should not segregate. Since both hormone production and hormone reception were changed in all sexual variants, Dr. Ko proposed that production of hormone  $\alpha^1$  and the existence of the hormone  $\alpha^2$  receptor in the  $A^1$  mating type are controlled by two linked genes ( $P^1R^2$ ), and that production of hormone  $\alpha^2$  and the existence of the hormone  $\alpha^1$  receptor in the  $A^2$  mating type are controlled by another linked pair ( $P^2R^1$ ). To account for the reversible conversion of mating types, it is postulated that the transcription of such linked genes is regulated by a repressor which, with one molecular configuration, represses the expression of the  $A^1$  mating type ( $P^1R^2$ ), and that another configuration represses the  $A^2$  type ( $P^2R^1$ ). Based on this hypothesis, aging and chloroneb treatment would have changed the mating type through alteration of the molecular configuration of the repressor. Recently, Dr. Ko and his associates found that the  $A^1$  mating type of *P. parasitica* can be converted by another fungicide, truban, to the  $A^2$  mating type, which in turn can be converted back to the  $A^1$  mating type by chloroneb. This novel sexual phenomenon provides a new tool for studying the regulation of microbial sexuality at the molecular level. The discovery of the initiation of sexual reproduction in a population of a self-sterile species by the transformation of certain individuals to an opposite mating type also reveals a possible evolutionary origin of sex in microorganisms.