Emergence of self-fertile *Phytophthora colocasiae* is a possible reason for the widespread expansion and persistence of taro leaf blight in Japan

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Abstract
Since 2015, the leaf blight of taro caused by *Phytophthora colocasiae* has resulted in severe economic loss in Japan. In order to investigate the causes of disease expansion and persistence, we need to clarify the mating type distribution of this pathogen, and to characterize each mating type. We collected 317 *P. colocasiae* isolates from 99 agricultural plots in seven prefectures from 2014 to 2020. We examined the mating type of each isolate and the distribution of mating types in each region and location. Five mating types were identified: heterothallic A1 and A2 and self-fertile (SF) A1, A2, and A1/A2. We found complex mating type distributions in some plots, and some leaves with multiple lesions carried more than one mating type. In addition, the variability of each mating type was checked after growth of single colonies from hyphal tips, zoosporangia, and zoospores. The SF type isolates were genetically unstable and segregated into both heterothallic and SF types after propagation. On the other hand, the heterothallic A1 and A2 isolates were stable. In pathogenicity tests, the heterothallic A1 isolates were less pathogenic than the heterothallic A2 and SF isolates. The SF strains can self-fertilize or mate with the heterothallic strains and produced abundant oospores. Therefore, the SF strains have the ability to reproduce at high rates and survive long term in the environment. The characteristics suggest that one possible causal factor for the rapid expansion and persistence of this disease is the appearance of the SF mating types in Japan.

Keywords Heterothallic · Homothallic · Transmission · Oospore formation

Introduction

*Phytophthora colocasiae* Raciborski causes a leaf blight disease of taro (*Colocasia esculenta* (L.) Schott) and was first identified in Java in 1900 (Raciborski 1900). It is widely distributed in tropical and subtropical areas, including Southeast Asia, many Pacific territories, and parts of Oceania (Singh et al. 2012). The disease has caused significant yield losses up to 50% or more in many locations (Tchameni et al. 2017). This disease was first reported in Japan in 1967, but there were no severe outbreaks until 2014, and since then the disease has been spreading rapidly. In August 2015, serious outbreaks occurred simultaneously in Miyazaki, Kagoshima, and Ehime Prefectures, with losses of around 60% in Ehime Prefecture (Kurogi 2017). The disease expanded to Chiba, Saitama and Fukui, and Gifu in 2018, 2019, and 2020, respectively, and it continues to spread. The pathogen can even infect the corms of taro, putting taro storage and seeding at risk.

*Phytophthora colocasiae* produces asexual spores (zoospores) that are released from zoosporangia and can spread rapidly through water (Brooks 2005). During wet climate, zoosporangia are abundantly produced on the lesions of infected leaves or petioles, and dissemination through rain splash is a common dispersal mechanism (Singh et al. 2012). A heavy rainstorm or typhoon is usually the main or one of the main trigger for the invasive spread of *P. colocasiae* between adjacent taro leaves, plants, and agricultural plots. Zoosporangia have been considered the most important
survival structure of this pathogen in soil (Quitugua and Trujillo 1998); however, the zoosporangia cannot survive for long time periods. Gómez (1925) reported that P. colocasiae zoosporangia can survive up to three months on taro leaf tissue. Besides this, Gollifer et al. (1980) found that zoosporangia can last no longer than 21 days in either naturally or artificially infested soil. The longest reported survival periods were more than three months in soil at – 1500 J/kg matric potential, and less than 1 year in the absence of the host (Quitugua and Trujillo 1998). Therefore, given the long-term recurrence of taro leaf blight, we need to investigate potential sources and routes of infestation other than zoosporangia.

Oospores of Phytophthora produced through sexual reproduction can survive for long periods under adverse natural conditions (Sivamani et al. 1987). The oospores of homothallic species such as Phytophthora sojae and Phytophthora cactorum, which produce oospores in single cultures, can survive in soil for a long period (Schmitthenner 1985; Sneh and McIntosh 1974). Heterothallic species depend on the presence of opposite mating types (A1 and A2) for oospore formation (Weste 1983). Heterothallic Phytophthora infestans produces oospores on diseased tomato leaflets and fruits in field crops (Cohen et al. 1997). Phytophthora coloreasiae is heterothallic, and the A2 mating type appears to be predominant (Ann et al. 1986; Tyson and Fullerton 2007; Mellow et al. 2018). The A1 type has been isolated only in Hawaii, USA (Ko 1979), India (Narula and Mehrotra 1980), and Hainan Island in China (Zhang et al. 1994). Lin and Ko (2008) found seven self-fertile (SF) A1/ A2-type isolates in Taiwan.

Since 2015, taro leaf and petiole blight caused by P. coloreasiae has become a serious problem in Japan. The mechanisms for the widespread outbreaks in multiple taro production areas and the persistence of the disease over years in the same area are not clear. There has been no previous report on the mating-type distribution of P. coloreasiae in Japan. If multiple mating types and/or SF strains coexist in a field, oospore formation could occur and this would enhance the survivability of the pathogen. This could be a possible mechanism for the expansion and persistence of the disease. Therefore, in this study we examined the distribution of, and variation among, mating types, and compared the pathogenicity of different mating types in isolates collected from taro growing areas in Japan.

Materials and methods

Collection and maintenance of isolates

A total of 317 isolates were obtained from diseased taro leaves and petioles (Table S1). The diseased samples were collected from 11, 35, 17, 17, 7, 8, and 4 agricultural plots of Kagoshima, Miyazaki, Ehime, Chiba, Saitama, Fukui, and Gifu Prefectures, respectively, between 2014 and 2020. The isolates were recovered using selective cornmeal agar amended with nystatin, ampicillin, rifampicin, and miconazole (NARM) (Morita and Tojo 2007). All isolates were maintained on corn meal agar (CMA) or potato-dextrose agar (PDA) at 20 °C in the darkness.

Mating type tests

All isolates were grown on 60 mm Petri dishes with 5 mL of V8 juice agar (V8A) medium [15% clarified V8 juice (Campbell Soup Co., NJ, USA) with 2.5 g/L CaCO₃ and 2% agar] at 25 °C in the darkness. To select the Japanese isolates with strong mating reactions, we used an isolate with a known mating-type, P6317 (A2) from the World Phytophthora Genetic Resource Collection. At this stage we could not use a known A1 type isolate, because no such isolate had been deposited in the international culture collections. After 150 Japanese isolates were tested with P6317, we selected EPC201522 (A1 type) and EPC2017Ko1 (A2 type) to be used as the standard mating type isolates for this study. Three V8A plates were prepared for each isolate: one for incubation as a single culture and the other two for pairing with either EPC201522 or EPC2017Ko1. Sexual structure formation was examined after incubation for 6 to 14 days, and the mating types were estimated. The single culture plates were examined for sexual structures twice after more than a month to determine whether the isolate was heterothallic or self-fertile.

Variability of mating types after vegetative propagation

Isolates showing strong mating reactions were selected from three major taro production areas: Miyazaki, Kagoshima, and Ehime Prefectures (Table S2). For single hyphal cultures, each isolate was placed on 2% water agar (WA) medium. After incubation for 48 h at 25 °C, a single hyphal tip was isolated under an inverted microscope and placed on NARM medium. The colony from the single hypha was then transferred to a CMA slant for long-term storage at room temperature. For single zoosporangium and zoosporangia cultures, each isolate was grown on V8A medium for one week at 25 °C. A mycelial agar disk was excised from the margin of each colony using a 5-mm cork borer and transferred to a sterilized pond: distilled water (1:2) mixture. After 24–48 h incubation at 25 °C, when zoospores were released from the zoosporangia and zoosporangia were detached from the sporangiophores, the suspension was placed on NARM medium and incubated for 24 h at 25 °C. Colonies from single zoosporangium or zoospores were then transferred to
NARM medium for further incubation at 25 °C. Mycelial mats were sub-cultured onto CMA slants for long-term storage at room temperature. Mating tests were conducted as described above.

Pathogenicity tests

Seedlings of taro cultivar ‘Ishikawawase’ were propagated in a growth chamber at 25 °C with a 12 h light/12 h darkness cycle. Expanded leaves were detached and used in the pathogenicity tests. The leaves were cut into round discs approximately 50 mm in diameter, and each disc was placed in a 90-mm Petri dish with 5 mL sterile distilled water, after inoculation as follows. Isolates from the major taro production areas, Kagoshima, Miyazaki, and Ehime Prefectures (Fig. 3, Table S3) were sub-cultured on V8A plates and incubated at 25 °C in the darkness for 3–5 days. A circular block of agar was excised from the edge of each actively growing colony using an 11.5 mm cork borer and placed on a leaf disc. A 5-mm cork borer was then used to make a hole in the middle of the agar block, and 2–3 droplets of sterile distilled water were dropped onto the hole. The plate containing the inoculated leaf disc was incubated at 25 °C for 3 days at 25 °C with a 12 h light/12 h darkness cycle. Then the size of the lesion was measured to assess the virulence of the isolate. Each experiment was repeated 3 times.

Results

Mating-type diversity

All 317 isolates obtained from 99 agricultural plots in seven prefectures were grown as single cultures and in cultures paired with each of our selected standard mating types (A1, EPC201522 and A2, EPC2017Ko1). By observing the sexual structures in the single cultures and in the reacting zones between paired colonies, we identified four kinds of mating types: heterothallic A1 and A2 types, and self-fertile (SF) A2 and A1/A2 types (Figs. 1 and 2). There were eight heterothallic A1 and 200 heterothallic A2 mating types among the 317 isolates. The remaining 109 isolates were SF and produced sexual structures (oogonia, antheridia, and oospores) in single cultures. However, these SF isolates also strongly reacted with the A1 type strain (103 isolates) or with both the A1 and A2 type strains (six isolates), and produced abundant sexual structures in the reacting zones (Fig. 1, Table 1).

Most of the heterothallic A1 type isolates were found in Ehime Prefecture, and one of each were found in Kagoshima and Miyazaki Prefectures (Fig. 3, Table 1). A2 type isolates were detected in almost all the agricultural plots in the surveyed prefectures. The SF A2 type isolates were also detected in many plots and in all surveyed prefectures. Like the heterothallic A1 isolates, the SF A1/A2 isolates were found only in Kagoshima, Miyazaki, and Ehime Prefectures.
Agricultural plots that had only SF strains were found in Miyazaki and Ehime Prefectures.

**Compositions of mating types in agricultural plots and in different lesions on single leaves**

We found multiple mating types in 31 of the 64 taro agricultural plots where two or more isolates were collected. (Table S1). Thirty of the 64 plots had only heterothallic A2 type strains, and three plots had only SF A2 type strains. No field had only A1 type strains. On the other hand, two plots had both heterothallic A1 and A2 types, 22 plots had heterothallic A2 and SF A2, two plots had heterothallic A2, SF A2, and SF A1/A2, three plots had heterothallic A1, A2, and SF A2, and two plots had all four types (Table S1).

We collected multiple leaves (two or three) showing multiple lesions from each of five agricultural plots in Kagoshima Prefecture (Table 2). In all five plots, we found

![Fig. 2 The formation of sexual reproductive structures of *Phytophthora colocasiae* in contact zones between mating types A1 and A2. A1 EPC201522; A2 EPC2017KO1](image)
at least one leaf infected with multiple mating types. Eight of the 13 tested leaves were each infected with two mating types, and the combination of heterothallic A2 with SF A2 was observed most frequently.

**Variability in mating types after vegetative propagation**

To determine if variability in mating types would occur after vegetative propagation of different mating type strains, we propagated single cultures from hyphal tips, zoosporangia, and zoospores, and tested the mating reactions of the isolates (Table 3).

Whether the single cultures were derived from hyphal tips, zoosporangia, or zoospores, the heterothallic A1 and A2 strains produced only A1 and A2 isolates, respectively (Table 3). On the other hand, five of the seven tested SF strains produced mixtures of heterothallic and SF isolates when propagated using hyphal tips. Strain KS17Ai3-2 (SF A2) produced only heterothallic A2 isolates. The two SF A1/A2 strains segregated into SF A1 and SF A2 (KS16TaOki5) or into heterothallic A1, SF A1, and SF A2 (KS16TaYo2) after propagation from hyphal tips (Table 3).

After propagation from single zoosporangia, the SF A2 strains all produced heterothallic isolates (either A1, A2, or both A1 and A2) in larger numbers than SF isolates. The only SF isolates derived from the SF A2 strains were one SF A2 isolate from EPC201527 and three SF A1 isolates from MS28101. The SF A1/A2 strain KS16TaOki5 produced all four mating types from the single zoosporangium cultures,

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*Fig. 3* Distribution of mating-types of *Phytophthora colocasiae* in Japan based on the data from this study.
while KS16TaOki5 produced five A2 and three SF A2 isolates (Table 3).

After propagation from single zoospores, all of the SF mating types (both A2 and A1/A2) produced mainly heterothallic A2 type isolates. In addition, MS28101 and EPC201527 produced three and four SF A2 isolates, respectively. Strain KS17Ai3-2 produced five A1 and seven A2 heterothallic isolates (Table 3).

Comparison of pathogenicity between mating types

Detached leaves have not generally been used for bioassays; however, taro leaves were evaluated and found to be useful for the selection of cultivars resistant to P. colocasiae (Brooks 2008). Therefore, in this study, we used detached taro leaves in pathogenicity tests.

To compare the pathogenicity between mating types, we selected one isolate of each mating type (except SF A1) from Kagoshima, Miyazaki, and Ehime Prefectures. (Fig. 4, Table S3). In addition, we tested an SF A1 isolate that was derived from strain KS16TaYo2 after subculturing. Taro leaf discs were inoculated with agar plugs containing each isolate, and incubated for 3 days at 25 °C. Three isolates, one heterothallic A2 isolate from Miyazaki and two SF A2 isolates from Miyazaki and Kagoshima, expressed strong pathogenicity, with average growth of about 10 mm from the edge of the agar plug. Five isolates, including the three heterothallic A1 isolates, one SF A2 isolate from Ehime, and one SF A1/A2 isolate from Kagoshima, demonstrated weak or even no pathogenicity, with average growth of less than 3 mm from the edge of the agar plug. The other isolates showed moderate pathogenicity.

We also compared growth rates on V8A and found variability between the isolates; however, we saw no relationship between the growth rate on V8A and pathogenicity on taro. To evaluate the stability of the mating types in these isolates during the pathogenicity tests, we recovered isolates from the lesions and again tested them for mating type. The heterothallic A1 and A2 mating types were stable, however, several SF isolates changed their mating type, for example from SF A1 or A2 to SF A1/A2, or from SF A1/A2 to SF A2 (Table S3).

Discussion

A majority of the P. colocasiae isolates collected in South Asia were identified as the heterothallic A2 mating type (Ann et al. 1986; Tyson and Fullerton 2007; Mellow et al. 2018). The A1 type was common only in Hawaii, USA (Ko 1979) and India (Narula and Mehrotra 1980). On Hainan Island of China, the ratio of A1:A2 types was 1:1, suggesting that the island could be the center of origin of P. colocasiae (Zhang et al. 1994). Self-fertile isolates have previously been found only in Taiwan (Lin and Ko 2008). In this study, we examined 317 isolates collected over a period of six years from 99 agricultural plots in seven prefectures of Japan. In total, we found five kinds of mating types: heterothallic A1 and A2 and SF A1, A2, and A1/A2. The heterothallic A2 type was the most frequent (63%), followed by the SF A2 type (33%), and the frequency of the heterothallic A1 type was only 3%. This kind of mating type diversity in P. colocasiae has not been reported in any other country.

We surveyed taro agricultural plots from seven prefectures, including Kagoshima, Miyazaki, and Ehime Prefectures in the south, Fukui and Gifu Prefectures in central Japan, and Saitama and Chiba Prefectures in the east (Fig. 3). A diversity of mating types was found in the southern prefectures, while only A2 and SF A2 types were found in central and eastern Japan. This kind of mating diversity was also found in P. nicotianae in Japan and Indonesia (Afandi et al. 2019). Furthermore, we found multiple mating types in 64 plots and on 13 taro leaves that had more than one lesion. Both the heterothallic A1 and A2 types existed simultaneously in some plots, and one leaf carried both the A1 type and the SF A2 type. Approximately 35% of all isolates were self-fertile. These results suggest that oospores could be produced as survival structures in nature.

Early researchers suggested that the A1 mating type of oomycetes was relatively stable among self-progenies, while the A2 type produced highly variable mating types after self-propagation (Gallegly 1970; Timmer 1970; Ko 1988). In this study, we randomly selected several P. colocasiae isolates of each mating type to check the stability of mating types after growth of single colonies from hyphal tips, zoosporangia,

| Table 2 Mating types on leaves where two or more isolates were collected in Kagoshima Prefecture |
|-----------------------------------|------------------|------------------|------------------|
| Field no | No. of isolates | Heterothallic | Self-fertile |
|          |                 | A1     | A2 | A2    |
| 1         | 1                | 3      | 0   | 2     | 1     |
| 2         | 2                | 2      | 1   | 0     | 1     |
| 3         | 3                | 3      | 0   | 2     | 1     |
| 4         | 3                | 3      | 0   | 1     | 2     |
| 5         | 3                | 3      | 0   | 1     | 2     |

Mycological Progress (2022) 21:49–58
Table 3  Variability in mating-types among progenies after propagation from hyphae, zoosporangia, and zoospores in Phytophthora colocasiae

| Isolation method and tested isolate | No. of tested isolates | Heterothallic | Self-fertile |
|------------------------------------|------------------------|---------------|--------------|
|                                    |                        | A1  | A2  | A1  | A2  |
| Single hyphal tip isolation        |                        |     |     |     |     |
| A1 type                            | EPC201509              | 2   | 2   | 0   | 0   |
|                                    | EPC201522              | 4   | 4   | 0   | 0   |
| A2 type                            | KS17Ai1-2              | 10  | 0   | 10  | 0   |
|                                    | EPC2017Ko1             | 5   | 0   | 5   | 0   |
| Self-fertile A2 type               | MS28041                | 4   | 0   | 1   | 0   |
|                                    | MS28101                | 4   | 0   | 1   | 0   |
|                                    | KS17Ai3-2              | 12  | 0   | 12  | 0   |
|                                    | EPC201527              | 4   | 0   | 1   | 0   |
|                                    | EPC201534              | 7   | 0   | 2   | 0   |
| Self-fertile A1/A2 type            | KS16TaYo2              | 12  | 3   | 0   | 1   |
|                                    | KS16TaOki5             | 3   | 0   | 0   | 1   |
| Single zoosporangium isolation     |                        |     |     |     |     |
| A1 type                            | EPC201509              | 10  | 10  | 0   | 0   |
|                                    | EPC201522              | 10  | 10  | 0   | 0   |
| A2 type                            | KS17Ai1-2              | 7   | 0   | 10  | 0   |
|                                    | EPC2017Ko1             | 7   | 0   | 7   | 0   |
| Self-fertile A2 type               | MS28041                | 8   | 0   | 8   | 0   |
|                                    | MS28101                | 10  | 2   | 7   | 0   |
|                                    | KS17Ai3-2              | 15  | 0   | 15  | 0   |
|                                    | EPC201527              | 12  | 9   | 0   | 3   |
|                                    | EPC201534              | 14  | 0   | 14  | 0   |
| Self-fertile A1/A2 type            | KS16TaYo2              | 10  | 1   | 1   | 1   |
|                                    | KS16TaOki5             | 8   | 0   | 5   | 0   |
| Single zoospore isolation          |                        |     |     |     |     |
| A1 type                            | EPC201509              | 9   | 9   | 0   | 0   |
|                                    | EPC201522              | 11  | 11  | 0   | 0   |
| A2 type                            | KS17Ai1-2              | 10  | 0   | 10  | 0   |
|                                    | EPC2017Ko1             | 7   | 0   | 7   | 0   |
| Self-fertile A2 type               | MS28041                | 10  | 0   | 10  | 0   |
|                                    | MS28101                | 7   | 0   | 4   | 0   |
|                                    | KS17Ai3-2              | 12  | 5   | 7   | 0   |
|                                    | EPC201527              | 7   | 0   | 3   | 0   |
|                                    | EPC201534              | 6   | 0   | 6   | 0   |
| Self-fertile A1/A2 type            | KS16TaYo2              | 10  | 0   | 10  | 0   |
|                                    | KS16TaOki5             | 10  | 0   | 10  | 0   |
and zoospores. The SF type isolates were genetically unstable and segregated into both heterothallic and SF types after propagation. On the other hand, the heterothallic A1 and A2 isolates were stable. Similar results have been found in several other *Phytophthora* species. Mortimer et al. (1977) and Fyfe and Shaw (1992) found that the SF A1/A2 types of *P. drechsleri* and *P. infestans* could segregate into heterothallic A1 or A2 types after vegetative propagation or from zoospores. A hypothesis was put forward that the mating types of *Phytophthora* spp. are regulated by the molecular configuration of a repressor (Ko 1988). Many factors are believed to affect the variation in mating types during asexual reproduction, including aging, fungicide exposure, changes in nutritional conditions, metabolite stimulation from soil microorganisms, and mechanical damage (Ann and Ko 1989; Ko 1994, 2007). Genetic factors including heterokaryosis and polyploidy are also likely to affect mating type variation (Jung et al. 2017; Shrestha et al. 2017). The causes of mating-type variation in *P. colocasiae* remain unclear and will be the subject of further studies. We also plan to investigate the conditions needed for efficient oospore germination, and then explore the variability of mating types in progeny grown from single oospores.

We examined the pathogenicity of different mating-types on taro leaves. Generally, the heterothallic A2 isolates tended to be more virulent than the heterothallic A1 types. On the other hand, the virulence of the SF isolates was more variable. This could be explained by their genetic instability, but the mating types of the SF isolates did not change after they were recovered from the inoculated taro leaves and re-tested. In addition, there was no obvious correlation between mating-type and growth rate or between virulence and growth rate. Moreover, we found some isolates had weak or even no virulence on taro leaves. These could be important materials for studying the pathogenic mechanisms of this pathogen.

One possible causal factor in the rapid and extensive outbreak of this disease in Japan is the appearance of the SF mating types. These strains have both high virulence and the ability to reproduce at high rates. We noted that more oospores were produced in mating cultures between heterothallic A1 and A2 types than in single cultures of the SF isolates (data not shown). However, the SF isolates also mated with either the heterothallic A1 or A2 types, or with both the A1 and A2 types, and produced abundant oospores. Therefore, the SF strains have the ability to reproduce at high rates and survive long term in the environment. This will enable them to be transmitted between different taro production areas and to persist in the same area over multiple years. A primary source of infection could be infected seed corms, and the SF strains of *P. colocasiae* could have arrived in Japan when infected corms were imported from other countries. This possibility could be clarified using population structure analyses based on simple sequence repeat and single nucleotide polymorphism markers (Afandi et al. 2019; Masanto et al. 2019; Shrestha et al. 2014).

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**Fig. 4** A column graph comparing the pathogenicity of different *Phytophthora colocasiae* mating-type isolates identified in this study. The bars on the diagram represent standard errors.
Authors’ contributions WF, KO, and KK performed the experiments and analyzed the data. WF, AH, KO, SH, and KK conceived, drafted, and edited the manuscript. All authors have approved the final version of the manuscript.

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Data availability Not applicable.

Code availability Not applicable.

Declarations

Conflicts of interest The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as potential conflicts of interest.

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References

Afandi A, Hieno A, Wibowo A, Subandiyah S, Afandi SH, Tsuchida K, Kageyama K (2019) Genetic diversity of Phytophthora nicotianae reveals pathogen transmission mode in Japan. J Gen Plant Path 85:189–200

Ann PJ, Ko WH (1989) Effect of chloroneb and ethazol on mating type of Phytophthora parasitica and P. cinnamomi. Bot Bull Acad Sinica 30:207–210

Ann PJ, Kao CW, Ko WH (1986) Mating-type distribution of Phytophthora colocasiae in Taiwan. Mycopathologia 93:193–194. https://doi.org/10.1007/BF00443524

Brooks F (2005) Taro leaf blight. In: Oomycetes. American Phytopathological Society https://www.apsne t.org/edcen ter/intro pp/lesso ns/fungi /Oomyc etes/Pages /TaroL caeBl ight.aspx. Cited 4 September 2018

Brooks F (2008) Detached-leaf bioassay for evaluating taro resistance to Phytophthora colocasiae. Plant Dis 92:126–131. https://doi.org/10.1094/PDIS-92-1-0126

Fyfe AM, Shaw DS (1992) An analysis of self-fertility in field isolates of Phytophthora infestans. Mycol Res 96:390–394. https://doi.org/10.1016/S0953-7562(99)80958-1

Gallegly ME (1970) Genetics of Phytophthora. Phytopathology 60:135–141. https://doi.org/10.1094/Phyto-60-1135

Cohen Y, Farkash S, Reshiti Z, Baider A (1997) Oospore production of Phytophthora infestans in potato and tomato leaves. Phytopathology 87:191–196. https://doi.org/10.1094/PHYTO.1997.87.2.191

Gollifer DE, Jackson G, Newhook FJ (1980) Survival of inoculum of the leaf blight fungus Phytophthora colocasiae infecting taro, Colocasia esculenta in the Solomon Islands. Ann Appl Biol 94:379–390. https://doi.org/10.1111/j.1744-7348.1980.tb03953.x

Gómez ET (1925) Leaf Blight of Gagli Philagr. Agric 14:429–440

Jung T, Jung MH, Scano B, Seress D, Kovács GM, Maia C, Pérez-Sierra A, Chang T-T, Chandelier A, Heungens K, van Poucke K, Abad-Campos P, Léon M, Cacciola SO, Bakonyi J (2017) Six new Phytophthora species from ITS Clade 7a including two sexually functional heterothallic hybrid species detected in natural ecosystems in Taiwan. Persoonia 38:100–135

Ko WH (1979) Mating-type distribution of Phytophthora colocasiae on the island of Hawaii. Mycologia 71:434–437. https://doi.org/10.1080/00275519.1979.12021021

Ko WH (1988) Hormonal heterothallism and homothallism in Phytophthora. Ann Rev Phytopathol 26:57–73

Ko WH (1994) An alternative possible origin of the A2 mating type of Phytophthora infestans outside Mexico. Phytopathology 84:1224–1227. https://doi.org/10.1094/Phyto-84-1224

Ko WH (2007) Hormonal regulation of sexual reproduction in Phytophthora. Bot Stud 48:365–375. https://doi.org/10.1007/s10022-007-425

Kurogi S (2017) The occurrences of taro leaf blight caused by Phytophthora colocasiae in Miyazaki prefecture and its control measures (in Japanese). Plant Protect 71:458–462

Lin MJ, Ko WH (2008) Occurrence of isolates of Phytophthora colocasiae in Taiwan with homothallic behavior and its significance. Mycologia 100:727–734. https://doi.org/10.3852/08-070

Masanto HA, Wibowo A, Subandiyah S, Shimizu M, Suga H, Kageyama K (2019) Genetic diversity of Phytophthora palmivora isolates from Indonesia and Japan using rep-PCR and microsatellite markers. J Gen Plant Path 85:367–381

Mellow KD, Tyson JL, Fullerton RA, Tugaga A, Maslen-Miller A (2018) Mating types of Phytophthora colocasiae on the island of Upolu Samoa. New Zealand Plant Prot 71:289–292. https://doi.org/10.30843/nzpp.2018.71.143

Morita Y, Tojo M (2007) Modifications of PARP medium using fluaizin, miconazole, and nystatin for detection of Pythium spp. in soil. Plant Dis 91:1591–1599. https://doi.org/10.1094/PDIS-91-12-1591

Mortimer AM, Shaw DS, Sansome ER (1977) Genetic studies of secondary homothallism in Phytophthora drechsleri. Arch Microbiol 111:255–259. https://doi.org/10.1007/BF00393463

Narula KL, Mehrrota RS (1980) Occurrence of A1 mating type of Phytophthora colocasiae. Indian Phytopathol 33:603–604

Quitugua RJ, Trujillo EE (1998) Survival of Phytophthora colocasiae in field soil at various temperatures and water matric potentials. Plant Dis 82:203–207. https://doi.org/10.1094/Phyto-98.82.2.203

Raciborski M (1990) Parasitic algae and fungi. Java Batavia Bull 19:189

Schmitthenner AF (1985) Problems and progress in control of Phytophthora root rot of soybean. Plant Dis 69:362–368. https://doi.org/10.1094/ PD-69-362

Shrestha S, Hu J, Fryxell RT, Mudge J, Lamour K (2014) SNP markers identify widely distributed clonal lineages of Phytophthora colocasiae in Vietnam, Hawaii and Hainan Island, China. Mycologia 106:676–685

Shrestha SK, Miyasaka SC, Shinitsku M, Kelly H, Lamour K (2017) Phytophthora colocasiae from Vietnam, China, Hawaii and Nepal: intra- and inter-genomic variations in ploidy and a long-lived, diploid Hawaiian lineage. Mycol Progress 16:893–904. https://doi.org/10.1007/s12273-017-0132-z

Singh D, Jackson G, Hunter D, Fullerton R, Lebot V, Taylor M, Iosefa T, Okpul T, Tyson J (2012) Taro leaf blight—a threat to food security. Agriculture 2:182–203. https://doi.org/10.3390/agriculture2030182
Sivamani E, Anuratha CS, Gnanamanickam SS (1987) Toxicity of _Pseudomonas fluorescens_ towards bacterial plant pathogens of banana (_Pseudomonas solanacearum_) and rice (_Xanthomonas campestris pv. oryzae_). Curr Sci (Bangalore) 56:547–548

Sneh B, McIntosh DL (1974) Studies on the behavior and survival of _Phytophthora cactorum_ in soil. Revue Canadienne De Botanique 52:795–802. https://doi.org/10.1139/b74-103

Timmer LW, Castro J, Erwin DC, Belser WL, Zentmyer GA (1970) Genetic evidence for zygotic meiosis in _Phytophthora capsici_. Am J Bot 57:1211–1218. https://doi.org/10.1002/j.1537-2197.1970.tb09926.x

Tchameni SN, Mbiakeu SN, Sameza ML, Jazet PMD, Tchoumbougnang F (2017) Using _citrus aurantifolia_ essential oil for the potential biocontrol of _Colocasia esculenta_ (taro) leaf blight caused by _Phytophthora colocasiae_. Environ Sci Pollut Res 25:29929–29935

Tyson JL, Fullerton RA (2007) Mating types of _Phytophthora colocasiae_ from the Pacific region, India and South-east Asia. Australas Plant Dis Notes 2:111–112. https://doi.org/10.1071/DN07046

Weste G (1983) Population dynamics and survival of _Phytophthora_. In: Erwin DC, Bartnicki-Garcia S, Tsao PH (eds) _Phytophthora_: its biology, taxonomy, ecology, and pathology. American Phytopathological Society, St. Paul, pp 237–258

Zhang KM, Zheng FC, Li YD, Ann PJ, Ko WH (1994) Isolates of _Phytophthora colocasiae_ from Hainan island in China: evidence suggesting an Asian origin of this species. Mycologia 86:108–112. https://doi.org/10.2307/3760724

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