

# The genus *Pythium* in Taiwan, China (1) – a synoptic review

Hon-Hing HO

Department of Biology, State University of New York, New Paltz, NY 12561, USA

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**Abstract** The genus *Pythium*, with slightly over 280 described species, has been classified traditionally with other filamentous, coenocytic, sporangia-producing fungi as “Phycomyetes”. However, with recent advances in chemical, ultrastructural and molecular studies, *Pythium* spp. are now considered as “fungus-like organisms” or “pseudo-fungi” and are placed in the Kingdom Chromista or Kingdom Straminopila, distinct from the true fungi of the Kingdom Fungi or Kingdom Mycota. They are widely distributed throughout the world as soil saprophytes or plant pathogens. Because of the warm moist maritime climate, Taiwan, China, is especially rich in *Pythium* species. To date, 48 species of *Pythium* have been reported from Taiwan, China, with the dominant species being *Py. vexans*, *Py. spinosum*, *Py. splendens*, *Py. aphanidermatum*, *Py. dissotocum* and *Py. acanthicum*. There is no definite geographical distribution of *Pythium* spp. in Taiwan, China. Twenty nine species of *Pythium* have proven to be plant pathogens attacking a wide variety of woody and herbaceous plants primarily causing pre- and post-emergence seedling damping-off, root rot, stem rot and rotting of fruits, tubers and ginger rhizomes, resulting in serious economic losses. The most important plant pathogenic species include *Py. aphanidermatum* and *Py. Myriotylum*, which are most active during the hot and wet summer months; whereas *Py. splendens*, *Py. spinosum*, *Py. ultimum* and *Py. irregulare* cause the greatest damage in the cool winter. Most *Pythium* spp. are non-specific pathogens, infecting mainly juvenile or succulent tissues. This review attempts to assess the taxonomic position of the genus *Pythium* and provide details of the historical development of the study of *Pythium* as pathogens in Taiwan, China, causing diseases of sugarcane, trees, vegetables, fruits, specialty crops and flowering plants, as well as measures to control these diseases. Of special note is the introduction of the S-H mixture which, when used as soil amendment, effectively controls many soil-borne *Pythium* diseases during the early

stages of plant growth. The diversity of *Pythium* species in Taiwan, China, is discussed in comparison with the situation in the mainland of China and suggestions are made to fully utilize *Pythium* spp. as agents for biological control, in industry and medicine.

**Keywords** Pythiaceae, oomycetes, Chromista, Straminopila, plant pathogens, soil-borne disease, saprophytes, mycoparasites, biodiversity

## 1 Introduction

The classification of the genus *Pythium* Pringsheim (Pringsheim, 1858), with 284 described species (www.mycobank.org), has been problematic. For a long time members of this genus were placed in the Plant Kingdom of the traditional two-kingdom classification, within class Phycomyceteae (Pycomycetes) and division Eumycophyta (Eumycetes) (Smith, 1955; Fitzpatrick, 1930). Whittaker (1969) first proposed the five Kingdom Classification System and included all fungi in the Kingdom Fungi. *Pythium* along with *Phytophthora* and other oomycetes that have oogamous sexual reproduction by producing oogonia and oospores in their life cycles were placed in the Kingdom Fungi based on the fact that they are similar to most other fungi in being eukaryotic, heterotrophic and absorptive organisms with the vegetative phase in the form of a mycelium composed of branched tubular hyphae and reproducing by means of spores. However, over time there has been sufficient biochemical and structural evidence to suggest that oomycetes are different from other fungi primarily in the production of heterokont zoospores with two flagella of unequal length, the posterior one being whiplash while the anterior one being tinsel, bearing hair-like processes (mastigonemes), cell walls composed predominantly of  $\beta$ -glucans and cellulose, tubular cristae in the mitochondria and diploid coenocytic or nonseptate hyphae (Barr, 1992). Most fungi are non-motile except for members of the Chytridimycota that produce single posterior whiplash flagella on the zoospores, have cell

walls made up of chitin, mitochondria with flat cristae, and with the hyphae (except for members of the Zygomycota) septate with each cell containing one, two or more haploid nuclei (Alexopoulos et al., 1996). Molecular studies based on DNA sequence have confirmed that oomycetes are different from other fungi and instead share a common ancestor with other algal groups, namely the Phaeophyta (brown algae), Xanthophyta (yellow-green algae), Chrysophyta (golden algae) and Bacillariophyta (diatoms) which also produce heterokont motile cells, have tubular mitochondrial cristae and other ultrastructural similarities (Barr, 1992; Gunderson et al., 1987; Forster et al., 1990). Subsequently, the oomycetes have been treated as “fungus-like organisms” or pseudo-fungi (Cavalier-Smith, 1987) belonging to the Phylum Pseudomycota, distinct from the true fungi in the Phylum Eumycota (McLaughlin and McLaughlin, 2000). New Kingdoms have been proposed to accommodate the oomycetes and the related algal groups producing heterokont motile cells: the Kingdom Chromista (Cavalier-Smith, 1981, 1986) and the Kingdom Stramenopila (Patterson and Sogin, 1992; Dick, 2001). Many mycologists embraced the Kingdom Chromista (Kirk et al., 2001; Kendrick, 2001; Carlile et al., 2001), whereas Alexopoulos et al. (1996) and Webster and Weber (2007) accepted the Kingdom Stramenopila to distinguish the oomycetes from the true fungi. In Taiwan, China (wrote as “the study area” in the following text) the genus *Pythium* has been officially classified by the Taiwan Biodiversity Information Network under Family Pythiaceae, Order Pythiales, Class Oomycetes, Phylum Oomycota and Kingdom Chromista (taibnet.sinica.edu.tw). In contrast, mycologists have retained the Kingdom Myceteae and erected a new family Phytophthoraceae to separate *Phytophthora* and *Halophytophthora* from the Family Pythiaceae so that *Pythium* is classified under Family Pythiaceae, Order Peronosporales, Class Oomycetes, Phylum Oomycota and Kingdom Myceteae (Yu, 1998).

Historically, there has also been confusion regarding the validity of *Pythium* as a distinct genus. The genus *Pythium* was created by Pringsheim (1958) and placed in the family Saprolegniaceae. However, *Pythium* Pringsh. was antedated by both *Pythium* Nees and *Artotrogus* Montagne. Subsequently, the genus *Pythium* Pringsh. was conserved and the genus *Artotrogus* was rejected (van der Plaats-Niterink, 1981a, b). There were attempts to split the genus *Pythium* into two genera to differentiate species with spherical sporangia from those with filamentous sporangia. Schröter (1897) erected the family Pythiaceae in which he placed the genera *Pythium* with globose sporangia and *Nematosporangium* with filamentous sporangia. On the other hand, Sparrow (1931) proposed that species of *Pythium* with globose sporangia be placed in a new genus: *Sphaerosporangium*. Others tried to create various infra-generic taxa within *Pythium* but all these proposals have now been rejected (van der Plaats-Niterink, 1981a) and *Pythium* is now widely accepted as the type genus of the

family Pythiaceae in the order Peronosporales of class Oomycetes (Waterhouse, 1974) or order Pythiales of class Peronosporomycetes (Dick, 2001).

In distribution, the species of *Pythium* are cosmopolitan, widely distributed throughout the world ranging from tropical to temperate (van der Plaats-Niterink, 1981a) and even arctic (Hoshino et al., 1999) and antarctic regions (Knox and Paterson, 1973). They exist as saprophytes, mutualists and parasites in soil, water, on plants, fungi, insects, fish, animals and even human beings (Yu, 2001). Economically they are especially important as pathogens of higher plants, causing serious damage to agricultural crops and turf grasses, causing primarily soft rot of fruit, rot of roots and stems, and pre- and post-emergence of seeds and seedlings by infecting mainly juvenile or succulent tissues (Hendrix and Campbell, 1973). They are rarely host-specific and often more than one species of *Pythium* may be involved in causing the disease.

According to Waterhouse (1974), *Pythium* species can be readily identified by the delicate, hyaline, coenocytic, freely branching flexuous hyphae (about 5  $\mu\text{m}$  on average). Non-deciduous sporangia are produced only in water with variable shapes ranging from spherical, subspherical, ovate, obovate, ellipsoidal, pyriform (non-papillate or sometimes papillate without apical thickening) to lobulate and filamentous, terminal or intercalary on undifferentiated, simple, irregular or sympodially branched sporangiophores. Zoospores are not formed within the sporangium. Instead, the sporangial protoplasm passes through an exit tube into a thin membranous globose vesicle within which zoospores are differentiated and dispersed by rupture or dissolution of the vesicle membrane. The sexual reproduction is oogamous, producing spherical female oogonia, and the antheridium is paragynous or occasionally hypogynous. The number, shape and origin of the antheridia vary with the species and the oospore can be aplerotic or plerotic and some species produce more than one oospore per oogonium. It may be difficult to distinguish some *Pythium* species that produce spheroidal sporangia from *Phytophthora* species characterized by obovate, obpyriform or occasionally spherical sporangia. However, *Phytophthora* species always produce terminal sporangia which may be caducous or persistent, non-papillate to papillate with apical thickening, and zoospores are differentiated within the sporangium. Some species of *Phytophthora* can produce sporangia in air. Furthermore, the antheridium of *Phytophthora* is paragynous or amphigynous and the oogonium always produces only one oospore which is basically aplerotic. The hyphae of *Phytophthora* are usually coarse (6–14  $\mu\text{m}$  wide) and grow in a more tortuous pattern (Erwin and Ribeiro, 1996). In general, most *Pythium* species grow faster than *Phytophthora* species on common agar media and have higher maximum temperatures for growth, sometimes up to 40°C or above (Yu and Ma, 1989); whereas the maximum growth temperature for the

*Phytophthora* species is usually below 37°C with the exception of *P. insolita* which can tolerate high temperatures up to 39°C–40°C (Ho et al., 1995). The characteristics used in speciation are the morphology and dimensions of the sporangia, oogonia, oospore, antheridia, colony characteristics, growth rate and the maximal growth temperature (Middleton, 1943; Waterhouse, 1967; van der Plaats-Niterink 1981a; Dick, 1990). However, due to the limited number and the variability of the morphological characters used in identification of the *Pythium* species (Hendrix and Papa, 1974), the speciation within this genus has always been difficult and was recently substantiated with molecular techniques (Kong et al., 2004; Wang and White, 1997; Bailey et al., 2002).

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## 2 Historical background

The study area, situated about 160 km off the southeastern coast of the mainland of China, is 394 km long and 144 km wide, with an area of 35962 km<sup>2</sup>. Due to its mountainous topography, the arable land is limited primarily to the narrow coastal plain, amounting to about 1000000 hectares and consequently, intensive farming is the norm for agriculture in the study area. The warm, moist maritime climate and continuous multiple cropping practice on very limited arable land has made the study area a potential hotbed for *Pythium* species which thrive under these conditions. In general, they are most abundant in moist, fertile and cultivated lands, especially in the rhizospheric soil (Yu and Ma, 1989).

The study of *Pythium* in the study area has been largely pragmatic, focusing primarily on plant diseases caused by members of this genus due to the economic losses resulting from the diseases. Consequently, phytopathological work was carried out mainly by the Phytopathological Laboratory (later the Department of Plant Pathology) of the Taiwan University in Taipei, College of Agriculture at the Taiwan Provincial Chung Hsing University in Taichung, the Taiwan Agricultural Research Institute at Wufung, Taichung and the Taiwan Forestry Research Institute in Taipei (Lo, 1961). The research findings were published almost exclusively in the local journals, especially Plant Protection Bulletin, Journal of Chinese Agricultural Society, Plant Pathology Bulletin and Quarterly Journal of Chinese Forestry.

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## 3 *Pythium* as plant pathogens

It was Kaneyoshi Sawada who initiated the study of *Pythium* more than 80 years ago. Sawada and Chen (1926) determined that the putrefaction of the *Antirrhinum majus* L. seedlings was due to a new species of *Pythium*: *Py. spinosum* Sawada. Based on artificial inoculation, they discovered that *Py. spinosum* caused diseases of a wide variety of vegetables

and fruits (onion, garlic, turnip, parsley, cucumber, carrot, lettuce, tomato, radish and eggplant) and flowering plants (marigold, canterbury bells, chrysanthemum and carnation) leading to seedling damping-off and rotting of the roots, stems and fruits. The disease was most serious when the soil was warm and moist. One year later Sawada (1927) provided a more detailed morphological description and diagrams of *Py. spinosum* and reported that *Py. hydosporum* was associated with leaves of *Boehmeria nivea* infected by *Phytophthora cactorum*. He further reported damping-off of seedlings of *Cucumis melo* caused by *Pythium debaryanum* (Sawada, 1942, 1943) and identified *Pythium aphanidermatum* as the causal agent of fruit rot in *Solanum melongena* and *Cucumis sativus* (Sawada, 1943).

### 3.1 Diseases of sugarcane

Sugarcane has played a major role in the economy of the study area, and was the second staple crop after rice, with 50% of the sugar product exported to other countries (Poon and Kuo, 1980). Much attention has thus been paid to this area by the Sugar Experimental Station of the Taiwan Sugar Cooperation in Tainan in order to understand and control diseases of sugarcanes. In the early 60s it was discovered that sugarcanes suffered from *Pythium*-induced root rot disease resulting in poor growth or death of the seedlings (Lo, 1961). Hsu and Chu (1962) isolated four species of *Pythium* associated with sugarcane root rot: *Py. arrhenomanes*, *Py. aphanidermatum*, *Py. debaryanum* and an unidentified species of *Pythium*. By artificial inoculation, they demonstrated that *Py. arrhenomanes* and *Pythium* sp. caused the heaviest damage to the sugarcane roots and could infect the plant by direct penetration, whereas the other three species entered the roots through wound sites. The root rot disease caused by *Py. arrhenomanes* was most serious when inoculation was made in April under the Tainan weather condition and the roots were more susceptible in sandy loam, loam, and clay loam soil (Hsu, 1963). Later, Hsu (1965a, b) identified the *Pythium* species causing root rot of sugarcane as *Py. catenulatum* based on the morphological and physiological characteristics. Hsu and Liu (1966) also isolated *Py. mamillatum* in addition to *Py. arrhenomanes* and *Py. catenulatum* causing damping-off of new sugarcane cuttings in the breeding bed of the Taiwan Sugar Experiment Station, resulting in more than 80% loss. *Pythium catenulatum* proved to be the most virulent species, but the combination of all these three pathogenic species of *Pythium* caused damage greater than any single *Pythium* species. Although sugarcanes in the study area were usually planted fresh, either every 18 months for early or autumn cane or every 12 months for late or spring cane (Poon and Kuo, 1980), ratooning of perennial sugarcane became more popular for economic reasons. However, poor ratoon standing was a serious problem. In the severely damaged fields, the unemerged or emerged ratoon canes had generally poor

root systems, and buds or young shoots sprouted from the cane stubbles were blighted or softened and sometimes completely collapsed. Although the cause of the problem might be complex, Chu et al. (1966) isolated *Pythium* spp. from ratoon cane fields, and by artificial inoculation, demonstrated conclusively that *Py. arrhenomanes*, *Py. catenulatum* and *Py. mamillatum* prevented the germination and reduced the number of germinated buds of ratoon stubbles as well as fresh cane cuttings. The treatment of soil with fungicides proved to be effective in controlling the disease. In order to find out the cause of poor ratooning of sugarcane in the study area, Watanabe et al. (1974) isolated 13 species of *Pythium* from the underground parts of unemerged ratoon canes: *Py. acanthicum*, *Py. aphanidermatum*, *Py. arrhenomanes*, *Py. catenulatum*, *Py. deliense* Meurs, *Py. elongatum*, *Py. graminicolum* (= *Py. graminicola*), *Py. myriotylum*, *Py. oligandrum*, *Py. pulchrum* and three unidentified *Pythium* spp. They further demonstrated that under growth chamber conditions, *Py. catenulatum* and *Pythium* sp. X107 caused severe root rot of sugarcane cuttings whereas under semi-field conditions, *Py. arrhenomanes* and *Py. catenulatum* also caused root rot. Similarly, Watanabe (1974) also isolated 5 species and 3 species complexes of *Pythium*: *Py. acanthicum*-*Py. oligandrum* complex, *Py. afertile*, *Py. aphanidermatum*, *Py. catenulatum*, *Py. debaryanum* complex, *Py. deliense*, *Py. graminicolum*-*Py. arrhenomanes* complex and *Py. inflatum*.

### 3.2 Diseases of trees

Beginning in the early 50s, the establishment of forests was encouraged in the study area on the island and consequently, tree nurseries sprung up throughout the island ranging from the coastal plains to the mountainous highlands. However, various diseases, especially damping-off of tree seedlings, developed in the nurseries. Thus, Chen (1962) as well as Jong and Chen (1966) reported damping-off of China fir due to *Py. Debaryanum*, which was also isolated from various diseased coniferous seedlings. It was the most virulent pathogen to *Pinus elliottii*, causing germination failure, radicle decay, basal stem rot and taproot rot, and inhibited the initial development of surviving seedlings. However, it was more or less suppressed in the field by other soil-borne parasites or saprophytes. Chen et al. (1969) demonstrated that *Pythium* spp. existed widely in forest nursery soils, including *Py. aphanidermatum*, *Py. spinosum*, and *Py. vexans*. By adding these *Pythium* species into the soil it was found that the seed germination of *Pinus luchuensis* was greatly reduced and the seedlings that survived were stunted. Of all the *Pythium* isolates tested, *Py. aphanidermatum* and *Py. spinosum* exhibited the greatest virulence and they concluded that an epidemic might happen whenever a favorable condition for disease development prevailed. Between 1977 and 1987 Hsieh,

working for the Taiwan Forestry Research Institute, published a series of papers on the diseases of woody plants in the study area. Again, seedling damping-off due to *Pythium* spp. was prevalent in nurseries. They could have been caused by single species of *Pythium*, like *Py. spendens* attacking *Schefflera arbuticola* (Hsieh, 1981, 1983b), *Cunninghamia konishii* (Hsieh, 1980), *Abroma augusta*, *Eucommia ulmoides* (Hsieh, 1982), *Broussonetia papyrifera* (Hsieh, 1984), *Cinnamomum camphora*, *Casuarinaglauca*, and *C. equisetifolia* (Hsieh, 1986a) and *Py. aphanidermatum* infecting seedlings of *Acacia mangium* (Hsieh, 1985). However, in most cases, more than one species of *Pythium* were implicated: *Py. myriotylum*, *Py. spinosum* and *Py. splendens* on *Pawlonia fortunei*, *Pawlonia kawakamii*, *Pawlonia taiwaniana* and *Pawlonia tomentosa*; *Py. spinosum* and *Py. splendens* on *Phellodendron* spp.; *Py. spinosum* and *Py. ultimum* on *Acrocarpus fraxinifolius*; *Py. irregulare*, *Py. spinosum*, *Py. splendens* and *Py. ultimum* on *Leucaena leucocephala*; *Py. aphanidermatum*, *Py. splendens* and *Py. ultimum* on *Calotropis procera*, *Pinus taiwansensis* and *Pinus lechuensis*; *Py. spinosum*, *Py. splendens* and *Py. ultimum* on *Cryptomeria japonica*; *Py. spinosum*, *Py. ultimum* and *Py. vexans* on *Liquidambar formosana* and *Py. irregulare* and *Py. spinosum* on *Pinus elliottii*, *Pinus kasiya*, *Pinus patula* and *Pinus taeda* (Hsieh, 1979, 1982, 1983a, 1983b, 1983c, 1985; Hsieh and Fung, 1980). In addition to causing seedling damping-off, *Pythium* spp. also caused root rot. Thus, Hsieh (1983a) reported that root rot of woody seedlings and cuttings of *Paulownia fortunei*, *Pawlonia kawakamii*, *Pawlonia taiwaniana* and *Pawloniatomentosa* was caused by *Py. splendens* and *Py. spinosum*; seedling root rot of *Schizolobium paraphyba* was incited by *Py. aphanidermatum* (Hsieh, 1982), whereas seedling root rot of *Pinus thunbergii* (Hsieh, 1987) and *Camelia oleifera*, *Camelia tenuifolia* (Hsieh, 1986b) and *Michelia compressa* (Fu and Chen, 2005) was attributed to *Py. splendens*. Chang (1992) found that *Py. spendens* caused root rot of cuttings of *Cinnamomum kanchirai* and isolated eight species of *Pythium* from the rhizosphere of the host: *Py. deliense*, *Py. oligandrum*, *Py. pleroticum*, *Py. spinosum*, *Py. splendens*, *Py. ultimum* var. *ultimum*, *Py. vexans* and an unidentified *Pythium* sp. (Chang, 1993). Based on artificial inoculation, all these species of *Pythium* except *Pythium* sp. were pathogenic to *Cinnamomum kanchirai* cuttings with *Py. splendens* and *Py. vexans* being the most virulent, followed by *Py. deliense*, often leading to the death of the cuttings.

### 3.3 Diseases of vegetables and other specialty crops

Vegetables have become popular in the study area at the expense of rice due to the higher profits per acre gained by growing a mixture of different vegetables with short growing periods. However, vegetables are especially susceptible to soil-borne *Pythium* species which cause

serious pre- and post-emergence seedling damping-off and root rot as well as fruit rot primarily by producing pectin lyase, an enzyme that macerates the host tissues quickly (Chen et al., 1994; 1998). Kuo et al. (1991) frequently isolated seven species of *Pythium*: *Py. afertile*, *Py. aphanidermatum*, *Py. deliense*, *Py. polymastum*, *Py. sylvaticum* and *Py. ultimum* var. *ultimum* from cruciferous vegetable field soils throughout the study area and occasionally *Py. catenulatum*, *Py. marsipium* and *Py. oligangrum* from Tainan. Using soils infested with seven common *Pythium* spp. to test for the pathogenicity on nine cultivars of vegetables, they found that all species of *Pythium* except for *Py. afertile* showed various degrees of pathogenicity, with *Py. aphanidermatum*, *Py. spinosum*, *Py. sylvaticum* and *Py. ultimum* var. *ultimum* being the most virulent on cucumber, *Py. sylvaticum* and *Py. ultimum* on Chinese cabbage and *Py. sylvaticum* on rapeseed, broccoli and kale, causing pre-emergence and post-emergence damping-off as well as stunting of the surviving vegetables. However, although vegetables growing in soil infested with *Py. deliense* or *Py. polymastum* showed stunting symptoms, the pathogens could not be recovered from the infected plants. Kuo and Hsieh (1991) further reported that the diseases caused by *Py. aphanidermatum* were most serious during the summer months when daily average temperatures reached 23°C–32°C, whereas *Py. ultimum* var. *ultimum* and *Py. spinosum* caused the greatest damage at cooler temperatures 12°C–22°C. Similarly, Lo and Lin (1990) demonstrated that the rotting of cucumber roots by *Py. aphanidermatum* was highest in the field when the daily average temperatures were above 27.2°C and between 32°C–36°C in laboratory tests. On the other hand, *Py. spinosum* was most virulent towards cucumber root in winter when the field temperature dropped below 27.2°C or between 24°C–28°C under experimental conditions. Cucumber seedling blight was also reported by Wu (1995). In the central part of the study area, *Pythium*-incited diseases of vegetables grown continuously under cheese cloth or a plastic cover were also common and serious (Liu, 1993). Various *Pythium* spp. caused the damping-off and basal stem rot of cruciferous vegetables (Chinese mustard, field mustard and especially black mustard) as well as non-cruciferous vegetables like lettuce and edible amaranth, with the latter infected primarily by *Py. aphanidermatum* causing stem rot. Due to the limited arable land in the study area and to avoid soil-borne diseases there was a movement in the early 80s to promote hydroponics by growing plants in soilless mineral solution. However, it was later discovered that even plants grown in hydroponics could not escape infection by *Pythium* spp. Thus, Lin and Huang (1993) reported the occurrence of *Pythium* root rot in hydroponic vegetables. Five species of *Pythium* were consistently isolated from the diseased roots: *Py. coloratum*, *Py. aphanidermatum* and *Pythium* “group F” caused mild root rot and stunting of plants in winter, whereas *Py. myriotylum*, *Py. aphanidermatum* and

*Pythium* “group G” caused severe root rot, stunting and wilting of plants in summer. Similarly, Huang (1993) as well as Huang and Lin (1998) studied root rot of vegetable pea seedlings in a soilless cultural system caused by *Py. aphanidermatum* and *Py. ultimum*, leading to death or severe stunting of seedlings. Again, they confirmed that *Py. aphanidermatum* was the most predominant pathogen during the warm summer, with an air temperature higher than 24°C, whereas *Py. ultimum* played a more important role during the cool winter when air temperature was lower than 20°C. The source of the *Pythium* inoculum in hydroponics was a mystery and it has been speculated that the inoculum might have been present in the water, on the seeds, insects or air dust, or inadvertently transferred by people handling the soilless culture (Davis, 1980). Huang et al. (1994) demonstrated that *Pythium* spp. was carried by dust to the greenhouse to attack the hydroponic vegetables. The inoculum was initially low and diseased plants were not noticeable especially at the early stage. However, since *Pythium* spp. produced abundant zoospores in infested trough and nutrient solution, they quickly caused serious root rot especially of the subsequent crops. Lin et al. (2002) showed that root rot of vegetable pea seedlings in a soilless cultural system (sawdust in a seedling tray used as the cultural substrate) was caused by *Py. aphanidermatum* in summer and *Py. ultimum* in winter. They also proved that *Pythium* spp. were probably introduced into the cultural system through cultural substrate (sawdust) and the original infection source could possibly come from contaminated soil dust. The small amounts of inocula from sawdust infected only a few pea seedlings but the disease could spread from plant to plant via hyphae, zoospores and by overhead irrigation. Although no obvious symptoms could be detected when a new seedling tray was used to grow pea seedlings for the first time, severe root rot appeared when the infested trays were used repeatedly. Species of *Pythium* also affected the production of other crops. For instance, *Py. myriotylum* caused soft rot of ginger which is commonly consumed by the local people in the study area and exported as well. Soft rot of ginger rhizome occurred in the field when the temperature was high and coupled with heavy rainfall, resulting in as much as 70% or more loss (Lin et al., 1971). The disease was so serious that ginger could not be planted in the same infested field (Sun, 1992). By artificial inoculation, the pathogen also induced soft rot of the fruits of asparagus bean, cucumber, watermelon, eggplant, tomato, carrot and tubers of potato. Peanut is an important special upland food crop covering about 100000 acres on the island. Its production has been limited by *Pythium myriotylum* which causes pre- and post-emergence damping-off, rotting of the roots and stems causing wilting of the plants, as well as pod rot and pre-mature abscission of the pods (Jan and Wu, 1972; Sun et al., 1973; Cheng et al., 1989). With the government mandate in the early 80s promoting the production of corn instead of rice, increasingly more

acreage has been devoted to the cultivation of corn plants. However, these efforts have been hampered by *Py. aphanidermatum* causing stalk rot which could lead to the collapse of the entire corn plant. The pathogen infects the host plant by penetrating the base of the stalk, especially through wound sites of young plants (Tu et al., 1985; Tsai et al., 1991). Other economically important special crops were also affected by species of *Pythium*. It was found that *Pythium* spp. caused root rot and heart rot of pineapple (Anonymous, 1944; Lo, 1961), fruit rot of papaya (Sun, 1955), seedling damping-off of sugar beet (Chu and Hu, 1959) and rice (Lo, 1961; Wong and Chen, 1972), post-harvest rotting of water chestnut (Anonymous, 1955) and *Py. spinosum* incited mottle necrosis of sweet potato (Lo, 1961). Seedling damping-off of tobacco and papaya was caused, respectively, by *Py. aphanidermatum* and *Py. myriotylum* (Matsumoto, 1946; Lo, 1961; Liu, 1976) as well as *Py. aphanidermatum*, *Py. ultimum* (Liu, 1977) and *Pythium* sp. (Tsai, 1970). Root rot of rosemary in warm and wet summers was caused by *Py. myriotylum*, *Py. oedocheilium* and *Py. catenulatum* (Wu, 2007).

#### 3.4 Diseases of flowering plants

Diseases of flowering plants have also received close attention due to their high value and popularity as ornamental plants or cut flowers. Seedling damping-off and root rot diseases due to *Pythium* spp. are especially common. Hsieh (1983d, e) reported that seedling damping-off of *Anthriscum majus* L. by *Py. ultimum*, damping-off and root rot of *Impatiens balsamina* L. and *Papaver rhoeas* L., respectively by *Py. splendens* and a combination of *Py. irregulare*, *Py. spinosum* and *Py. ultimum*. *Pythium aphanidermatum* was associated with the basal stem rot of chrysanthemum (Hsieh and Lo, 1976); *Py. spinosum* induced lily root rot (Chen and Wu, 1968); *Py. splendens* and *Py. aphanidermatum* were responsible for the seedling blight of poinsettia (Wu, 1995), and *Py. palingenes* caused the root rot of *Tibouchina semidecandra* (Huang, 2008).

#### 3.5 Application of molecular biology techniques to the study of *Pythium*

Since the identification of *Pythium* species based solely on the limited and often variable morphological characteristics proved to be difficult, molecular techniques have been developed since the early 90s to facilitate speciation. Buu et al. (1992) conducted a selection of species-specific probes to distinguish the mitochondrial DNA RFLP patterns of 17 species of *Pythium*, and a cloned mtDNA probe was developed successfully for the detection of *Py. aphanidermatum* (Buu et al., 1993). By using booster PCR with DNA primers developed from mitochondrial DNA, Wang et al. (2002) also detected *Py. aphanidermatum* from naturally infected nutrient solutions and roots of vegetables in a field hydroponic system. Similarly,

*Py. myriotylum*, the soft rot pathogen, was detected in infected ginger rhizomes using the new PCR method (Wang et al., 2003). The molecular characterization of five *Pythium* species from plant hosts in the study area: *Py. aritosporum* from *Cucumis melo*, *Py. dimorphum* from *Euphorbia longana*, *Py. hydrosorum* from *Brassica* sp., *Py. irregulare* from *Daucus carota* and *Py. myriotylum* from *Brassica chinensis*. along with other *Pythium* isolates from various countries was conducted (Wang and White, 1997). A species-specific PCR primer for *Py. dimorphum* was one of the five successfully developed from the ribosomal ITS1 region and the fungus could be detected both from artificially inoculated and natural soil (Wang et al., 2003). To understand the genes involved in the pathogenesis, Chen (1994) established a DNA transformation system for *Py. aphanidermatum*.

#### 3.6 Plant disease control

Identification of the pathogen that causes any plant disease is only the first step in the study of the disease. Ultimately, control measures have to be developed to control and/or prevent the disease. Since *Pythium* spp. thrive in moist soil (Sun, 1991) by producing abundant zoospores and persist as resistant oospores in the diseased plant debris and/or infested soil, the treatment of soil or seeds with fungicides to control *Pythium*-induced plant diseases has been common practice. In the early days substances like charcoal, lime and sulfur were added to the soil (Sawada and Chen, 1926) to control damping-off of snapdragon due to *Py. spinosum*. Later on, other more effective chemicals were developed, for instance, Similton for poor ratoon standing of sugarcane (Chu et al., 1966), Granosan, Semesan and Upsulun for damping-off of China fir seedlings (Chen, 1962), and since the early 80s, Ridomil (Metalaxyl), Dexon and Etridizole became popular fungicides to control *Pythium* diseases both in the field and in hydroponics (Lo and Lin, 1990; Huang et al., 1994). The chemical could be used to coat the seeds or be applied to the soil or nutrient solution. In order to control *Pythium* root rot of pea seedlings in soilless cultural systems, using sawdust as the germination medium, drying the used seedling trays under sunlight for months or immersing the trays in a calcium hypochlorite solution for 24 hours before planting was effective in preventing the disease. Soil sterilization with steam or methyl bromide was also effective in eradicating the *Pythium* inoculum (Lo and Lin, 1990; Cheng et al., 1989). Detailed physiological studies of *Py. sylvaticum* and *Py. spinosum* were conducted to determine the most vulnerable point in their life cycles in order to develop an effective disease control method (Lee, 1989). However, with increasing awareness of the dangers of chemicals and their residues to the ecosystem, human beings, animals and other living organisms, the government, research institutions and universities have cooperatively developed measures towards establishing sustainable

organic agriculture in the study area (Lin, 2005). The addition of soil amendment to suppress the pathogen could be a safer and cheaper alternative control method. The use of fresh S-H mixture, named after its developers (Sun and Huang, 1983) is made up of 4.4% bagasse, 8.4% rice husks, 4.25% oyster shell powder, 1.04% potassium nitrate, 13.6% calcium superphosphate, 8.25% urea and 60.5% siliceous slag (mineral ash). When used as soil amendment at the rates of 0.5% to 2% (w/w), the mixture greatly or completely inhibits damping-off and root rot of cucumber caused by *Py. aphanidermatum* under greenhouse and field conditions (Lin and Lo, 1987, 1988). Lin et al. (1990) considered that the disease suppression in soils amended with the S-H mixture was probably attributable to multiple effects of several factors in the mixture. Thus the high level of calcium and the fertilizer content of the mixture might promote seedling growth, resulting in a shorter susceptible period and probably an increase of beneficial mycorrhizal fungi and other soil microorganisms. Urea, in combination with mineral ash inhibited zoospore germination and mycelial survival of *Pythium aphanidermatum*. Chitin in the oyster shell powder might promote an antagonistic actinomycete population in the soil. Lo and Lin (1992) further demonstrated that the high amounts of ammonia gas produced from the amended soils reduced oospore germination of *Py. aphanidermatum*. However, the period of disease suppression due to S-H amendment was effective for only about 40 days. Other agricultural wastes, especially spent forest mushroom compost (SFMC), proved to be effective in controlling the disease by reducing the production of zoospores by the pathogen and suppressing the germ tube growth of encysted zoospores (Wang and Huang, 2000).

Biological control is also a viable option. Wu (1992) reported that *Trichoderma pseudokoningii* and *T. viride* were antagonistic to *Py. spinosum* and *Py. aphanidermatum* by inhibiting their mycelial growth. When added to the soil infested with either *Pythium* species, *Trichoderma* spp. increased the survival rate of cucumber and muskmelon, whereas tomatoes and hot and sweet pepper were effectively protected when the soil or seeds were treated with *Trichoderma* spp. Kuo (1990) obtained 11 isolates of fungi, including *Penicillium* sp., *Aspergillus* sp. and *Pyrenochaeta* sp. from the rhizosphere of field vegetables and these fungi showed varying antagonistic effects against *Py. aphanidermatum*, *Py. spinosum*, *Py. sylvaticum* and *Py. ultimum*. *Streptomyces griseobrunneus* proved to be mycoparasitic on *Pythium aphanidermatum* by germinating and growing on and inside the hyphae (Yang et al., 2005). Mycoparasitism of *Py. deliense*, *Py. splendens* and *Py. ultimum* was also demonstrated by *Py. oligandrum* and to a lesser extent, *Py. periplocum* and *Py. acanthicum* (Wu and Hsieh, 1993; Wu, 1995). It is widely recognized that *Bacillus cereus* used in wettable powder or liquid formulation is a highly effective biofungicide against *Pythium* soft rot, basal stem rot and damping-off by

producing iturin, which altered the permeability of the pathogen cell membrane allowing rapid leakage of potassium ions and subsequent inhibition of spore germination and mycelial growth ([www.ag.168.com](http://www.ag.168.com)). Chang et al. (2007) demonstrated that the culture supernatant of *B. cereus* grown on shellfish chitin wastes not only produced antifungal hydrolytic enzymes that inhibit the growth of *Py. ultimum* but also compounds that enhance the growth of Chinese cabbage. Yang (2007) isolated five gas-producing bacterial strains from field and rhizosphere soils in the study area and three of them (*Pseudomonas putida* and two species of *Enterobacter*) inhibited the mycelial growth of *Py. aphanidermatum* and might be used to control damping-off of lettuce seedlings grown in solution culture. In a recent study of the antimicrobial activity of 14 medicinal plants used by the local people in the study area, Muto et al. (2005) showed that water and ethanol extracts of fresh tissues of *Clematis tashiroi* and *Drymaria diandra* completely inhibited the mycelial growth of *Py. aphanidermatum*, whereas 50% inhibition was obtained by using water extracts from dry tissues of *Arenga engleri*.

Other effective measures include improved soil drainage (Sawada and Chen, 1926), crop rotation (Huang et al., 2002) and development of resistant cultivars (Ho et al., 1998; Tsai et al., 1991). In practice, it is important to use pathogen-free planting materials. Thus, a new PCR method has been developed to monitor for the presence of *Py. myriotylum*, the soft rot pathogen, in ginger rhizomes as a way of disease diagnosis in order to select for healthy seed gingers for planting. A knowledge of the *Pythium* inoculum density in the field soil is also important in deciding whether any susceptible crops should be planted or not. Using a potato baiting bioassay technique, Lin et al. (1992) demonstrated a significant correlation between the percentage of potato bait colonization and that of damping-off of cucumber seedlings, and established a correlation between inoculum density and absolute inoculum potential, which served as the basis to determine whether the field soil is suppressive enough for the planting of cucumbers. The PCR method used to screen for healthy seed ginger has also been used to detect oospores of *Py. myriotylum* from soil before ginger planting as a way to reduce or eliminate soft rot disease (Wang and Chang, 2003).

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#### 4 Diversity of *Pythium* species

Species of *Pythium* are widely distributed in soil, water and on plant roots throughout the study area. Hsieh (1976), as well as Hsieh and Chang (1976), conducted the first comprehensive survey of *Pythium* species in the study area and provided a detailed description of the 16 species isolated: *Py. acanthicum*, *Py. adhaerens*, *Py. afertile*, *Py. aphanidermatum*, *Py. catenulatum*, *Py. deliense*, *Py. dissotocum*, *Py. elongatum*, *Py. gracile*,

*Py. graminicolum*-*Py. arrhenomanes* complex, *Py. irregulare*, *Py. marsipium*, *Py. oligandrum*, *Py. pulchrum*, *Py. spinosum* and *Py. tardescens*. *Pythium spinosum* and *Py. dissotocum* were the most abundant species, followed by *Py. aphanidermatum*, *Py. irregulare* and *Py. debaryanum*. He further provided an annotated list of 27 species known at that time by including *Py. arrhenomanes*, *Py. carolinianum*, *Py. debaryanum*, *Py. graminicolum*, *Py. helicandrum*, *Py. hydno sporum*, *Py. mamillatum*, *Py. myriotylum*, *Py. paroecandrum*, *Py. splendens* and *Py. undulatum* (Hsieh, 1978). Ho (2004) isolated 34 species of *Pythium*: *Py. acanthicum*, *Py. aphanidermatum*, *Py. arrhenomanes*, *Py. carolinianum*, *Py. catenulatum*, *Py. coloratum*, *Py. debaryanum*, *Py. deliense*, *Py. dissotocum*, *Py. graminicola*, *Py. helicoides*, *Py. inflatum*, *Py. intermedium*, *Py. irregulare*, *Py. middletonii*, *Py. monospermum*, *Py. myriotylum*, *Py. oedochilum*, *Py. oligandrum*, *Py. paroecandrum*, *Py. periplocum*, *Py. perplexum*, *Py. pulchrum*, *Py. rostratum*, *Py. salpingophorum*, *Py. spinosum*, *Py. splendens*, *Py. sylvaticum*, *Py. tardescens*, *Py. torulosum*, *Py. ultimum*, *Py. vexans* and *Py. volutum* with *Py. vexans*, *Py. splendens*, *Py. aphanidermatum*, *Py. spinosum* and *Py. acanthicum* as the dominant species. The discrepancy in the dominant *Pythium* spp. found in the study area may be due to the different sites studied, samples collected, methods of isolation and the ecological changes over time. There was no distinct pattern in the geographic distribution of *Pythium* spp. in the study area. A new species of *Pythium* was isolated from the soil of an undisturbed natural forest in northern the study area: *Py. sukuiense* (Ko et al., 2004). In contrast to most *Pythium* species, *Py. splendens* and *Py. sylvaticum* are heterothallic, but all isolates of the latter proved to be male (Lee and Hsieh, 1991), whereas both male and female isolates of the former have been found in the study area (Ho, unpublished). Using an unidentified Basidiomycetous fungus as bait, three mycoparasitic species of *Pythium* were obtained from 64.5% of cultivated soil samples and 10.7% of non-cultivated soil samples from various sites on the island: 31 isolates of *Py. oligandrum*, 10 isolates each of *Py. acanthicum* and *Py. periplocum* (Wu and Hsieh, 1993; Wu, 1995). Based on the mycoparasitic ability test, all three species, especially *Py. oligandrum*, proved to be pathogenic to *Py. deliense*, *Py. splendens*, *Py. ultimum*, *Botrytis cinerea* and *Phytophthora parasitica* by entwining and invading the hyphae. *Pythium debaryanum* has also been isolated from dead eggs of rainbow trout (*Salmo gairdneri*) (Chien, 1980, 1981). By using the first-instar larvae of mosquitoes (*Aedes aegypti* and *A. albopictus*) as bait, Chen et al. (2005) obtained four *Pythium* spp. from various soil samples and found that zoospores of these *Pythium* species could infect the first-instar larvae by attaching to the anal gill and sometimes the region between the head and thorax. *Pythium* sp. was also found on cultivated mushrooms causing rotting of the fruiting bodies (Hsieh, 1976).

## 5 Discussion

In nature, *Pythium* species thrive in warm and moist soil or water and the subtropical maritime climate of the study area, favoring the existence of a wide variety of saprophytic and plant pathogenic *Pythium* species. To date, 48 species of *Pythium* have been recorded in the study area with one new taxon: *Py. sukuiense* Ko, Wang & Ann. In the mainland of China, which has an enormous area considerably much larger than the study area, 55 species have been reported (Yu, 1998; Fu et al., 2004; Yuan and Lai, 2004; Lou and Zhang, 2004; Su, 2006) with 10 erected as new species: *Py. acrogynum* Yu, *Py. amasculinum* Yu, *Py. boreale* Duan, *Py. connatum* Yu, *Py. falciforme* Yuan & Lai, *Py. guiyangense* Su, *Py. hypoandrum* Yu & Wang, *Py. kunmingense* Yu, *Py. nanningense* Lai & Yuan and *Py. sinensis* Yu. A comparison of *Pythium* species found in the study area, and the mainland of China is listed in Table 1. It is of interest to note that *Py. Splendens*, which is abundant and found throughout the study area causing a wide variety of plant diseases, has been only recently isolated from Guangxi (Yuan and Lai, 2004), Zhejiang (Wang et al., 1995) and Hainan Island (Chen, 2007). None of the 10 new species of *Pythium* in the mainland of China has been found in the study area, and *Py. sukuiense* has not been isolated either in the study area or in the mainland of China since its first report in 2004 (Ko et al., 2004).

There is no doubt that the presence of *Pythium* spp. in the study area has been closely tied with plant diseases for economic reasons. They attack a wide variety of woody and herbaceous plants, causing primarily pre- and post-emergence seedling damping, root rot, stem rot and rotting of various fruits, tubers and rhizomes by producing cell wall-degrading enzymes like pectin lyase that breaks down the intercellular middle lamella, leading to rapid maceration, softening and subsequent death of infected tissues (Chen et al., 1998). In addition, there was one report of mottle necrosis of sweet potato leaves (Lo, 1961). To date, 24 species of *Pythium* have been found to be plant pathogens in the study area and their hosts are listed in Table 2. The most important plant pathogenic species include *Py. aphanidermatum* and *Py. myriotylum* which are most active during the hot, wet summer months due to their maximum growth temperature (above 40°C), whereas *Py. spinosum*, *Py. splendens*, *Py. ultimum* and *Py. irregulare*, which stop growing at 34°C–35°C (Plaats-Niterink, 1981a), cause the greatest damage in the cool winter. It is refreshing to note the growing trend of using non-chemical measures to control *Pythium* species in order to maintain a healthy environment for human beings and all other live forms in the study area.

Although *Pythium* spp. are known as common soil inhabitants causing a wide variety of plant diseases, their beneficial effects on human beings have been overlooked especially in the study area. Several mycoparasitic *Pythium*

**Table 1** Presence of *Pythium* species in the study area and the mainland of China

species	study area	mainland of China	species	study area	mainland of China
<i>acanthicum</i> Drechsler	+	+	<i>irregulare</i> Buisman	+	+
<i>acanthophoron</i> Sideris	–	+	<i>kunmingense</i> Yu	–	+
<i>acrogynum</i> Yu	–	+	<i>mamillatum</i> Meurs	+	+
<i>adherens</i> Sparrow	+	–	<i>marsipium</i> Drechsler	+	+
<i>afertile</i> Kanouse & Humphrey	+	–	<i>middletonii</i> Sparrow	+	+
<i>amasculinum</i> Yu	–	+	<i>monospermum</i> Pringsheim	+	+
<i>aphanidermatum</i> (Edson) Fitzpatrick	+	+	<i>myriotylum</i> Drechsler	+	+
<i>aquatile</i> Hohnk	–	+	<i>nagaii</i> Ito & Tokunaga	–	+
<i>aritosporum</i> Vanterpool	+	+	<i>nanningense</i> Lai & Yuan	–	+
<i>arrhenomanes</i> Drechsler	+	+	<i>oedochilum</i> Drechsler	+	–
<i>boreale</i> Duan	–	+	<i>orthogonon</i> Ahrens	–	+
<i>carolinianum</i> Mathews	+	+	<i>oligandrum</i> Drechsler	+	+
<i>catenulatum</i> Matthews	+	+	<i>palpingenes</i> Drechsler	+	–
<i>chamaehyphon</i> Sideris	–	+	<i>paroecandrum</i> Drechsler	+	+
<i>coloratum</i> Vaartja	+	+	<i>peridium</i> Drechsler	–	+
<i>connatum</i> Yu	–	+	<i>periplocum</i> Drechsler	+	+
<i>debaryanum</i> Hess	+	–	<i>perplexum</i> Kouyeas & Theohari	+	+
<i>deliense</i> Meurs	+	+	<i>pleroticum</i> Drechsler	+	–
<i>diclinum</i> Ito & Tokunaga	–	+	<i>polymastum</i> Drechsler	+	–
<i>dimorphum</i> Hendrix & Campbell	+	–	<i>polypapillatum</i> Ito	–	+
<i>dissotocum</i> Drechsler	+	+	<i>pulchrum</i> Minden	+	+
<i>echinocarpum</i> Ito & Tokunaga	–	+	<i>rostratum</i> Butler	+	+
<i>elongatum</i> Mathews	+	+	<i>salinum</i> Hohnk	–	+
<i>falciforme</i> Yuan & Lai	–	+	<i>salpingophorum</i> Drechsler	+	+
<i>gracile</i> Shenk	+	–	<i>sinensis</i> Yu	–	+
<i>gramincola</i> ( <i>graniicolum</i> ) Subramanian	+	+	<i>spinousum</i> Sawada	+	+
<i>guiyangense</i> Su	–	+	<i>splendens</i> Braun	+	–
<i>helicandrum</i> Drechsler	+	–	<i>sukuiense</i> Ko, Wang & Ann	+	–
<i>helicoides</i> Drechsler	+	+	<i>sylvaticum</i> Campbell & Hendrix	+	+
<i>hemmianum</i> Takashashi	–	+	<i>tardicrescens</i> Vanterpool	+	+
<i>hydno sporum</i> (Mont.) Schroet.	+	–	<i>torulosum</i> Coker & Patterson	+	+
<i>hypoandrum</i> Yu & Wang	–	+	<i>ultimum</i> Trow	+	+
<i>indigoferae</i> Butler	–	+	<i>undulatum</i> Peterson	+	–
<i>inflatum</i> Mathews	+	+	<i>vexans</i> de Bary	+	+
<i>intermedium</i> de Bary	+	+	<i>volutum</i> Vanterpool & Truscott	+	–

species have been isolated, like *Py. oligandrum*, *Py. periplocum*, and *Py. acanthicum*, but they have yet to be utilized commercially as biological controls of soil-borne diseases prevalent in the study area. The isolation of *Pythium* spp. from mosquito larvae is of special interest because of its potential for limiting the population of mosquitoes, which often carry the human pathogenic virus causing deadly dengue fever disease, especially in the southern part of the study area during the hot summer

months. The copious production of hydrolytic enzymes like pectinase, amylase and cellulase by many *Pythium* spp. might find uses in industry, for instance, in the breakdown of plant wastes for fermentation to produce biofuel. In addition, some species of *Pythium* can be utilized in medicine since they can synthesize biotin, folic acid, pantothenic acid, riboflavin, thiamine and vitamin C, etc. and are capable of transforming sterols such as cholesterol, ergosterol and sitosterol (Yu, 2001).

**Table 2** Plant pathogenic species of *Pythium* in Taiwan, China and their hosts

species	hosts	species	hosts
<i>acanthicum</i>	<i>Saccharum officinarum</i> L.		<i>Cryptomeria japonica</i> D. Don, <i>Cucumis sativus</i> L.,
<i>afertile</i>	<i>Oryza sativum</i> L., <i>Saccharum officinarum</i> L.		<i>Daucus carota</i> L., <i>Dianthus chinensis</i> L., <i>Eleocharis</i>
<i>aphanidermatum</i>	<i>Acacia mangium</i> Willd., <i>Amaranthus mangostanus</i> L., <i>Capsicum frutescens</i> L., <i>Calotropis procera</i> (Ait.) Ait., <i>Carica papaya</i> L., <i>Chrysanthem</i> sp., <i>Cucumis</i> <i>sativus</i> L., <i>Diospyros kaki</i> Thunb., <i>Euphorbia</i> <i>pulcherrima</i> Willd. Ex. Klotzsch, <i>Lactuca sativa</i> L., <i>Nicotiana tabacum</i> L., <i>Phaseolus aureus</i> R., <i>Phaseolus vulgaris</i> L., <i>Pinus luchuensis</i> Mayr., <i>Pisum</i> <i>sativum</i> L., <i>Saccharum officinarum</i> L., <i>Schizolobium</i> <i>paraphyba</i> Vell., <i>Solanum melongena</i> L., <i>Solanum</i> <i>tuberosum</i> L., <i>Zea mays</i> L.		<i>plantaginea</i> R. Br. var. <i>tuberosa</i> Makino, <i>Hordeum</i> <i>vulgare</i> L., <i>Ipomea reptans</i> Poir, <i>Lactuca sativa</i> L., <i>Leucaena leucocephala</i> (Lam.) de Wit., <i>Lilium</i> spp., <i>Liquidambar formosana</i> Hance, <i>Lycopersicon</i> <i>esculentum</i> Mill., <i>Oryza sativa</i> L., <i>Papver rhoeas</i> L., <i>Phaseolus aureus</i> Roxb., <i>Phellodendron</i> spp., <i>Pinus</i> <i>elliotti</i> Engelm., <i>Pinus kaysia</i> Royle & Gord, <i>Pinus</i> <i>luchuensis</i> Mayr, <i>Pinus patula</i> Schlechtend & Champ, <i>Pinus taeda</i> L., <i>Pawlonia fortunei</i> Hemle., <i>Pawlonia</i> <i>kawakamii</i> Itl., <i>Pawlonia taiwaniana</i> He & Chang.
<i>aritisporum</i>	<i>Cucumis melo</i> L.		<i>Pawlonia tomentosa</i> Steud, <i>Raphanus sativus</i> L.,
<i>arrhenomanes</i>	<i>Oryza sativa</i> L., <i>Saccharum officinarum</i> L.		<i>Solanum melongena</i> L., <i>Zinnia elegans</i> Jacq.
<i>debaryanum</i>	<i>Cucumis melo</i> L., <i>Cunninghamia lanceolata</i> (Lamb.) Hook., <i>Pinus elliotti</i> Engelm., <i>Saccharum officinarum</i> L.	<i>splendens</i>	<i>Abroma angusta</i> Stevc., <i>Broussonetia papyrifera</i> (L.) L'Herit ex. Vent., <i>Calotropis procera</i> (Ait.) Ait., <i>Camellia</i> <i>oleifera</i> Abel., <i>Camellia tenuifolia</i> (Hay.) Cohen-Stuart.,
<i>catenulatum</i>	<i>Rosmarinus officinales</i> L., <i>Saccharum officinarum</i> L.		<i>Casuarina glauca</i> Sieb., <i>Casuarina equisetifolia</i> Forst.,
<i>coloratum</i>	hydroponic vegetables		<i>Cinnomum camphora</i> Presl., <i>Cinnamomum</i> <i>kanchirai</i> Hay., <i>Cryptomeria japonica</i> D. Don,
<i>deliense</i>	<i>Cucumis sativum</i> L., <i>Cunninghamella kanchirai</i> Hay., <i>Saccharum officinarum</i> L.		<i>Cunninghamia konishii</i> Hayata, <i>Eucommia ulmoides</i> Oliv., <i>Euphorbia pulcherrima</i> Willd. Ex. Klotzsch,
<i>dimorphum</i>	<i>Euphorbia longana</i> Lamarck		<i>Impatiens balsamina</i> L., <i>Leucaena leucocephalia</i> (Lam.) de Wit., <i>Michelia compressa</i> (Maxim.) Sargent,
<i>dissotocum</i>	<i>Citrus</i> spp., <i>Oryza sativa</i> L.		<i>Phellodendron</i> spp., <i>Pinus lectuensis</i> Mayr, <i>Pinus</i> <i>thunbergii</i> Parl., <i>Pinus taiwansensis</i> Hayata,
<i>elongatum</i>	<i>Oryza sativa</i> L., <i>Saccharum officinarum</i> L.		<i>Pawlonia fortunei</i> Hemsl., <i>Pawlonia kawakamii</i> Itl., <i>Pawlonia taiwaniana</i> He & Chang, <i>Pawlonia</i> <i>tomentosa</i> Steud.
<i>graminicola(um)</i>	<i>Saccharum officinarum</i> L.	<i>sylvaticum</i>	<i>Brassica chinensis</i> L., <i>Brassica oleracea</i> var. <i>acephala</i> DC., <i>Brassica oleracea</i> L., var. <i>botrytis</i> L., <i>Brassica</i> <i>rapa</i> L., <i>Cucumis sativum</i> L.
<i>hydno sporum</i>	<i>Brassica</i> sp.		<i>ultimum</i>
<i>inflatum</i>	<i>Saccharum officinarum</i> L.		<i>Acrocarpus fraxinifolius</i> Wright & Arn, <i>Antirrhinus majus</i> L., <i>Brassica chinensis</i> L., <i>Calotropis procera</i> (Ait.) Ait., <i>Carica papaya</i> L., <i>Cinnamomum tanchiria</i> Hay.,
<i>irregulare</i>	<i>Cryptomeria japonica</i> D., <i>Daucus carota</i> L., <i>Leucanea</i> <i>leucocephala</i> (Lam.) de Wit., <i>Papver rhoeas</i> L., <i>Pinus</i> <i>kasiya</i> Royle & Gord., <i>Pinus patula</i> Schlechtend & Chen <i>Pinus taeda</i> L., <i>Saccharum officinarum</i> L.		<i>Cryptomeria japonica</i> D. Don, <i>Leucaena leucocephalia</i> (Lam.) de Wit., <i>Liquidambar formosana</i> Hance, <i>Papver</i> <i>rhoeas</i> L., <i>Pinus luchuensis</i> Mayr., <i>Pinus taiwansensis</i> Hayata, <i>Pisum sativum</i> L., <i>Saccharum officinarum</i> L.
<i>mamillatum</i>	<i>Saccharum officinarum</i> L.		<i>vexans</i>
<i>myriotylum</i>	<i>Arachis hypogaea</i> L., <i>Asparagus officinalis</i> L., <i>Brassica campestris</i> L., <i>Citrullus lanatus</i> L., <i>Cucumis</i> <i>sativus</i> L., <i>Daucus carota</i> L., <i>Lycopersicon esculentum</i> L., <i>Nicotiana tabacum</i> L., <i>Pawlonia fortunei</i> Hemsl., <i>Pawlonia kawakamia</i> Itl., <i>Pawlonia taiwaniana</i> He & Chang, <i>Pawlonia tomentosa</i> Steud., <i>Saccharum offici-</i> <i>narum</i> L., <i>Solanum melongena</i> L., <i>Solanum tuberosum</i> L.		<i>Cinnamomum kanchirai</i> Hay., <i>Pinus luchuensis</i> Mayr., <i>Liquidambar formosana</i> Hance.
<i>obigandrum</i>	<i>Cinnamomum kanchiria</i> Hay., <i>Saccharum officinarum</i> L.	<i>unidentified</i>	<i>Ananas cosmos</i> L., <i>Beta vulgaris</i> L., <i>Carica papya</i> L.,
<i>spinosum</i>	<i>Allium fistulosum</i> L., <i>Allium schaeenoprasum</i> L. <i>Antirrhinum majus</i> L., <i>Arctium lappa</i> L., <i>Brassica</i> <i>campestris</i> L., <i>Calendula officinalis</i> L., <i>Campanula</i> <i>medium</i> L., <i>Chrysanthemum coronarium</i> L., <i>Cinnamomum kanchirai</i> Hay., <i>Coriandrum sativum</i> L.,	<i>spp</i>	<i>Oryza sativa</i> L., <i>Pachira aquatica</i> Aubl.

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