

(Invited review paper)

## Taiwan *Phytophthora*

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## Introduction

The genus *Phytophthora* (Gr. *Phyton*, a plant; *phthora*, destroyer) was established by de Bary (1876) with *P. infestans* de Bary as the type species. He recognized that the fungus causing late blight of potato in Europe in the 1840's, previously identified as *Botrytis infestans* Montagne, later *Peronospora infestans* (Montagne) Caspary, had unique conidiophore characteristics, which he considered distinct enough to be assigned a new genus name.

Despite earlier controversies over the taxonomic position of *Phytophthora*, it is now accepted as a genus in the family Pythiaceae of the order Peronosporales (Waterhouse, 1973). A fungus can be readily identified as a species of *Phytophthora* by the aseptate hyphae with slight constriction at the base of its initially right-angled branches; by ovoid, obpyriform to limoniform sporangia produced in succession on a typically sympodially branched sporangiophore of indeterminate growth; by differentiation of mature laterally biflagellate zoospores within the sporangium proper; by its globose oogonium with single spherical oospore and thin or no periplasm; by antheridial configuration being amphigynous and/or paragynous. But speciation within this genus has always been difficult due to the variability and overlapping of morphological characteristics used in taxonomy. To date, over eighty different species of *Phytophthora* have been described. Most of them are plant pathogens of seed plants and their distribution is world-wide (Zentmyer, 1983), resulting in more than a thousand combinations of host plant and *Phytophthora*, some of which have attained the status of major epidemics (Gregory, 1983). For instance, *P. cinnamomi* Rands attacks over 1000 plant species from 67 countries (Zentmyer, 1983) causing root and collar rot of conifers, (e. g. *Pinus* L., *Abies* Mill., *Cedrus* Loud., *Juniperus* L., *Cupressus* L., *Taxus* L., *Larix* Mill.), broad-leaved trees (e. g. *Eucalyptus* L'Her, *Quercus* L., *Castanea* Mill., *Juglans* L., *Betula* L., *Platanus* L., *Acer* L.), fruit trees (*Persea* L., *Macademia* F. Muell., *Pyrus* L., *Prunus* L., *Ananas* L., *Carica* L.) and ornamental shrubs (e.g. *Camellia* L., *Rhododendron* L., *Calluna* Salisb.). Newhook and Podger (1972) regarded *P. cinnamomi* in Australia and New Zealand forests as "unquestionably the most destructive pathogen ever recorded in native vegetation of this and possibly any

region". *Phytophthora palmivora* (Butl.) Butl. attacks 138 plants like *Theobroma* L., *Hevea* Aubl., *Citrus* L., *Ananas* L. and members of the family Palmaceae by infecting every part of the plant (Chee, 1974). It has been described by Zentmyer (1974) as "one of the most important pathogens of tropical plantation crops". According to Hickman (1958), *P. parasitica* Dast. occurs on members of 72 genera in 42 families of angiosperms, e.g. *Nicotiana* L., *Lycopersicon* Mill., *Gossypium* L., *Citrus* L., *Cucumis* L., and *Capsicum* L.; *P. cactorum* (Leb. & Cohn.) Sohrbet. infects plants belonging to 83 genera in 44 families, causing damping-off of seedlings, root rot, collar and trunk canker as well as leaf and fruit rot of many valuable ornamental shrubs and fruit trees including *Malus* Mill., *Pyrus* L. and *Paeonia* L.. Whereas *P. cinnamomi* is found in temperate to tropical areas, *P. palmivora*, *P. parasitica* (*P. nicotianse* Breda de Haan) and *P. citrophthora* (R. & E. Smith) L. are characteristic of tropical and subtropical regions and *P. infestans*, *P. syringae* (Kleb.) Kleb. and *P. fragariae* Hick. occur more commonly in temperate zones, but the most important factor in *Phytophthora* disease development is high moisture (Hickman, 1958).

The moist oceanic climate and the continuous multiple cropping system on very limited arable land ranging from tropical/subtropical coastal plains to temperate mountainous areas has made Taiwan potentially a hotbed for *Phytophthora* diseases. Information on Taiwan *Phytophthora* is not only important for local agriculture but would be of great interest to *Phytophthora* researchers in other parts of the world. Unfortunately, the study of *Phytophthora* in Taiwan has been sporadic and in many cases, the information was recorded in Chinese or Japanese, published in regional periodicals not readily available to foreign scientists. The purpose of this review is to provide a synopsis of studies on Taiwan *Phytophthora* in light of current global information on this economically important fungal genus.

## Historic Background

The study of *Phytophthora* in Taiwan was initiated more than 70 years ago by Kaneyoshi Sawada. Working for the Formosan (Taiwan) Government Agricultural Experimental Station, Sawada studied *Phytophthora* diseases extensively throughout the island, resulting in numerous publications on this genus between 1911 and 1943. His last publication on *Phytophthora* and

other fungi (Sawada, 1959) was actually compiled by Imazeki *et al.* after his death, based on his notes. Sawada described a total of 22 species of *Phytophthora* attacking various plants in Taiwan, cultivated as well as wild. Waterhouse (1956) includes *P. persica* Sawada in the genus *Phytophthora* and stated that the name was "reported to have been published in Agric. Mag. Formosa, 38, 2, p.95, 1942." I have not been able to locate this species in this or any of Sawada's publications on *Phytophthora*. The epithet "*persica*" was not listed under *Phytophthora* or other fungal genera in Sawada's list of fungi found in Taiwan (Sawada, 1961). Thus *P. persica* must be deleted from the genus *Phytophthora* until its publication in literature can be verified.

Sawada described 16 *Phytophthora* species as new taxa, but one of them, *P. tabacci* Saw. was isolated from tobacco, *Nicotiana tabacum* L. in Honshu, Japan (Sawada, 1927) and is not taken into consideration here. He published exclusively in Japanese in regional periodicals and failed to give English or Latin descriptions of his new species. Subsequently, based on Sawada's original descriptions, Tanaka (1917) and Ito and Tokunaga (1935) provided, respectively, English and Latin diagnosis of some of his new taxa. Ito (1936) further summarized and included most of Sawada's findings of Taiwan *Phytophthora* at that time, as part of his comprehensive study of the mycological flora of Japan. Most of Sawada's new *Phytophthora* species have not been confirmed by later researchers due to the lack or unavailability of type cultures or specimens. Thus Waterhouse (1963) accepted only three of Sawada's sixteen new taxa as good species and rejected the others based almost exclusively on original diagrams and translated, abridged diagnosis or on technicalities governing the validity and legitimacy of published epithets in accordance with the International Code of Botanical Nomenclature.

After Sawada's death, *Phytophthora* research in Taiwan came virtually to a halt. Interest on *Phytophthora* was not resumed until the mid-60's when the impact of *Phytophthora* diseases on some of Taiwan's important fruit crops was finally recognized. Thus Chen (1966) conducted an intensive study on the etiology, epidemic factors and control of pineapple (*Ananas cosmosus* Merr.) rot due to *P. nicotianae*. Beginning around the mid-70's, there was a marked increase of publications on *Phytophthora* diseases. The fruit and root rot of papaya (*Carica papaya* L.) was re-

-investigated in detail and the pathogen was determined as *P. palmivora* (Huang *et al.*, 1976) instead of *P. parasitica* as originally implicated (Sun, 1955) and control measures were developed (Wang and Chien, 1975). Leu and Lee (1976) and Lin and Chang (1982) studied *Phytophthora* blight, root rot and collar rot of passion fruit (*Passiflora edulis* Sims.) due to *P. nicotianae* var. *parasitica* and suggested various methods to control the disease. Severe fruit rot of strawberry, *Fragaria chiloensis* Duch. var. *ananossa* Bail. was also caused by *Phytophthora* spp. including *P. cactorum*, *P. citricola* Saw. and *P. citrophthora* (Kao and Leu, 1979; Chang, 1988). The most exhaustive study of *Phytophthora* disease of fruit crops was done on citrus probably because of its economic importance. Citrus brown rot, gummosis and foot rot were first reported to be caused by *P. citrophthora* (Anonymous, 1944b) or *P. parasitica* (Lo *et al.*, 1952). Lee, from 1966 to 1968, conducted a survey of *Phytophthora* diseases of citrus orchards and nurseries. He found that fibrous root rot or foot rot (gummosis) was caused by *P. parasitica*, *P. palmivora*, *P. citrophthora* and *P. cinnamomi*, bud and leaf blight by *P. parasitica*, *P. palmivora* and *P. citrophthora* whereas brown rot was due to *P. palmivora*, *P. citrophthora*, *P. citricola* and *P. parasitica*. But his results were not published until 1976 by Hsieh on his behalf and Hsieh (1977a,b) himself also confirmed and extended some of Lee's studies. Ann (1980, 1984) completed a comprehensive study on the distribution and mating types of *Phytophthora* spp. in citrus orchards in Taiwan. She found both A<sub>1</sub> and A<sub>2</sub> mating types of *P. parasitica* and *P. palmivora* only from the tropical central and southern counties, *P. citricola* and only A<sub>1</sub> mating type of *P. citrophthora* and *P. cinnamomi* from the subtropical central and northern counties, and they were all pathogenic to sweet oranges, *Citrus sinensis* Osb.

Vegetables are becoming popular crops in Taiwan because of the rapid growth and higher profits. However, vegetables are especially susceptible to soil-borne *Phytophthora* diseases which then came into focus. Peppers (*Capsicum annum* L.) throughout Taiwan suffered serious damages due to *P. capsici* Leon. (Kao and Leu, 1977; Leu and Kao, 1981). Extensive loss of cucumber (*Cucumis sativus* L.) as a result of blight and fruit rot was attributable to *P. drechsleri* Tuck. (Kao and Leu, 1977) or *P. melonis* Kat. (Kao *et al.*, 1982; Lin and Wu, 1985; Chang, 1986). Other major *Phytophthora* diseases include the late blight of tomato (*Lycopersicon es-*

*culentum* Mill.) and potato (*Solanum tuberosum* L.) caused by *P. infestans*, and *Phytophthora* rot of eggplant (*Solanum melongena* L.) by *P. parasitica* and *P. capsici* (Chang, 1983).

Recently, *Phytophthora* diseases also received the close attention of florists due to the high value of cut flowers and flowering plants. Seedlings and young plants are especially susceptible to *Phytophthora* damping-off. The causal agent of damping-off of Rozelle (*Hibiscus sabdariffa* L.) first attributed to *Phytophthora* sp. (Yu, 1975), was determined to be *P. parasitica* (Chang, 1983). Chang (1983) also reported the damping-off of *Gerbera hybrida* Hort. by *P. cryptogea* Peth. & Laff. and *Gypsophila elegans* Bieb. by *P. parasitica*. Ann P.J. (unpublished) noted extensive loss of carnation (*Dianthus caryophyllus* L.) in nurseries and isolated *P. parasitica*, *P. cryptogea* and *P. capsici* from the diseased plants and soil. Serious black (soft) rot of *Phalaenopsis* Blume and other orchids was caused by *P. palmivora* and *P. parasitica* (Chen and Hsieh, 1977a,b; 1978).

### *Phytophthora* Species Found in Taiwan

So far, 35 species of *Phytophthora* have been found in Taiwan but many of Sawada's 15 new species are questionable and the taxonomic status of some of the others is controversial. I have included here only 21 species that are distinct enough based on the information available at this point (Table 1 and Fig. 1). I have re-examined Sawada's collection of *Phytophthora* specimens deposited with the Department of Plant Pathology, National Taiwan University, the type or authentic cultures of a few of Sawada's new species available from the American Type Culture Collection at Rockville, Maryland, and cultures of all *Phytophthora* species hitherto found in Taiwan, except *P. cactorum*, *P. infestans* and *P. vignae* Purss.

#### *P. boehmeriae* Sawada

Described by Sawada (1927) on the leaves of ramie, *Boehmeria nivea* (L.) Guad., this is one of the three Sawada's new taxa accepted by Waterhouse (1963). The type culture (ATCC 60238) is indeed a good species, easily recognized by the production in single culture of abundant oogonia with amphigynous antheridia and broadly ovoid to sub-spherical conspicuously papillate sporangia. Both sporangia and sex organs could be found on Sawada's dried type specimen

although the sporangia on the leaf were mostly obpyriform to broadly ellipsoidal. *Phytophthora boehmeriae* has not been reported again in Taiwan since its original description. In mainland China, *P. boehmeriae* has been reported on cotton (*Gossypium* sp.) (Zhuang, 1981) and paper-mulberry (*Broussonetia papyrifera* L'Her) (Zheng and Lu, 1989a), whereas in other countries, it has been found on *Citrus* spp. and *Pinus* spp. (Gerrettson-Cornell, 1989).

#### *P. cactorum* (Lebert & Cohn) Schroeter

The earliest record of *P. cactorum* was on the leaves of *Boehmeria nivea* in Taipei (Sawada, 1927). Upon re-examination of Sawada's dried specimen of ramie I found conspicuously papillate, broadly ovoid to obpyriform sporangia, sometimes arranged in close sympodia, distinctive of this species.

Recently, *P. cactorum* drew the attention of plant pathologists in Taiwan because it caused serious strawberry fruit rot (Kao and Leu, 1979; Chang, 1988). In addition to the sporangial characteristics described above, this species can be readily identified by the production in single culture of abundant oogonia with predominantly paragynous antheridia.

It is surprising that *P. cactorum* which attacks a wide variety of plants, especially those in the Family Rosaceae on all continents has not been reported more frequently in Taiwan. In mainland China, *P. cactorum* has been found on apple (*Malus pumila* Mill.) and rubber (*Hevea brasiliensis* Muell.-Arg.) (Zhuang, 1981; Ho *et al.*, 1984b; Yu *et al.*, 1986b). While *P. cactorum* from temperate regions usually grow at 5°C, Taiwan isolates have a higher minimum temperature for growth, about 8–10°C (Sawada, 1927; Kao and Leu, 1979). Isolates from rubber in subtropical regions of mainland China also have similar high minimal growth temperature (Ho *et al.*, 1984b; Yu *et al.*, 1986a).

#### *P. capsici* Leonian

It was not too long ago when *P. capsici* was first reported in Taiwan (Kao and Leu, 1977; Leu and Kao, 1977), but it proved to be an important pathogen causing serious damages not only to different varieties of pepper but also to other vegetables like cucumber, tomato, eggplant, onion (*Allium cepa* L.) and flowering plants including *Dianthus barbatus* L. and *Enkianthus quinquefolius* Lour. (Leu and Kao, 1981). The species is widespread on the island especially in the warmer cen-

Table 1. *Phytophthora* species found in Taiwan

Species	Ref. <sup>1</sup>	Host	Mating Type <sup>2</sup>	Distribution among counties
<i>P. boehmeriae</i> Saw.	a	<i>Boehmeriae nivea</i> (L.) Guad.	H	Ilan, Taipei
<i>P. cactorum</i> (Leb. & Cohn.) Schroet.	a	<i>Boehmeriae nivea</i> (L.) Guad.	H	Miaoli, Nantou, Taichung,
	a	<i>Fragaria chilensis</i> Duch. var. <i>ananassa</i> Bail.	H	Taipei, Yunlin
<i>P. capsici</i> Leon.	a	<i>Allium cepa</i> L.	A <sub>1</sub>	Changhua, Chiayi, Hualien,
	a	<i>Aloe</i> sp.	A <sub>1</sub>	Nantou, Pingtung, Taichung,
	a	<i>Capsicum annum</i> L.	A <sub>1</sub>	Tainan, Taitung, Yunlin
	a,b	<i>Capsicum annum</i> L. var. <i>grossum</i> Sendt.	A <sub>1</sub>	
	d	<i>Cosmos</i> sp.	A <sub>1</sub>	
	a,b	<i>Cucumis sativa</i> L.	A <sub>1</sub>	
	b,d	<i>Dianthus caryophyllus</i> L.	A <sub>1</sub>	
	a	<i>Dianthus barbatus</i> L.	A <sub>1</sub>	
	a	<i>Enkianthus quinquefolius</i> Lour.	A <sub>1</sub>	
	a	<i>Lycopersicon esculentum</i> L.	A <sub>1</sub>	
	b	<i>Phaseolus</i> sp.	A <sub>1</sub>	
	a,c	<i>Piper betle</i> L.	A <sub>1</sub>	
	a,b	<i>Solanum melongena</i> L.	A <sub>1</sub>	
<i>P. cinnamomi</i> Rands = <i>P. cinchonae</i> Saw.	a,b	<i>Ananas cosmosus</i> (L.) Merr.	A <sub>1</sub>	Chiayi, Hsinchu, Kaohsiung,
	a	<i>Azalea</i> sp.	A <sub>1</sub>	Miaoli, Nantou, Pingtung,
	a	<i>Camellia</i> sp.	A <sub>1</sub>	Taichung, Tainan, Taipei,
	a	<i>Cinchona ledgeriana</i> Moeus.		Taitung, Taoyuan
	a	<i>Cinchona succirubra</i> Pav.		
	a	<i>Citrus</i> spp. and soil	A <sub>1</sub>	
	a	<i>Persea americana</i> L. and soil	A <sub>2</sub> (A <sub>1</sub> )	
	a	Forest soil	A <sub>1</sub> , A <sub>2</sub>	
<i>P. citricola</i> Saw.	a	<i>Citrus sinensis</i> Osb.	H	Hsinchu, Miaoli, Taichung,
	a	<i>Citrus tankan</i> Hay.	H	Taipei
	a	<i>Citrus</i> spp. and soil	H	
	a	<i>Fragaria chiloensis</i> Duch. var. <i>ananassa</i> Bail.	H	
<i>P. citrophthora</i> (R. & E. Smith) L.	a	<i>Citrus medica</i> L.		Chiayi, Hsinchu, Hualien,
	a	<i>Citrus</i> spp. and soil	A <sub>1</sub>	Ilan, Miaoli, Nantou,
	a	<i>Fragaria chiloensis</i> Duch. var. <i>ananassa</i> Bail.	A <sub>1</sub>	Taichung, Taipei, Taitung, Taoyuan
<i>P. colocasiae</i> Rac.	a	<i>Colocasia antiquorum</i> Schott.	A <sub>2</sub>	Changhua, Chiayi, Hsinchu,
	a	<i>Colocasia esculenta</i> Schott.	A <sub>2</sub>	Hualien, Ilan, Kaohsiung, Miaoli, Nantou, Pingtung, Taichung, Tainan, Taipei, Taitung, Taoyuan, Yunlin
<i>P. cryptogea</i> Peth. & Laff.	b	<i>Chrysanthemum</i> sp. and soil	A <sub>1</sub>	Chiayi, Taichung

Table 1. Continued

Species	Ref. <sup>1</sup>	Host	Mating Type <sup>2</sup>	Distribution among counties
	b	<i>Dianthus caryophyllus</i> L. and soil	A <sub>1</sub>	
	a,d	<i>Gerbera jamesoni</i> Bolus ( <i>G. hybrida</i> Hort.) and soil		
	c	<i>Lactuca sativa</i> L.		
<i>P. cyperi</i> (Ideta) Ito	a	<i>Cyperus iria</i> L.	H*	Ilan, Taichung, Tainan,
= <i>P. cyperi-iriae</i> Saw.	a	<i>Cyperus malaccensis</i> (Miyabe) Roxb.	H*	Taipei, Taoyuan
= <i>P. cyperi-rotundati</i> Saw.	a	<i>Cyperus rotundus</i> L.	H*	
	a	<i>Cyperus tegetiformis</i> Roxb.	H*	
<i>P. drechsleri</i> Tuck.	a,c	<i>Cucumis melo</i> L. and soil	A <sub>1</sub>	Chiayi, Hualien, Kaohsiung
= <i>P. melonis</i> Kat.	a,b	<i>Cucumis sativus</i> L.	A <sub>1</sub> , A <sub>2</sub>	Nantou, Pingtung, Tainan
	c	<i>Luffa aegyptiaca</i> Mill. and soil	A <sub>1</sub>	
<i>P. heveae</i> Thomp.	b	<i>Ananas cosmosus</i> (L.) Merr. soil	H	Changhua, Chiayi, Nantou,
	b	<i>Areca catechu</i> L. and soil	H	Taichung
	a	Citrus soil	H	
	a	Forest soil	H	
<i>P. humicola</i> Ko & Ann	a	Citrus soil	H	Changhua, Yunlin
	a	<i>Phaseolus vulgaris</i> L.	H	
<i>P. infestans</i> (Mont.) de Bary	a	<i>Lycopersicon esculentum</i> Mill.		Hualien, Taichung, Taipei
	a	<i>Solanum melongena</i> L.		
	a	<i>Solanum tuberosum</i> L.		
	e	<i>Tubocapsicum anomalum</i> Makino		
<i>P. insolita</i> Ann & Ko	a	Citrus soil	H	Changhua
<i>P. katsurae</i> Ko & Chang	a	Forest soil	H	Nantou
<i>P. leersiae</i> Saw.	a	<i>Leersia hexandra</i> Swartz.	H*	Taipei
<i>P. lepironae</i> Saw.	a	<i>Lepironiae mucronatae</i> Rich.	H*	Taichung, Taipei
<i>P. macrospora</i> (Sacc.) I. & T.	a	<i>Oryza sativa</i> L.	H*	Taipei
<i>P. nicotianae</i> Breda	a	<i>Allium fistulosum</i> L.		Changhua, Chiayi, Hsinchu,
de Haan ( <i>P. parasitica</i> Tuck.)	a	<i>Allium odorum</i> L.		Hualien, Kaohsiung, Nantou,
= <i>P. allii</i> Saw.	a,b	<i>Ananas cosmosus</i> (L.) Merr.	A <sub>1</sub>	Pingtung, Taichung, Tainan,
= <i>P. formosana</i> Saw.	b	<i>Averrhoa carambola</i> L.	A <sub>1</sub>	Taipei, Taitung, Yunlin
= <i>P. lycopersici</i> Saw.	d	<i>Cactus</i> sp.	A <sub>2</sub>	
= <i>P. melongenae</i> Saw.	a,b	<i>Carica papaya</i> L.	A <sub>2</sub> (A <sub>1</sub> )	
= <i>P. murrayae</i> Saw.	b	<i>Cattleya</i> sp.	A <sub>1</sub>	
	a	<i>Citrus</i> spp. and soil	A <sub>1</sub> (A <sub>2</sub> )	

Table 1. Continued

Species	Ref. <sup>1</sup>	Host	Mating Type <sup>2</sup>	Distribution among counties
= <i>P. ricini</i> Saw.	d	<i>Dendrobium phalaenopsis</i> Fitzg.	A <sub>2</sub>	
= <i>P. taihokuensis</i> Saw.	b	<i>Dendrobium</i> sp.	A <sub>2</sub>	
	c	<i>Dianthus barbatus</i> L.		
	b,c	<i>Dianthus caryophyllus</i> L. and soil	A <sub>2</sub> (A <sub>1</sub> )	
	b	<i>Dracena sanderiana</i> Sander ex M.T. Mast.	A <sub>1</sub>	
	b	<i>Fragaria chiloensis</i> Duch. var. <i>ananassa</i> Bail. and soil	A <sub>2</sub>	
	a	<i>Gypsophila elegans</i> Bieb.		
	b	<i>Gypsophila paniculata</i> L.	A <sub>1</sub>	
	d	<i>Hemerocallis fulva</i> L.	A <sub>1</sub>	
	a,b	<i>Hibiscus sabdorriffa</i> L.	A <sub>2</sub>	
	b	<i>Lilium longiflorum</i> Thunb. var. <i>eximium</i> Baker	A <sub>1</sub>	
	b	<i>Lilium</i> sp.	A <sub>1</sub> (A <sub>2</sub> )	
	a	<i>Lycopersicon esculentum</i> Mill.		
	a,c	<i>Murraya paniculata</i> L.	A <sub>2</sub>	
	a	<i>Nicotiana tabaccum</i> L.		
	a	<i>Paulownia</i> spp.		
	a,b	<i>Passiflora edulis</i> Sims. and soil	A <sub>2</sub>	
	a	<i>Phalaenopsis</i> sp.	A <sub>1</sub> ,A <sub>2</sub>	
	a,b,c	<i>Piper betle</i> L. and soil	A <sub>2</sub> (A <sub>1</sub> )	
	b	<i>Poinsettia</i> sp.	A <sub>1</sub>	
	a,b	<i>Psidium guajava</i> L. and soil	A <sub>1</sub> ,A <sub>2</sub>	
	b	<i>Pyrostegia venusta</i> (Ker.-Gawl.) Miers.	A <sub>1</sub>	
	a	<i>Ricinus communis</i> L.		
	b,d	<i>Schlumbergera</i> sp.	A <sub>1</sub> ,A <sub>2</sub>	
	b	<i>Solanum melongena</i> L.	A <sub>2</sub>	
	c	<i>Vinca rosea</i> L.	A <sub>1</sub>	
<i>P. palmivora</i> (Butl.) Butl.	a,b	<i>Carica papaya</i> L.	A <sub>1</sub> (A <sub>2</sub> )	Changhua, Chiayi, Kaohsiung,
= <i>P. carica</i> (Hora) Hori	a	<i>Citrus</i> spp. and soil	A <sub>1</sub> (A <sub>2</sub> )	Nantou, Pintung, Tainan, Yunlin
	b	<i>Eriobotrya japonica</i> Lindl. (soil)	A <sub>1</sub>	
	a	<i>Eugenia javanica</i> Lamk.		
	a	<i>Ficus carica</i> L.		
	d	<i>Fuchsia magellanica</i> Lam.	A <sub>2</sub>	
	b	<i>Mangifeera indica</i> L.	A <sub>2</sub>	
	a	<i>Paulownia</i> spp.	A <sub>1</sub>	
	b	<i>Persea americana</i> L.	A <sub>2</sub>	
	a	<i>Phalaenopsis</i> sp.	A <sub>1</sub> ,A <sub>2</sub>	
	b	<i>Zizyphus jujuba</i> Mill.	A <sub>2</sub>	
<i>P. vignae</i> Purss	a	<i>Vigna sinensis</i> (L.) Erdl.	H	Nantou

<sup>1</sup>Reference source:

- a. published literature cited.
- b. unpublished data of P. J. Ann.
- c. unpublished data of H. H. Ho.
- d. unpublished data of H. H. Ho and H. C. Yang.
- e. unpublished data of K. Sawada.

<sup>2</sup>H=Homothallic; \*Known only on host; mating type in parenthesis of infrequent occurrence.

tral and southern regions. It can be distinguished from other similar heterothallic *Phytophthora* species that produce papillate sporangia by the variable sporangial shapes from nearly spherical to elongated with tapering base many with two papillae, the long pedicels of sporangia when deciduous and the absence or rarity of chlamydospores in culture under normal growing conditions. So far, only A<sub>1</sub> mating type has been found in Taiwan, although both mating types commonly occur in other countries. For instance, in mainland China, both A<sub>1</sub> and A<sub>2</sub> mating types have been reported from pepper and rubber (Ho *et al.*, 1983; Yu *et al.*, 1986a).

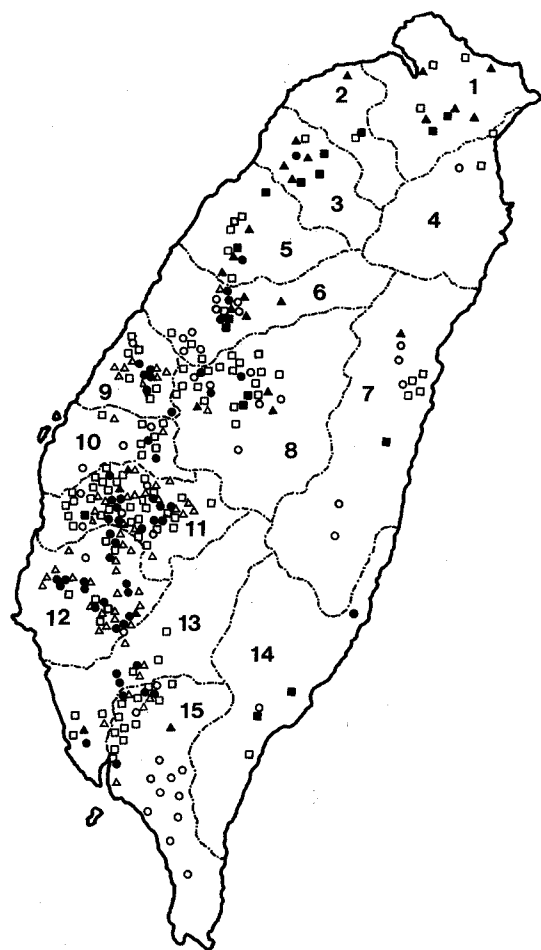


Fig. 1. Distribution of major *Phytophthora* species in Taiwan: ○, *P. capsici*; ■, *P. citrophthora*; ▲, *P. cinnamomi*; □, *P. colocasiae*; ●, *P. nicotianae* (*P. parasitica*); △, *P. palmivora*. (1) Taipei, (2) Taoyuan, (3) Hsinchu, (4) Ilan, (5) Miaoli, (6) Taichung, (7) Hualien, (8) Nantou, (9) Changhua, (10) Yunlin, (11) Chiayi, (12) Tainan, (13) Kaohsiung, (14) Taitung, (15) Pingtung.

#### *P. cinnamomi* Rands

= *P. cinchonae* Sawada

*Phytophthora cinchonae* was described by Sawada (1936, 1942b) as a new species causing seedling damping-off of *Cinchona* spp. in Kaohsiung. Waterhouse (1963) considered it an insufficiently described taxon for lack of information on the sexual organs. Since this species has never been confirmed and no type culture or specimen is available, I concur with Waterhouse's judgement that it is "possibly the same as *P. cinnamomi*" based on Sawada's description and diagrams. It is strange that Sawada never compared *P. cinchonae* with *P. cinnamomi*. According to Novotol'Nova (1974), *P. cinnamomi* is a pathogen of various species of *Cinchona* including *C. ledgeriana* Moeus, one of the type hosts of *P. cinchonae*.

If we accept *P. cinchonae* synonymous with *P. cinnamomi* which has priority, then *Cinchona* is the first host plant recorded for *P. cinnamomi* in Taiwan. Later, *P. cinnamomi* was found to be one of the *Phytophthora* spp. causing heart rot of pineapple (Anonymous, 1965) and fibrous root rot and foot rot of *Citrus* spp. (Lee, 1976). The species can be readily recognized by its relatively broad coralloid hyphae with large botryose swellings and thin-walled chlamydospores, ovoid to ellipsoidal non-papillate sporangia and fairly large oogonia often with long, bicellular antheridia, normally produced only in dual cultures.

Ko *et al.* (1978) conducted an extensive survey of *P. cinnamomi* in Taiwan and found that it was widely distributed in the soil throughout the island, but often did not affect the native flora. In a natural forest at Lenhuachih, Nantou, both A<sub>1</sub> and A<sub>2</sub> mating types existed in a ratio approximating 1:1 and the local plants remained healthy. They speculated that Taiwan probably lies within the center of origin of this cosmopolitan fungus. Their hypothesis was further substantiated by the diversity of biological variants of *P. cinnamomi* on the island (Ann and Ko, 1985). This species has an extremely wide host range in other countries especially among woody trees and shrubs but in Taiwan, it has so far been reported only from avocado (*Persea americana* L.), *Camellia* sp., pineapple and citrus. Whereas A<sub>2</sub> mating type of *P. cinnamomi* dominates the world, isolates from citrus, pineapple and camellia are all A<sub>1</sub> and A<sub>2</sub> mating type has been found on avocado only (Ko *et al.*, 1978; Ann, 1984). In contrast, both isolates from avocado in Fujian of mainland



China belong to A<sub>1</sub> mating type although isolates from *Cedrus deodora* (Roxb.) G. Don. are predominantly A<sub>2</sub> (Zheng and Lu, 1989a).

*P. citricola* Sawada

Erected by Sawada (1927) as a new taxon on the fruits of *Citrus sinensis* Osb. and *C. tankan* Hay. in Taipei this is another of Sawada's new species of *Phytophthora* accepted by Waterhouse (1963). There is no type culture or type specimen but this species has been studied previously by many researchers. It can be distinguished from other *Phytophthora* species by its often "chrysanthemum" growth pattern, semi-papillate sporangia which may assume irregular or bizarre shapes in water and the production in single culture of numerous oogonia with predominantly paragynous antheridia. Besides infecting *Citrus* spp. in Taiwan, it is one of the *Phytophthora* spp. involved in strawberry fruit rot (Chang, 1988). In distribution, it has been found mainly in the northern part of the island probably because of its lower maximal temperature for growth (30–31°C).

*P. citrophthora* (Smith & Smith) Leonian

Described first by Sawada (1915a, 1919c) as *Pythiacystis citrophthora* R. & E. Smith on the fruits of *Citrus medica* L., this species continues to be best known as one of the causal agents in brown rot of citrus (Anonymous, 1944b; Lee, 1976) in Taiwan. Recently, it has been implicated in strawberry fruit rot (Kao and Leu, 1979; Chang, 1988). *Phytophthora citrophthora* can be identified based on its finely radiate appressed growth pattern, the non-deciduous papillate sporangia whose shapes often become distorted in water and the absence or paucity of sexual capacity. When fertile, it is heterothallic and both A<sub>1</sub> and A<sub>2</sub> mating types are known to exist but all isolates of *P. citrophthora* in Taiwan belong to A<sub>1</sub> mating type (Kao and Leu, 1979; Ann, 1984). Although found so far only on citrus and strawberry in the central and northern counties of the island, this species is known to attack 75 plant species in 28 families especially from subtropical areas (Novotel'Nova, 1974). In mainland China, *P. citrophthora* has been proved to cause diseases not only in citrus, but also in rubber, papaya, carambola (*Averrhoa carambola* L.) and *Euonymus japonicus* L. (Ho *et al.*, 1983; Yu *et al.*, 1986a,b; Zheng and Lu, 1988).

*P. colocasiae* Raciboski

*Phytophthora colocasiae* was first reported in Taiwan by Sawada (1915c, 1919b) as the pathogen causing leaf blight of taro, *Colocasia antiquorum* Schott and *C. esculenta* Schott, albeit initially under the binomial *Kawakamia colocasiae* (Rac.) Sawada (Sawada, 1911). It is distinguished from other heterothallic *Phytophthora* species with papillate sporangia primarily in the elongated, deciduous sporangia with pedicels of medium length and its association with *Colocasia*.

*Phytophthora* leaf blight continues to be the major disease of taro in Taiwan. A recent intensive study by Ann *et al.* (1986) showed that *P. colocasiae* is present in every county on the island and all isolates belong to A<sub>2</sub> mating type. They concluded too, that Taiwan is not within the center of origin for *P. colocasiae* although Ko (1979) speculated that it should be in Asia. So far, only A<sub>2</sub> isolates have been reported from Asian countries while A<sub>1</sub> but not A<sub>2</sub> mating type was found in Hawaii. It is interesting to note that *P. botryosa* Chee (mating type A<sub>1</sub>) but not *P. colocasiae* has recently been isolated from the leaves of *C. esculenta* in Fujian of mainland China (Zheng and Lu, 1989a).

*P. cryptogea* Pethybridge & Lafferty

*Phytophthora cryptogea* has recently appeared in the central counties of Taiwan as a major pathogen of cut flower plants including *Chrysanthemum* sp., *Gerbera jamesoni* Bolus (*G. hybrida* Hort.) and carnation (Chang, 1983; P. J. Ann, unpublished; H. C. Yang, unpublished). It can be recognized by the often conspicuous network of small hyphal swellings and the regularly obpyriform non-papillate sporangia in water and by its heterothallism producing medium-sized oogonia with amphigynous antheridia. So far, only A<sub>1</sub> mating type has been found on the island although both mating types are known to exist in other parts of the world. This pathogen has a long list of 84 host plant species from 23 families (Novotel'Nova, 1974) including flowering plants, e.g. *Kalanchoe* Adans., *Primula* L., *Lupinus* L., *Petunia* Juss., *Aster* L. and *Saintpaulia* Wendl. as well as vegetables like tomato, *Brassica* spp. and members of the Family Curcubitaceae. Given the very short history of this species in Taiwan, more host plants are expected in the future. It has been isolated from the root of *Cedrus deodara* in Nanjing of mainland China (Zheng and Lu, 1989a) and from imported Fuzhou citrus seedling (P.J. Ann, personal communica-

tion).

*P. cyperi* (Ideta) Ito

= *P. cyperi-iriae* Sawada

= *P. cyperi-rotundati* Sawada

*Phytophthora cyperi* was first described on the stems and leaves of *Cyperus tegetiformis* Roxb. as *Kawakamia cyperi* (Miy. & Ideta) Miyabe (Sawada, 1915b, 1916b, 1919c) and later on *C. malaccensis* Roxb. as *K. cyperi* (Ideta) Sawada (Sawada, 1942g, 1943). This species has never been grown in culture. I have re-examined Sawada's specimens but could not find the semi-papillate sporangia supposedly produced by the fungus. I did find thick-walled, spherical, smooth oogonia with predominantly paragynous antheridia characteristic of the species.

*Phytophthora cyperi-iriae* was recorded on the leaves and peduncles of *C. iria* L. from Taipei (Sawada, 1931) but later Sawada (1942g, 1943) changed it to *K. cyperi-iriae* (Saw.) Sawada. Sawada (1927) described the pathogen on *C. rotundus* L. as *P. cyperi-rotundati* and later as *K. cyperi-rotundati* (Saw.) Sawada (Sawada, 1942g, 1943). *Phytophthora cyperi-iriae* was supposed to be distinguished by the rare amphigynous antheridia whereas *P. cyperi-rotundati* differed from *P. cyperi* with only paragynous antheridia in having paragynous and more commonly amphigynous antheridia. I found that the oogonia of *P. cyperi-iriae* and *P. cyperi-rotundati* are similar to those of *P. cyperi* and the antheridia are all predominantly paragynous. All three species caused similar leaf spots on *Cyperus* spp. producing semi-papillate, ovoid to ellipsoidal sporangia. Without the opportunity to collect fresh materials and compare the asexual and sexual stages of the pathogens, I am inclined to treat them as conspecific (Waterhouse, 1963).

*P. drechsleri* Tucker

= *P. melonis* Katsura

*Phytophthora drechsleri* was first reported by Kao and Leu (1977) as the causal agent of cucumber blight in Taiwan. It is very similar to *P. cryptogea* (Ho and Jong, 1986). As far as Taiwan isolates are concerned, it differs slightly from *P. cryptogea sensu stricto* in having larger, more irregular and more elongated sporangia and less conspicuous network of small hyphal swellings. For the time being, it is retained as a separate species until the species concept of *P. cryptogea* is re-

-defined. It has also been isolated from *Cucumis melo* L. and *Luffa aegyptiaca* Mill. (Chang, 1983; H.H. Ho, unpublished) and the pathogenicity of Taiwan isolates has been restricted to the Family Cucurbitaceae. Both A<sub>1</sub> and A<sub>2</sub> mating type have been isolated (P.J. Ann, unpublished) primarily from the central and southern counties of the island. This species also caused serious damage to cucumber and other cucurbits in Iran, Japan and mainland China.

*Phytophthora melonis* was described initially by Katsura as the causal agent of foot rot of cucumber in Japan but Ho (1986) showed that it is very similar to and should be treated as synonymous with *P. drechsleri* which has nomenclatural priority. Similarly, *P. sinensis* Yu & Zhuang from cucumber in Nanjing of mainland China is considered conspecific with *P. drechsleri*.

*P. heveae* Thompson

This species can be easily recognized by its small, smooth oogonia with conspicuously tapering oogonial base and very small amphigynous antheridia, produced abundantly in single culture. It has been isolated recently from soil and from the roots of *Areca catechu* L. (Ann, 1984; Chang and Shu, 1988; P.J. Ann, unpublished). So far, it has not caused any plant disease in Taiwan although it is a known pathogen of rubber, cacao, avocado, mango (*Mangifera indica* L.) and guava (*Psidium guajava* L.) (Gerrettson-Cornell, 1989). It is possible that it was brought into Taiwan along with rubber tree decades ago (Chang and Shu, 1988). On the other hand, this species is absent from rubber plantations in mainland China (Ho *et al.*, 1984b; Yu *et al.*, 1986a).

*P. humicola* Ko & Ann

This species was recently isolated from citrus soil as well as rotten root of kidney bean, *Phaseolus vulgaris* L. and described as a new species (Ko and Ann, 1985) non-pathogenic to citrus. It is similar to *P. megasperma* Drechs. in the nonpapillate sporangia and the production in single culture of large oogonia with predominantly paragynous antheridia, but differs in having large distinctive hyphal swellings with radiating hyphae and long oogonial stalk. But these characteristics have been described and diagrammed for *Pythiomorpha miyabeana* Ito & Nagai (Ito and Nagai, 1931) considered by Waterhouse (1963) as synonymous with *P. megasperma*. Further comparative studies are

needed to determine the relationship between *P. humicola* and *P. megasperma* especially in view of the complexity of the species concept of *P. megasperma* (Hansen *et al.*, 1986).

*P. infestans* (Montagne) de Bary

This species upon which the genus *Phytophthora* is based, is actually distinct from all species of *Phytophthora*, with the exception of *P. phaseoli* Thaxter, in having an aerial, differentiated, "tree-like", nodose sporangiophore with compound sympodial branches bearing ovoid to obpyriform, slightly papillate sporangia which fall off in air with short occluded pedicels.

*Phytophthora infestans* is known to exist in Taiwan for a long time causing late blight of potato, tomato and eggplant (Sawada, 1915c, 1919c) but apparently, there has been no further report on the disease or the pathogen after Sawada. So far, the great majority of isolates of *P. infestans* in the world including all isolates from mainland China belong to A<sub>1</sub> mating type, but I have not been able to obtain a Taiwan isolate to determine its mating type. I have re-examined Sawada's specimens and found the sporangiophores and sporangia characteristic of the species. In addition, I also came across a specimen of *P. infestans* on the leaves of *Tubocapsicum anomalum* Makino from Hualien, which has not been reported as a host for this species by Sawada or by researchers in other countries.

*P. insolita* Ann & Ko

This interesting new species of *Phytophthora* was isolated from citrus soil only about ten years ago (Ann and Ko, 1980). It is unique in producing in single culture abundant oogonia without antheridia and can thus be easily distinguished from all other *Phytophthora* species. It is not pathogenic to citrus and has not been found anywhere since its first report.

*P. katsurae* Ko & Chang

*Phytophthora katsurae*, previously known as *P. castanae* Kat. is characterized by the production in single culture of abundant, small, verrucose oogonia with tapering base and small antheridium. It has been isolated from forest soil only (Ko and Chang, 1979; Chang and Shu, 1988) although it is reportedly a pathogen of chestnut (*Castanea crenata* Sieb. & Zucc.) and coconut (*Cocos nucifera* L.) (Gerrettson-Cornell, 1989).

*P. leersiae* Sawada

Sawada (1941, 1942b) described *P. leersiae* as a new species of *Phytophthora* on the leaves of *Leersia hexandra* Swartz. from Taipei. It was never isolated and has not been reported by other researchers. My recent re-examination of the type specimen has confirmed the absence of sporangia and the presence of clusters of exceptionally large, thick-walled and pigmented oogonia often with undulated surface and tapering oogonial base, aplerotic to markedly aplerotic oospore and entirely amphigynous antheridia as described by Sawada. Although Waterhouse (1963) rejected this species as insufficiently described for lack of description on the sporangia, I consider the characteristics of its sexual structures distinct enough to be a good species. Attempts should be made to collect new specimens to study the asexual stage. It is possible that *P. leersiae*, like many downy mildews, produce sporangia only during certain hours of the day or under certain laboratory conditions when the environmental conditions are most conducive to sporulation.

*P. lepironiae* Sawada

*Phytophthora lepironiae* was first reported on the stems of *Lepironia muronata* Rich. by Sawada (1919a,b) who subsequently renamed it as *Nozemia lepironiae* (Saw.) Sawada (Sawada, 1919c) and then *Kawakamia lepironiae* (Saw.) Sawada (Sawada, 1942g, 1943). He was unable to culture it and this species has not been verified by other researchers. Waterhouse (1963) accepted it as a good species different from *P. cyperi* primarily because of the supposedly broader sporangia and larger oogonia. I could not find sporangia on Sawada's type specimen and the oogonia did not appear to be significantly larger than those of *P. cyperi sensu lato*. However, the antheridia were entirely paragynous in contrast to the predominantly paragynous antheridia of *P. cyperi*. Tentatively, I have accepted this as a distinct species found in Taiwan but attempts should be made to collect fresh specimens to confirm its identity.

*P. macrospora* (Saccardo) Ito & Tanaka

This species was initially reported on the leaves of *Oryza sativa* L. by Sawada (1927) as *Sclerospora oryzae* Brizi (= *Sclerospora macrospora* Sacc.). Tanaka (1940) transferred *S. macrospora* to *Phytophthora*. Chen (1956) listed *P. macrospora* as the pathogen causing downy

mildew of rice. Thirumalachar *et al.* (1953) made it the type species of the genus *Sclerophthora* partly based on the union of the oogonial wall with the oospore wall, but Waterhouse (1963) retained it as a species of *Phytophthora*. The taxonomic status of this species is still confusing but for the time being, I have accepted Waterhouse's taxonomic treatment.

On Sawada's specimen, I found abundant distinctively large, thick-walled, smooth oogonia close together in parallel series within the leaves. Although the large, plerotic oospore nearly fills up the entire oogonial space, the oospore wall is not fused with the oogonial wall. Instead, the intact oospore could be easily released by crushing open the oogonial wall, as experienced by Waterhouse (1963). Although no sporangia were found on the specimen nor reported by Sawada, this species can be easily distinguished from other *Phytophthora* spp. known only on the hosts.

*P. nicotianae* Breda de Haan (*P. parasitica* Dastur)

= *P. allii* Sawada

= *P. formosana* Sawada

= *P. lycopersici* Sawada

= *P. melongenae* Sawada

= *P. murrayae* Sawada

= *P. ricini* Sawada

= *P. taihokuensis* Sawada

Recently, Ho and Jong (1989) based on detailed comparative studies, concluded that *P. nicotianae* and *P. parasitica* should be treated as conspecific. Although the binomial *P. parasitica* is popular especially among plant pathologists, the present International Code of Botanical Nomenclature dictates that *P. nicotianae* which has priority, should be the correct name to be used. Waterhouse (1963) distinguished *P. nicotianae* into *P. nicotianae* var. *nicotianae* and *P. nicotianae* var. *parasitica*, but Ho and Jong (1989) proved such distinction to be impossible and unnecessary. Indeed, in his thorough study of pineapple heart rot in Taiwan, Chen (1966) found that many isolates possessed characteristics of both varieties and the most practical and logical way was to identify the pathogen simply as *P. nicotianae*. Zheng and Lu (1989b) compared isolates of *P. nicotianae* from various parts of mainland China and arrived at a similar conclusion.

Regardless of its nomenclatural controversies, there is no doubt that *P. nicotianae* (*P. parasitica*) is the single most important *Phytophthora* species attacking a

wide variety of plants throughout Taiwan. To date, it has been isolated from 33 plant species and soil on the island (Table 1) and more hosts are expected, considering the versatility of this species as a plant pathogen. It is characterized by its often tufted mycelial growth on agar media, good growth at 35°C, conspicuously papillate, broadly ovoid, obpyriform to obturbinate, usually nondeciduous sporangia, spherical chlamydospores and relatively small oogonia with short antheridia. Both mating types have been found in Taiwan, as in other parts of the world. In distribution, it is interesting to note that nearly all of the citrus isolates were from the tropical regions in the central and southern counties. This is probably attributable to the higher optimal and maximal temperatures for growth (about 30 and 37°C respectively).

It is puzzling that many of Sawada's new *Phytophthora* species are so similar to *P. nicotianae* that they should be treated as synonymous (Waterhouse, 1963). Presumably, Sawada epitomizes the "splitter" philosophy in classification so that he erected new species based on minor differences which could be accepted by others as intra-specific variations.

*P. allii* Sawada. This species was described on the leaves of *Allium fistulosum* L. from Taipei (Sawada, 1915c, 1919b). Waterhouse (1963) suggested that it is "probably the same as *nicotianae* var. *nicotianae*". The culture is no longer in existence. I found from the type specimen only irregular *Phytophthora*-like intercellular hyphae. Nevertheless, I discovered on the dried leaves of *Allium odorum* L. from Taipei, a fungus that Sawada labeled as *Phytophthora* sp. with sporangia and chlamydospores closely resembling *P. nicotianae* and it seems reasonable to treat *P. allii* as such. Ito (1936) also considered *P. allii* so similar to *P. parasitica* that it might be treated as a biotype of the latter. Novotel' Nova (1974) listed *Allium* spp. including *A. fistulosum* as one of the hosts for *P. nicotianae* var. *parasitica*. However, *P. palmivora* instead of *P. nicotianae* has been reported on *Allium tuberosum* Roxb. ex Spreng (= *A. odorum*) in mainland China (Ho *et al.*, 1983).

*P. formosana* Sawada, *P. ricinis* Sawada. Sawada described *P. formosana* (Sawada, 1942f, 1943) and *P. ricinis* (Sawada, 1942e, 1943) as new species respectively on the cotyledons and leaves of *Ricinus communis* L. in Kaohsiung and Taipei. Waterhouse (1963) considered them "probably the same as *nicotianae* var. *parasitica*". Unfortunately, no type culture or specimen can be

located. I did find dried specimens of *Ricinus communis* leaves from Taipei that Sawada labeled as "*Phytophthora* sp." which showed conspicuously papillate, broadly obpyriform sporangia characteristic of *P. nicotianae*. Chang and Hsieh (1977) considered *P. ricini* the same as *P. palmivora* based on the rather elongated sporangia in Sawada's diagrams. But elongated sporangia were no common on Sawada's specimen of *Ricinus communis*. In fact, the length/breadth ratio of sporangia produced *in vitro* was determined by Sawada as 1.361 and the culture grew well at 35°C. Furthermore, Sawada found sex organs in single culture of *P. ricini*. To the best of my knowledge, *P. palmivora* almost never produces sex organs in single cultures but they can occasionally be found around the inoculum disc in old cultures of *P. nicotianae*. It seems justifiable to treat *P. ricini* synonymous with *P. nicotianae* based on these evidences. *Phytophthora parasitica* has been recorded as causing castor bean seedling blight in Taiwan (Anonymous, 1944a).

*P. lycopersici* Sawada. No type culture or specimen is available for confirmation. Based on Sawada's original descriptions and diagrams (1942d, 1943). I concur with Waterhouse (1963) that *P. lycopersici* on tomato fruit is "probably the same as *nicotianae* var. *parasitica*" although I do not think the variety epithet is necessary.

*P. melongenae* Sawada. This species was described on *Solanum melongena* L. (Sawada, 1914, 1915c, 1919c, 1927). Waterhouse (1963) considered it "the same as *nicotianae* var. *nicotianae*". The general characteristics of an authentic culture of the species (ATCC 64535) would undoubtedly place it under *P. nicotianae*. Ito (1936) also felt that *P. melongenae* was very similar to *P. parasitica*.

*P. murrayae* Sawada. Sawada (1942a, 1943) erected this new species solely based on the papillate sporangia which were distinct from the nonpapillate sporangia of *P. cryptogea* and the semi-papillate sporangia of *P. pini* Leon. (= *P. citricola*). Most sporangia that I found on the type specimen (leaves of *Murraya paniculata* L. from Taipei) are broadly obpyriform with distinct hemispherical apical thickenings. I also discovered on some leaves spherical straw-colored chlamydospores not mentioned in Sawada's description. Based on these findings, I believe it can be treated the same as *P. nicotianae*. Indeed, this species has recently been isolated from the leaves and stem of *Murraya paniculata*

at the nursery of National Taiwan University.

*P. taihokuensis* Sawada. This species was described on the fruits of *Solanum melongena* from Taipei but it was actually published after Sawada's death (Sawada, 1959). No type culture or specimen could be located. Waterhouse (1963) rejected *P. taihokuensis* as insufficiently described for lack of information on its sexual stage. Based on Sawada's original description and diagrams, I agree with Chang and Hsieh (1977) and Chang (1983) that it is probably the same as *P. nicotianae* (*P. parasitica*). Sawada himself considered it near *P. melongenae* (= *P. nicotianae*).

*P. palmivora* (Butler) Butler

= *P. carica* (Hora) Hori

*Phytophthora palmivora* can be readily distinguished from other similar heterothallic *Phytophthora* spp. with conspicuously papillate sporangia, in the production on agar media of abundant chlamydospores and elongated, ellipsoidal to ovoid sporangia which fall off easily in water with short occluded pedicels. It is well-known in Taiwan as the pathogen causing fruit and root rot of papaya, black rot of orchids and brown rot of citrus. A *Phytophthora* sp. associated with betel (*Piper betle* L.) decline was initially designated as an atypical form of *P. palmivora* (Chang and Shu, 1981) but later considered closer to *P. parasitica* (Chang, 1983). The reclassification is appropriate since most isolates from betel in Taiwan can be identified as *P. nicotianae* (*P. parasitica*) (P.J. Ann, unpublished; H.H. Ho, unpublished) and some as *P. capsici* (Leu and Kao, 1981; Chang and Ma, 1985; H.H. Ho, unpublished). More recently, *P. palmivora* has also been isolated from other tropical fruit crops including *Eugenia javanica* Lamk, mango, *Zizyphus jujuba* Mill. and avocado (Chang, 1983; P.J. Ann, unpublished). Given the fact that *P. palmivora* is the most important *Phytophthora* species in the tropics attacking a wide variety of plants, many of which are found in Taiwan, it is expected that more hosts will be discovered on the island especially from the tropical regions of the central and southern counties where most Taiwan isolates of *P. palmivora* hitherto originated.

*Phytophthora carica* was reported on the fruits of *Ficus carica* L. from Taipei (Sawada, 1916a, 1919c). Unfortunately, no Sawada's specimen or culture is available. Waterhouse (1963) considered *P. carica* as insufficiently described and "most likely this belongs in

group II near *palmivora*". Based on Sawada's description and diagrams, I believe that *P. carica* can be treated as a synonym of *P. palmivora* and in such a case, the common fig is the first host plant recorded for *P. palmivora* in Taiwan. Novotél'Nova (1974) also listed *Ficus* spp., including *F. carica* as hosts of the species.

#### *P. vignae* Purss

*Phytophthora vignae* has been reported only once from cowpea, *Vigna sinensis* (L.) Erdl. by Kao and Leu (1977, 1982). It can be recognized by its nonpapillate sporangia in water, the production in single culture of abundant oogonia with rather large amphigynous antheridia and its association with cowpeas. Hwang and Qi (1984) also found this species on yard-long bean, *V. sesquipedalis* (L.) Fruw. in Guangzhou area of mainland China.

#### Insufficiently Described and/or Unidentified Species

##### *P. fragariae* Hickman

Chang (1983) recovered an interesting isolate from brownish stem tissue of stunting strawberry at Dah-hu. Based on the sporangial characteristics, it was considered closest to *P. fragariae* and might be designated as a high temperature variant of *P. fragariae*. Ho and Jong (1988) found it so different in cultural and physiological characteristics that it should not be assigned to this species. The precise identification of this isolate is not possible until the characteristics of sexual organs can be determined.

##### *P. polygoni* Sawada

This species known only from the original description on the leaves of *Polygonum japonicum* Meisn. from Taipei and Taichung (Sawada, 1922) was later renamed by Sawada (1942g, 1943) as *Kawakamia polygoni* (Saw.) Sawada. It has not been grown in culture and no type specimen can be located. It was supposed to be distinguished from other *Phytophthora* spp. by its elongated sporangia, but for the time being, I concur with Waterhouse's judgment (1963) that this species is insufficiently described due to the absence of sexual stage and it should be rejected until fresh specimens can be collected for further studies.

##### *Phytophthora* sp.

Some species of *Phytophthora* causing plant dis-

eases in Taiwan have not been identified and were recorded as *Phytophthora* sp. for instance, on rice seedlings (Wong and Chen, 1972) and sugar beet (Chu and Hu, 1959). Further attempts should be made to re-investigate these species to determine their identity.

#### Remarks

Taking into consideration the short history of *Phytophthora* research in Taiwan, the small size of the island, the limited cultivated land and the fact that there are only about 40 good species of *Phytophthora* found in the world (Gerrettson-Cornell, 1989), the number of *Phytophthora* species hitherto discovered in Taiwan totalling 21 is impressive. Of these, 9 species are heterothallic: *P. capsici*, *P. cinnamomi*, *P. citrophthora*, *P. coloasiae*, *P. cryptogea*, *P. drechsleri*, *P. infestans*, *P. nicotianae* (*P. parasitica*) and *P. palmivora* and 12 species are homothallic: *P. boehmeriae*, *P. cactorum*, *P. citricola*, *P. heveae*, *P. humicola*, *P. insolita*, *P. katsuriae*, *P. vignae*, *P. cyperi*, *P. leersiae*, *P. lepironae* and *P. macrospora* with the last four species known only on the host. Of note is the concentration of *Phytophthora* spp. in the subtropical to tropical southwest plains of the island where crops abound (Poon and Kuo, 1980). Undoubtedly, with further *Phytophthora* research, more hosts and more *Phytophthora* species will be found in Taiwan. The recent discovery of *P. meadii* McRae on *Euonymus* in Hangzhou (Zheng and Lu, 1989a) and *P. robinicola* Lu, Xu & Fang sp. nov. on *Robinia pseudoacacia* L. in Jiangsu areas of mainland China (Lu, J.Y. personal communication) is of special interest because of geographic proximity. At present, *P. erythroseptica* Pethyb., *P. syringae* and *P. hibernalis* Cairne occurring commonly on potato, apple and citrus, respectively in other countries are absent on the island, presumably because they usually prefer cooler climate for disease development. On the other hand, the lack of reports for *P. cambivora* Buis. on trees and *P. megasperma* on soybean (*Glycine max* Merr.) and alfalfa (*Medicago sativa* L.) is interesting. Although *Phytophthora* spp. are known to cause damping-off diseases in tree nurseries (Poon and Kuo, 1980) little work has been done on the identity of the pathogen(s). *Phytophthora megasperma* attacks soybean, alfalfa and many other plants on a world-wide basis, causing notably root and stem rots (Gerrettson-Cornell, 1989), but there has been no report of this species or disease(s) attributable to *P. megasper-*

*ma* in Taiwan. It would be interesting to ascertain if *P. megasperma* is indeed absent and in case of its presence, determine why it has failed to incite diseases. The answer to these questions may throw light on the control of plant diseases caused by this species in other countries. It is intriguing that *Phytophthora megasperma* has never been reported from mainland China either, but is known to exist in Japan.

A slightly different situation exists for *P. cinnamomi* which is widely distributed in Taiwan but apparently causes little damage to the local flora. It may be true that this species has coevolved successfully with the local plants resulting in a dynamic equilibrium (Chang and Hsieh, 1977). However, with continual human efforts to exploit land for agricultural and other purposes, this delicate pathoecosystem can be easily disturbed, resulting possibly in the outbreak of epidemics. It is not inconceivable that the devastating destruction of forests in Australia (Gregory, 1983) may happen in Taiwan resulting not only in the loss of vegetation but further aggravates the existing soil erosion problem.

Most *Phytophthora* species are soil-borne, and like other soil-borne diseases, the control of *Phytophthora* diseases is often very difficult. The best means of control is to prevent the occurrence of the disease in the first place and one effective way is to avoid introducing potential host plants in a locality where certain *Phytophthora* species is/are known to exist. It is thus essential to know the distribution of *Phytophthora* species on the island. Concerted efforts must be made to isolate, identify and determine the population density of all *Phytophthora* species in Taiwan. For each *Phytophthora* species, the host range and the resistance of crops to be planted should be known. To this end, a culture collection center should be set up where *Phytophthora* isolates can be deposited and maintained permanently in liquid nitrogen, for future references and use by other researchers. Alternatively, the existing Culture Collection and Research Center of Food Industry Research and Development Institute at Hsinchu can be expanded to accommodate Taiwan *Phytophthora* isolates.

At present, in those areas already infested with *Phytophthora* diseases, farmers and growers have relied almost exclusively on fungicides (Anonymous, 1988) to keep the pathogens under control. In view of the limited cultivated land, and the contiguity of residential areas, the continual heavy application of chemicals will

ultimately create serious environmental problems and human health hazards. In the long run, cultural and biological methods (Shea and Broadbent, 1983) supplemented with minimal but timely application of selective fungicides probably provide better solutions. In Taiwan, it has been demonstrated that *Phytophthora* diseases could be reduced considerably by providing better ventilation and drainage, mulching of soil and the addition of soil amendments such as chicken manure (Leu and Lee, 1976; Leu and Kao, 1977; Tsai, 1983; Lin and Wu, 1985). But prerequisite to developing effective cultural and biological controls is a good understanding of the behavior of *Phytophthora* spp. in soil—how they survive and how they initiate and spread diseases. Unfortunately, we know very little about this important aspect of *Phytophthora* epidemiology, especially in Taiwan (Leu, 1975; Hwang, 1977). Previously, the behavior of *P. palmivora*, *P. parasitica*, *P. melonis* and *P. katsurae* in soil has been studied (Huang and Chen, 1974; Huang, 1975a,b; Chang, 1986). Since many *Phytophthora* spp. probably survive in soil as oospores, the physiology of oospore production and germination have been investigated (Yu, 1979; Yu and Chang, 1980; Chang *et al.*, 1984; Chang and Shu, 1988). Motile zoospores released from sporangia are essential in the initiation and spread of diseases (Gallegly, 1983) and so conditions governing the production of sporangia have been studied in *P. parasitica* (Wen, 1973) and *P. palmivora* (Huang and Leu, 1976). The role of pectic enzymes in disease development by *P. capsici* and *P. parasitica* has also been explored (Tseng and Tseng, 1980; Yuan and Tseng, 1980). Further studies along these lines of research are needed. There is little doubt that *Phytophthora* research deserves more attention and more support than it has received in the past.

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