Grace Marion Waterhouse

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Phytophthora Systematist and Taxonomist

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Grace Marion Waterhouse, a British mycologist, worked for more than 20 years at the Imperial Mycological Institute (later the Commonwealth Mycological Institute and then the International Mycological Institute) in Kew, England. She was first hired as an assistant editor for the Review of Applied Mycology. She became an expert in the identification of Phytophthora pathogens, and this earned her recognition as an authority on the genus. She is noted for her research on Phytophthora systematics and taxonomy. She gathered together a large collection of Phytophthora cultures and published a compilation of species descriptions from original papers. The well-authenticated and useable keys to species in the genus Phytophthora that she developed are still in use today. Her meticulous work was based on careful observation of the morphological characteristics of the pathogen, including sporangia, sexual reproductive organs, chlamydospores, and hyphal and cultural characteristics. She also developed taxonomic keys to species in the genera Pythium, Entomophthora, and Sclerophthora. She served as president of the British Mycological Society in 1961 and was later elected an honorary member of the society. Waterhouse left a legacy of materials that oomycete biologists still use today.

Grace Marion Waterhouse was the youngest of three children. She had two brothers, who both lived into their early nineties. Her life was long and active and full of challenge, enterprise, and achievement. Born in South-West London, she attended Godolphin School and then Royal Holloway College, one of the women's colleges of the University of London (1924–1927), where she studied botany. After graduation, she spent 12 years in the Botany Department at Royal Holloway College, where the department head, Elizabeth M. Blackwell, stimulated her interest in the genus *Phytophthora*.

In 1939, Waterhouse was awarded an M.Sc. degree based on her studies of *Phytophthora*.

Waterhouse was a student of Blackwell. Blackwell headed the Botany Department of the Royal Holloway College from 1922 to 1949 and trained many stellar mycologists over a 27-year period. The late Kitty Brady (coauthor of this chapter), who became the curator of the National Collection of Yeast Cultures, also trained with Blackwell. The department had boasted three former presidents of the British Mycological Society (BMS), including Helen Gwynne-Vaughan, 1928; Kathleen Sampson, 1938; and Blackwell, 1942. Waterhouse would become the fourth in 1961 (Fig. 1). Blackwell's zest and enthusiasm for fungi were transmitted to many students. Waterhouse learned how to bait water molds from rivers and ponds, how to use good culture techniques, and how to identify *Phytophthora* species. She long remained a supporter of the activities at the college.

One of Waterhouse's first publications was with her mentor, Blackwell, on the invalidity of the genus *Pythiomorpha* (2). They moved isolates previously described in this genus to the genus *Phytophthora*. While at Royal Holloway College, she also conducted a survey of the water molds of the Hogsmill River, a minor tributary of the Thames (8). She collected water samples from the river, used tomatoes as bait to isolate water molds, and described and illustrated species of the genera *Blastocladia*, *Phytophthora*, and *Pythium* and of chytrids (8).

Intending to embark on a teaching career, Waterhouse sought further qualifications by following the B.Sc. course in zoology at Birkbeck College



Figure 1. The Imperial Mycological Institute staff in 1947. Left to right, back row: Mason, unidentified, Wiltshire, Dade, Webster, Ellis, Hughes, and Madelin; and front row: Cross, unidentified, Hills, Waterhouse, Hickman, Macfarlane, and Fuller. (Reprinted, with permission, from Aitchison and Hawksworth [1])

(1937–1941), where she earned first-class honors. Her first teaching post was at Eastbourne (1942–1945), followed by a position at Lincoln Training College. While at Lincoln, she joined the Lincolnshire Naturalists' Union. She would later become the mycological secretary in 1943 and president of the Lincolnshire Naturalists' Union in 1956. She returned to research in the Botany Department at the Royal Holloway College from 1945 to 1946 and continued her studies of the genus *Phytophthora* under the guidance of Blackwell for another year.

In 1946, Waterhouse joined the staff of the Imperial Mycological Institute (IMI) (later the Commonwealth Mycological Institute [CMI] and then the International Mycological Institute) at Kew, where she remained until her retirement (Fig. 2). It was here that she made her most important contributions to plant pathology. The Review of Applied Mycology (RAM), later to be renamed Review of Plant Pathology, had been produced since 1922 by IMI as an abstracting journal to cover the world literature on plant diseases. In the early years, before the use of computers, abstracts were first written at the institute by a team composed mainly of linguists. Abstracts were then checked and edited for scientific content to provide a continuous record of developments in plant pathology. When Waterhouse joined the editorial staff, she became an assistant editor, replacing G. C. Ainsworth, who had gone on to another position. Collin Booth, an IMI employee, reminisced, "The production of the RAM was under the aegis of the director, but the organization and sub-editorial responsibilities were led by Grace Waterhouse and Jean Stamps, who together did most of the abstracting on the ground floor of the Kew buildings 59-61" (1). The houses round the Green were prone to flooding and, on one occasion in 1953, RAM materials, books, and other journals that were stored in the basement of No. 63 had to be salvaged from the ravages of the River Thames.

Jean Stamps (coauthor of this chapter) began working with Waterhouse in 1951. Her early images include "in the bay window of the corner house, No. 61, three figures huddled together in blankets and scarves, booted and mittened, one cuddling a large white cat as a hot-water bottle. Their desks were piled high with books, journals, scribbled manuscripts, and flimsy type-scripts, long galley proofs and packs of index cards, providing a clue to what was going on—production of the abstracting journal in the pre-computer age" (1). Waterhouse, who occupied the room opposite, did much to maintain the high standard and reliability of the RAM, which had long been an essential source of up-to-date information for plant pathologists before the days of computer databases and the Internet.

During the war, when bombs fell in the Kew area, the institute was spared any severe damage, but with air raid warnings and night duties, working conditions were far from ideal. Waterhouse described the postwar conditions of the institute and noted in her reminisces of the IMI that "it was very much after the war and things were rather down at the heel." She was "bequeathed a rather appalling microscope, which someone had quietly

exchanged for the one Ainsworth had left" (1). She used her own microscope during the time she worked at the institute. Eventually a fellow scientist went to a sale of "war loot" and acquired one or two quite good microscopes, including a Leitz, which her technician used.

The institute operated a pathogen identification service. Each mycologist specialized in a particular group of fungi, and isolates and specimens arrived from all over the world (Fig. 3). Waterhouse was charged with the taxonomy and identification of the phycomycetes, a task for which her earlier studies with Blackwell had prepared her well. This group includes many



Figure 2. Top, The Mycological Herbarium building, and **Bottom,** the front door piece of the old Imperial Mycological Institute, Kew Green, as it appeared in 1997.

plant pathogens, among which Phytophthora species are particularly important, causing major diseases of many field and glasshouse crops, ornamentals, plantation crops, and forest trees in many parts of the world. Some Phytophthora species have a wide range of hosts, while others are more specialized. The characteristics and life cycles of individual species are related to their ability to cause different types of infection. Identification to species level was, therefore, essential if the pathologist was to understand the disease and devise effective measures of control. IMI had a pool of plant pathologists in the field in the former British colonies. Samples were sent by the pathologists in the "pool" for identification back at the institute. Brian Wheeler, who worked with Waterhouse, reminisced that "collecting plant diseases in Malta gave me the opportunity to experience the identification service of the Institute at first hand, for all specimens which I collected were sent back to confirm or establish their identity. As ever, Grace Waterhouse enthused over the downy mildews and encouraged me to even greater efforts on oospore material" (1).

The institute's large collections of cultures and herbarium specimens were readily available for comparison, but published keys and other aids to identification were often lacking, out-of-date, or inadequate. Here was a real challenge, which Waterhouse met with great enthusiasm. Over a period of years, Waterhouse developed useful keys to the genus *Phytophthora*. This became her lasting legacy to the science of plant pathology (6,7,9,12,16,17). Waterhouse stated, "There has been a demand for some time that a bold attempt should be made to formulate a key to the known species. It is only when such a key is available that it is possible for workers to assess more precisely the similarities and differences between closely related taxa" (12).



Figure 3. Waterhouse at work in the International Mycological Institute herbarium in Kew. (Reproduced with permission of the British Mycological Society)

It is evident that Waterhouse had interest in the development of a key that would be useful not only for research but for practitioners in the field. "This key is put forward very much as a first effort, to be tested and moulded by use. It is only thus that a more perfect key will eventually emerge" (12). She began by preparing, with E. M. Blackwell, a key to the *Phytophthora* species recorded in the British Isles, which was published by the CMI in 1954 as number 57 in their series *Mycological Papers* (17).

In 1956, she published the first edition of "The genus *Phytophthora*: Diagnoses (or descriptions) and figures from original papers" as *Commonwealth Mycological Institute Miscellaneous Publications 12* (9). A revised edition of "The genus *Phytophthora*..." was published as *Mycological Papers 122* in 1970 (16). These papers contained original species descriptions and drawings for more than 40 *Phytophthora* species.

Mycological Papers 92 was a seminal paper for Waterhouse, entitled "Key to the species of Phytophthora de Bary" (12). She divided the genus into six groups based first on the morphology of the sporangia at their apex (markedly papillate, semipapillate, and nonpapillate) (Fig. 4). Homothallic isolates were then grouped separately from heterothallic ones and isolates were further subdivided by antheridial characteristics (paragynous or amphigynous) (Fig. 5). Those isolates that she considered good species were included in the key and those with inadequate descriptions were listed at the end of the key. She recommended that fresh cultures be used to measure sporangial morphology and said, "It is necessary at the outset to induce sporangial production and zoospore emission in order to make certain that species of Phytophthora (and not Pythium) are being dealt with" (12).

Waterhouse examined either type cultures or authentic isolates from infected hosts to confirm her descriptions and prepared permanent fixed slides. Her collections and slides are archived at CABI Bioscience, in

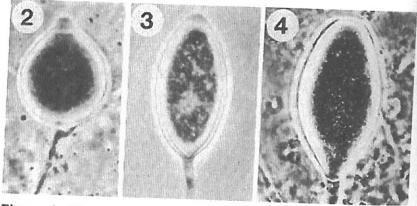


Figure 4. Phytophthora sporangia demonstrating papillate, semi-papillate, and nonpapillate species. (Reprinted, with permission, from Newhook et al. [6])

Egham, England. The importance of Waterhouse's reference collections cannot be overstated. She kept reference cultures and, as they accumulated, she adapted several means of preserving them, including under "oil" (1). Her cultures became part of the IMI Culture Collection, curated by H. A. Dade. Novel and established highly invasive pathogens, such as *Phytophthora ramorum* and *Phytophthora infestans*, still pose a threat to crops and native and planted landscapes around the world. Accurate species identification continues to be a necessary and important endeavor for plant quarantine, regulatory, and research work.

Collaboration with Frank Newhook and Stamps resulted in the publication of a tabular key to *Phytophthora* species, first as *Mycological Papers* 143 in 1978 (6) and revised as *Mycological Papers* 162 in 1990 (7). The tabular key format enabled researchers to use a simplified matrix-based approach to identify species in the genus. The first tabular key contained 48 species, varieties, or forms, and the revised edition listed 67 species. Sporangial, sexual reproductive, and cultural characteristics were entered in three separate tables and the terms used were illustrated by photomicrographs.

Waterhouse also published a key to the genus *Pythium* (14) and diagnoses from original papers (15), both in 1968. *Mycological Papers 148*, a collaboration with M. P. Brothers, dealt with the taxonomy of the genus *Pseudoperonospora* (19). *Commonwealth Mycological Institute Miscellaneous Publications 17* contained diagnoses from original papers and a key to the genus *Sclerospora* (13). With B. L. Brady, she published a key to *Entomophthora* species in the *Bulletin of the British Mycological Society* in 1982 (18). At the institute, she also was involved with other projects begun by S. P. Wiltshire, CMI/IMI director, including *Distribution Maps of Plant Diseases* and *Index of Fungi*.

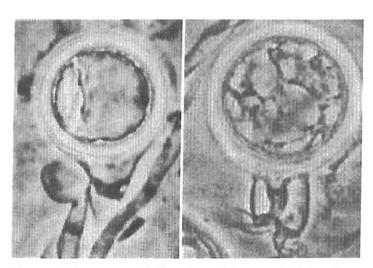


Figure 5. Paragynous (left) and amphigynous (right) antheridia. (Reprinted, with permission, from Newhook et al. [6])

Waterhouse joined the British Mycological Society in 1927 while still a student. She edited the Transactions of the British Mycological Society from 1959 to 1965, was elected president in 1961, and later was named honorary member (Fig. 6). In her presidential address entitled "The zoospore", she discussed the relationship between the parasitic zoospore and its host and the importance of this to the plant pathologist (11). She described in vivid detail the generation of zoospores from sporangia in many oomycete species. She also speculated on the ancestral origin of the species, suggesting, "Other groups with the heterokont, biflagellate type zoospore with one two-sided tinsel flagellum and one whiplash, are the brown algae and the chrysomonads, and it is here, possibly, that one might look for a descendent of a common ancestor" (11). Others, 30 years later, would confirm her hypothesis using molecular data from ribosomal and nuclear genes (3-5). Waterhouse's groups are still used in modern molecular phylogenies of the genus (4). Waterhouse was also a member of the Mycological Society of America (MSA). In fact, she cancelled her membership in the British Automobile Association in order to have funds to join MSA.

Waterhouse showed an interest in many mycological subjects in addition to microfungi. Her presidential address to the Lincolnshire Naturalists' Union in 1956 was on the larger fungi of lawns (10). She was an enthusias-



Figure 6. Grace Waterhouse shown in her presidential photograph in 1961 as president of the British Mycological Society. (Reproduced with permission of the British Mycological Society)

tic field worker and regularly took part in fungus forays. In 1989, she updated and produced with Ainsworth the publication *British County Foray Lists*, which included many fungal lists in addition to county records.

Throughout her career, many mycologists and plant pathologists received the benefit of her experience. Visitors came to the institute from far and wide to work with her and study *Phytophthora* taxonomy. In addition, her clearly identified cultures were used in many laboratories around the world. Through personal contact and correspondence, she made many friends, both in the United Kingdom and abroad. Among them was Eva Sansome (see page 129), another "pioneering woman" plant pathologist who worked on the cytology and genetics of *Phytophthora* species. Long after retirement, Waterhouse was still associated with work in progress all over the world on various aspects of the organisms in her group. She welcomed every opportunity for travel and spent several months in South Africa, working in the Botanical Herbarium at Cape Town. Waterhouse continued her mycological work after retirement and, in 1983, was awarded a D.Sc. degree from the University of London. Her total contribution to plant pathology was enormous.

Waterhouse immensely enjoyed life, contributing to and deriving the maximum from it. Accomplished on the hockey field and tennis court, she was in the college eleven and on the tennis team. She started to ski when she was more than 50 years old. She was an early motorist and continued to drive until the week before the stroke that brought about her death. She was also musical and sang in the choirs at school, college, Lincoln, St. Anne's Church Kew and St. Andrew's Church Ham. A dedicated Christian, she was an enthusiastic member of her local church and took part in all its activities, including a visit to the Holy Land.

She took up beekeeping while teaching and continued to keep hives both at Kew and at Middleton-on-Sea, Sussex, where she had a seaside retreat. Theatergoing, visiting Glyndebourne (the renowned rural opera house), folk dancing, and gardening were among her enthusiasms and, in later years when less active, she borrowed several library books weekly, including her favorite whodunnits.

Waterhouse was a life member of most of the societies she joined, which included the British Mycological Society, the Royal Horticultural Society, the Surrey Wildlife Trust, the Woodland Trust, and the Richmond Scientific Society (president 1966–1967 and 1979–1980). From 1974 to 1991, she was governor and honorary treasurer of the Botanical Research Fund, responsible for the award of small grants to amateur researchers.

Over the years, Grace Waterhouse carried out extensive international correspondence, which continued long after her retirement. Her letters covered a variety of topics and were written to many different people—including sailors studying botany during long voyages at sea. She is remembered as a seminal individual in *Phytophthora* taxonomy with respect, admiration, and affection by her many friends all over the world.

Acknowledgments

The authors dedicate this chapter to the late Kitty Brady who died while the book was in progress. The authors are also grateful to Brian Spooner, head of mycology, and Gill Butterfill at the Royal Botanic Gardens, Kew, and to Leslie Ragab, librarian, at CABI BioScience, United Kingdom, for providing photographs and archival materials on Grace Waterhouse.

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