Distribution of Mating Types of Phytophthora palmivora

G. A. Zentmyer, D. J. Mitchell, Laura Jefferson,
J. Roheim, and D. Carnes

Department of Plant Pathology, University of California, Riverside 92502. Present address of second author: University of Florida, Gainesville 32601.

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ABSTRACT

Mating type was determined for 206 isolates of *Phytophthora palmivora*; 116 were A^2, 80 were A^1, and ten did not form oospores with either test strain. These data were combined with previous records of intraspecific crosses in *P. palmivora* to give for the first time a world-wide summation of the geographical distribution of the two mating types and of their host relationships. Both types occur in Brazil, Cameroun, Ceylon, Costa Rica, Gabon, Ghana, India, Ivory Coast, Jamaica, Malaya, Mexico, Nigeria, Puerto Rico, Rhodesia, Sarawak, and the United States (Hawaii). New records are included of A^1 and A^2 types in a number of countries.

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Phytophthora palmivora (Butler) Butler is essentially a tropical plant pathogen with a wide variety of hosts (5) on which it causes various disease symptoms. This paper presents information on the geographical and host distribution of the two mating or compatibility types in this species, based on 206 isolates from our culture collection and on information published by other investigators, as well as information on specimens in the collection at the Commonwealth Mycological Institute, England.

TABLE 1. Geographical distribution of A^1 and A^2 mating types of *Phytophthora palmivora* on various hosts

Theobroma cacao L. (cacao)

Africa

**[a]	Belgian Congo (7)[b]
***	Cameroun (9)
*	Fernando Po (8)
***	Gabon (6)
**	Ghana (9)
***	Gold Coast (3) (1)
**	Ivory Coast (9)
***	Nigeria (9)
*	Sao Thome (7)
**	Sierra Leone (3)
***	Tanzania (3)

Americas

***	Brazil (9)
**	British Guiana (8)
**	Colombia (9)
**	Costa Rica (9)
**	Dominican Rep. (9)
**	El Salvador (9)
*	Guatemala (9)
**	Honduras (9)
***	Jamaica (7)
***	Mexico (9)
**	Nicaragua (9)
**	Panama (7)
**	St. Lucia (7)
**	Surinam (7)
**	Trinidad (9)
**	Venezuela (9)

Pacific and Asia

***	Ceylon (8)
**	Fiji (9)
**	Malaya (8)
**	New Guinea (9)
*	North Borneo (8)
*	Philippines (1)
**	Solomon Islands (9)
**	Truk (9)
**	Western Samoa (8)

Hevea brasiliensis Muell. Arg. (rubber)

Africa

**	Ghana (8)
**	Ivory Coast (8)
*	Nigeria (6)

Americas

*	Brazil (9)
*	Costa Rica (9)

Pacific and Asia

***	Cambodia & Vietnam (4)
***	Ceylon (9) (8)
*	India (5)
***	Malaya (9) (8)

Piper nigrum L. (Black pepper)

**	Brazil (9)
*	Guatemala (9)
***	Puerto Rico (9)
***	Sarawak (2)

Carica papaya L.

**	Australia (9)
**	Brazil (9)
**	Ceylon (9)
*	Hawaii (9)
**	Saipan (9)

Other Hosts

Africa

Congo

*	*Citrus* sp. (9)

Ghana (Gold Coast)

*	*Mimusops* sp. (1)

Ivory Coast

***	*Citrus* (4) (9)
**	*Ananus sativus* Schult. (pineapple) (4)
**	*Lycopersicon esculentum* Mill. (tomato) (4)
**	*Solanum melongena* L. (eggplant) (4)

Malawi (Nyasaland)

**	*Dianthus caryophyllus* L. (carnation) (3)

Mauritius

**	*Yucca* sp. (3)

Nigeria

**	*Nicotiana tabacum* L. (tobacco) (3)

Rhodesia (So.)

***	Bougainvillea (3)
*	*Clianthus dampieri* (3) A. Cunn.

Americas

Brazil

**	Tomato (9)

Puerto Rico

*	*Cocos nucifera* L. (coconut) (1)
**	Eggplant (9)

Uruguay

*	Mandarin citrus (3)

Europe

Italy

*	*Dianthus caryophyllus* L. (carnation) (1)

(Table 1 continued on next page)

Table 1 (continued)

TABLE 1. Geographical distribution of A^1 and A^2 mating types of *Phytophthora palmivora* on various hosts

Pacific and Asia	
Australia (Queensland)	
**	*Anona squamosa* L. (3)
Ceylon	
*	*Artocarpus* sp. (breadfruit) (1)
**	Cattleya orchid (3)
**	*Cocos nucifera* L. (coconut) (9)
*	*Dendrobium* sp. (1)
**	*Lasia aculeata* Lour. (9)
*	*Odontadenia* sp. (1)
**	Orchid (9)
Hawaii	
*	Orchid (9)
**	Vanda orchid (3)
India	
*	*Borassus flabellifer* L. (5)
***	Coconut (5) (1)
**	*Citrus* sp. (3)
*	Breadfruit (5)
*	*Spondias mangifera* Willd. (5)
*	*Citrus sinensis* (L.) Osbeck (5)
Java	
**	*Vanda* sp. (1)
**	*Cattleya* sp. (1)
Malaya	
*	*Eugenia aromatica* Baill. (clove) (1)
*	Durian (9)
*	Orchid (9)
Philippines	
*	Coconut (1)
*	Citrus (1)
Trust Territory of Pacific Islands	
	(Ponape)
*	*Artocarpus* sp. (9)

[a] * = A^1 type, ** = A^2 type, *** = both types.

[b] Numbers refer to publications or laboratory where mating type was reported or determined:

1 – Ashby (2, 3)
2 – Brasier (4)
3 – Commonwealth Mycological Institute
4 – Ravisé (14)
5 – Thomas (17)
6 – Turner (20)
7 – Turner (21)
8 – Turner (22)
9 – University of California, Riverside

When both mating types are present reference for A^1 is listed first. (See Literature Cited for references referred to above).

Ashby in 1922 (1) first reported production of oospores by *P. palmivora* (then designated *P. faberi* Maubl.); his observations were from paired cultures of isolates from cacao and coconut in Jamaica. Additional reports of oospore production in *P. palmivora* were published by Gadd in 1924(7), Lester-Smith in 1927 (11), Ashby in 1929 (2,3), Thompson in 1929 (18), Leonian in 1931 (10), Thomas et al. in 1947 (17), Turner in 1960 and 1961 (20,21,22), Satchuthananthvale in 1963 (15), Peries & Dantanarayana in 1965 (12), Savage et al. in 1968 (16), Brasier in 1969 (4), and Zentmyer & Mitchell in 1970 (26).

Gadd initiated the terms 'cacao' or + group and 'rubber' or – group in 1924 (7), based on formation of oospores between paired cultures from cacao and rubber as well as several other hosts.

Turner used several designations for the mating or compatibility types in his three papers (20, 21, 22): 'G' (Ghanaian), 'A', and 'Group I' for the typical 'cacao' types, and 'N', 'Group B' and 'Group II' for the typical 'rubber' types. He also recognized some atypical forms that did not produce oospores when paired with either the 'cacao' or 'rubber' types.

In recent years the commonly-used designation for mating or compatibility type in *Phytophthora*, indicating production of oospores in paired culture, is A^1 and A^2. This nomenclature is based on the studies of Gallegly and Galindo (9) with *P. infestans*, and has been used for all species of *Phytophthora* in which the two types have been found, including *P. cambivora, P. capsici, P. cinnamomi, P. citrophthora, P. cryptogea, P. drechsleri, P. infestans, P. meadii, P. nicotianae* v. *parasitica, P. nicotianae* v. *nicotianae*.

In a number of publications on the genus *Phytophthora*, the terms "mating type" and "compatibility type" have been used interchangeably. Galindo & Gallegly (8) pointed out, that with *P. infestans*, mating is controlled by compatibility factors, so that mating types are really compatibility types and not morphological sex types. The terms need clarification for the entire genus, but in this paper we will use the term mating type. For the purpose of this paper the two types were distinguished by pairing them with isolates of *P. palmivora* whose type had been standardized by pairing with A^1 and A^2 isolates of *P. infestans*. The great majority of isolates act as either A^1 or A^2 when tested in this manner.

In *P. palmivora* the typical 'rubber' isolates are in the A^1 group and the 'cacao' isolates in the A^2 group. Savage et al. (16) pointed out this general relationship in their pairing studies published in 1968, as did Zentmyer & Mitchell (26) in their report of mating type distribution.

There have been numerous publications on the occurrence of mating types of *P. palmivora* in various parts of the world. This paper brings together for the first time information on the two types on a world-wide basis, utilizing the 206 cultures examined here plus many reports in which mating types could be related to the A^1 or A^2 type.

MATERIALS AND METHODS.—Cultures of *P.*

palmivora used in these studies are in the *Phytophthora* collection in this Department. They were obtained from a number of sources, as follows: D.V.W. Abeygunewardene, F. Albuquerque, R. Alconero, P. de T. Alvim, G. Blaha, R. Fox, M. E. Gallegly, F. A. Haasis, E. P. Imle, H. Maia Rocha, A. G. Medeiros, R. A. Muller, S. Romero, M. Tarjot, B. H. Waite, A. Watson, the American Type Culture Collection, the Commonwealth Mycological Institute, and the Centraalbureau voor Schimmelcultures. Many of the cultures were isolated by the senior author in the Pacific area, Central and South America, the Caribbean, and Africa.

Additional information on occurrence of the two compatibility types was obtained by examining the collection of slides of species of *Phytophthora* in the Commonwealth Mycological Institute herbarium, through the courtesy of Director Anthony Johnston and with the cooperation of Miss Grace Waterhouse and Miss Jean Stamps. Some of the original cultures from which the slides were prepared had been paired with 'cacao' or 'rubber' strains of *P. palmivora* by Grace Waterhouse or Jean Stamps.

In the present studies, isolates were grown on clear V-8 agar (CV8A) prepared by adding 3.3 g of $CaCO_3$ to 235 ml of Campbell V8 juice and centrifuging the mixture at 1,000 *g* for 15 min; the supernatant was diluted 1:4 with deionized water and 15 g of agar per liter were added. Isolates were paired with isolates of *P. palmivora* previously designated as A^1 and A^2 mating types by comparison with A^1 and A^2 types of *P. infestans*. These tests were done in petri dishes containing 15 ml of CV8A, and incubated in the dark at 22-26 C for 7 to 10 days.

RESULTS.–In pairing tests with 206 cultures, 116 were of the A^2 mating type and 80 were A^1. The remainder of the cultures did not form oospores with either of our test strains, and thus cannot be classified as to mating type as present. One culture, an isolate from coconut in Ceylon, appeared at first to be homothallic. It was apparently a mixed culture, however, as single zoospore cultures from it did not produce the sexual stage. A few isolates, notably 253 (A^1 from Mexico provided by S. Romero) formed a few golden brown oospores near the inoculum plug, both in paired and unpaired cultures.

The results of the pairing tests are presented in Table 1, which gives the distribution of the two mating types by country and by host. This table combines the information on our tests with the information obtained from the Commonwealth Mycological Institute and from published results. Results of pairing tests on cultures in the collection at Riverside indicated in the tables by the designation '(9)' constitute the first definite record of A^1 or A^2 mating type on the particular host in a number of areas.

The A^1 type was found on cacao in Brazil and Guatemala, on black pepper in Guatemala and Costa Rica, on papaya in Hawaii, and on breadfruit in Ponape (Trust Territory of Pacific Islands). New records of the A^2 type on cacao include: Colombia, Dominican Republic, El Salvador, Fiji, Honduras, New Guinea, Nicaragua, Solomon Islands, Trinidad, Truk, and Venezuela; on black pepper: Brazil and Puerto Rico; and on papaya: Australia, Brazil, Ceylon, and Saipan.

The two mating types of *P. palmivora* both occur in the following countries based on our tests and the other reports: Africa – Cameroun, Gabon, Ghana, Ivory Coast, Nigeria, Rhodesia; Americas – Brazil, Costa Rica, Jamaica, Mexico, Puerto Rico, United States (Hawaii); Asia – Cambodia, Ceylon, Malaya, Sarawak, Vietnam. Both mating types occur on cacao in Cameroun, Gabon, Ghana, Nigeria, Brazil, Jamaica, Mexico and Ceylon. Both types occur on rubber in Cambodia and Vietnam, Ceylon and Malaya.

DISCUSSION.–*Phytophthora palmivora* is essentially a heterothallic species, although there have been a few reports of oospores in isolates grown alone (2,3,12,18). Possibly some of these were mixed cultures since in our tests a "homothallic" culture from coconut in Ceylon which did not produce oospores from single zoospore cultures produced oospores in the original mass transfer isolate.

When both types are present in the same locality there may be opportunity for hybridization and formation of new strains of the fungus. The variable nature of *P. palmivora* isolates (Fig. 1) may be an indication of such hybridization. An unknown factor in the situation at present is the role that interspecific crosses may play in variation in this, as well as in other, species of *Phytophthora*. Oospores have been reported in interspecific crosses between *P. palmivora* and several other species of the genus (1,6,16,24,25). In no case, however, has germination of such "hybrid" oospores been obtained. The recent report by Brasier (4) of stimulation of oospore production in single cultures of A^2 type of *Phytophthora* in the presence of *Trichoderma viride* and our report (23) of production of oospores in single zoospore cultures of *P. cinnamomi* and *P. drechsleri* in an avocado root extract also are significant in relation to the sexual stage of *P. palmivora*. Formation of oospores under such conditions, where the fungus is essentially acting as a homothallic species, does not negate the significance of oospore production by the two mating types.

The most prevalent type on cacao in Ghana is the A^2 type, based on cultures examined by Turner (20) and others, and on cultures isolated in Ghana by the senior author in 1969. The report of the A^1 type on cacao in Ghana is based on the Commonwealth Mycological Institute collection, which includes one isolate from the Gold Coast (now part of Ghana) in 1956 which was determined to be the 'rubber' strain. The A^1 type was also reported in 1929 by Ashby (3), on *Mimusops* sp. in the Gold Coast.

Some data from previous reports have not been included because of difficulty in interpretation. Some of Satchuthanthvale's (15) cultures were later shown by Peries and Dantanarayana (12) to be *P. meadii*. Thomas et al. (17) combined *P. arecae, P. faberi, P. meadii, P. parasitica* v. *nicotianae*, and *P. palmivora* isolates into one species, *P. palmivora*. Their pairing studies are thus of doubtful value in relation to

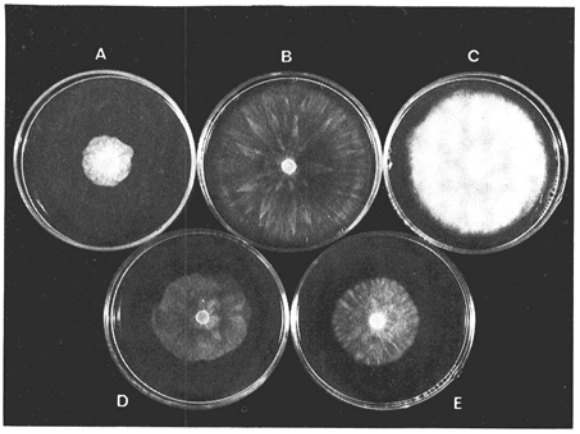

Fig. 1. Cultures of *Phytophthora palmivora* from cacao, in (A) Ceylon, (B) Brazil, (C) Mexico, (D) Nigeria, and (E) Costa Rica. C and D are A^1 mating type, the others are A^2. Cultures grown at 24 C for 4 days on potato-dextrose agar.

intraspecific crosses and mainly constitute another report of interspecific pairing in the genus. Ravise's (13) data also are somewhat confusing since many of his pairings were sterile.

This paper constitutes the most complete report possible at the present time of the geographical distribution of mating or compatibility types of *P. palmivora* and their host relationships, based on the 206 cultures tested in this laboratory plus records from the CMI, and previous reports by other authors. Obviously, changes and additions will be made as new cultures are examined.

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