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Phytophthora Leaf Blight of Taro (*Colocasia esculenta*) – A Review

Raj Shekhar Misra* • **Kamal Sharma** • **Ajay Kumar Mishra**

Central Tuber Crops Research Institute, Thiruvananthpuram, Kerala, 695017, India

Corresponding author: * **rajshekharmisra@gmail.com**

ABSTRACT

Taro (*Colocasia esculenta* (L.) *Schott*.) is an important tropical tuber crop for millions of people in developing countries. Leaf blight caused by *Phytophthora colocasiae* Rac. is the most destructive disease of taro causing a 25-50% loss in yield. Besides, the pathogen also causes the serious post-harvest decay of corms. Both A1 and A2 mating types have been reported and it is believed that the fungus originated from Hainan Island in Asia. The existence of races of *P. colocasiae* is not known. The pathogen is reported to survive inside the tubers during the off-season. Collateral hosts also play an important role in the perennation of the pathogen. Secondary spread is through sporangia and zoospores, which are shed in water but not in wind and are carried by splash between plants and plantings. It has been found that *Colocasia* blight epidemic occurs when night and day temperatures range between 20-22 and 25-28°C, respectively with a relative humidity of 65% during the day and 100% at night and accompanied by overcast, rainy weather. Resistant cultivars have been identified in India, which can be used in breeding resistance. Copper and metalaxyl fungicides have proved to be very effective in controlling leaf blight. More in-depth studies are required to find out the existence of races, if any, of *P. colocasiae*, survival, biology and ecology of pathogen, a disease-forecasting system, breeding for disease resistance and disease management practices.

Keywords: epidemiology, disease management, disease resistance, *in situ* conservation, *Phytophthora colocasiae*, post harvest decay, varietal resistance, yield losses

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INTRODUCTION

Taro (*Colocasia esculenta* (L.) Schott.), a tropical aroid with nearly 1000 cultivars, is an important staple or subsistence crop for millions of people in developing countries. Throughout the islands of the Pacific, Asian Archipelago, central Africa, West Indies and the islands of the Caribbean and Central America, taro forms an important part of peoples' diet (Chandra and Sivan 1984). Africa ranks first in area and production of taro, followed by Asia and Oceania. However, as a commercial crop, its cultivation is limited to only few countries such as Hawaii, Egypt, Philippines and few islands in the Pacific and the Caribbean.

In India, two taro types viz., *C. esculenta* var. *esculenta* and *C. esculenta* var. *antiquorum* are commonly cultivated throughout the country but its exact acreage and production are not known. The major area under this crop is located in the northern and eastern states of India. *Colocasia* has very high yield potential. During a survey of major colocasia growing areas, Misra (1991, 1999) observed tuber yield of 30-50 t/ha, especially in *C. esculenta* var. *antiquorum.* Taro tubers are rich in starch and used almost everywhere as a vegetable. Besides, this crop is of great medicinal value and is included in many Ayurvedic preparations. The nutritional value of *Colocasia* is much more superior than other tuber crops and potato in many constituents such as protein, minerals, fiber, phosphorus, iron, etc. (Misra and Chowdhury 1997) (**Table 1**).

Leaf blight of taro, caused by *Phytophthora colocasiae* Raciborski, is the most destructive disease of colocasia.

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Table 1 Nutritive value of taro compared with other tropical tuber crops and potato as cited by Misra and Chowdhury (1997).

Constituent (per 100 g fresh tuber)	Taro (*Colocasia esculenta*)	Potato (*Solanum tuberosum*)	Cassava (*Manihot esculenta*)	Sweet potato (*Ipomoea batatas*)	Elephant foot yam (*Amorphophallus paenifolius*)	Yams (*Dioscorea alata*)	Coleus (*Solenostemon rotundifolius*)
Moisture (g)	73.1	74.7	59.4	68.5	78.7	79.6	87.4
Protein (g)	3.0	1.6	0.7	1.2	1.2	1.3	0.3
Fat (g)	0.1	0.1	0.2	0.3	0.1	0.1	0.2
Minerals (g)	1.7	0.6	1.0	1.0	0.8	0.8	0.7
Fibre (g)	1.0	0.4	0.6	0.8	0.8	0.1	-
Carohydrate(g)	21.10	22.6	38.1	28.2	18.4	18.1	11.4
Energy Kcal	97.0	97.0	157	120	79	79	49
Calcium (mg)	40	10	50	46	50	16	153
Phosphorus (mg)	140	40	40	50	34	31	13
Iron (mg)	1.7	0.7	0.9	0.8	0.6	0.5	0.6
Vitamin A (IU)	24	24	-	6	260	-	93
Thiamine (mg)	0.09	0.10	0.05	0.08	0.06	-	0.04
Niacin (mg)	0.4	1.2	0.3	0.7	0.7	-	0.4
Vitamin C (mg)	-	17	23	24	-	-	-
Riboflavin (mg)	0.03	0.01	0.01	0.4	0.07	-	0.05

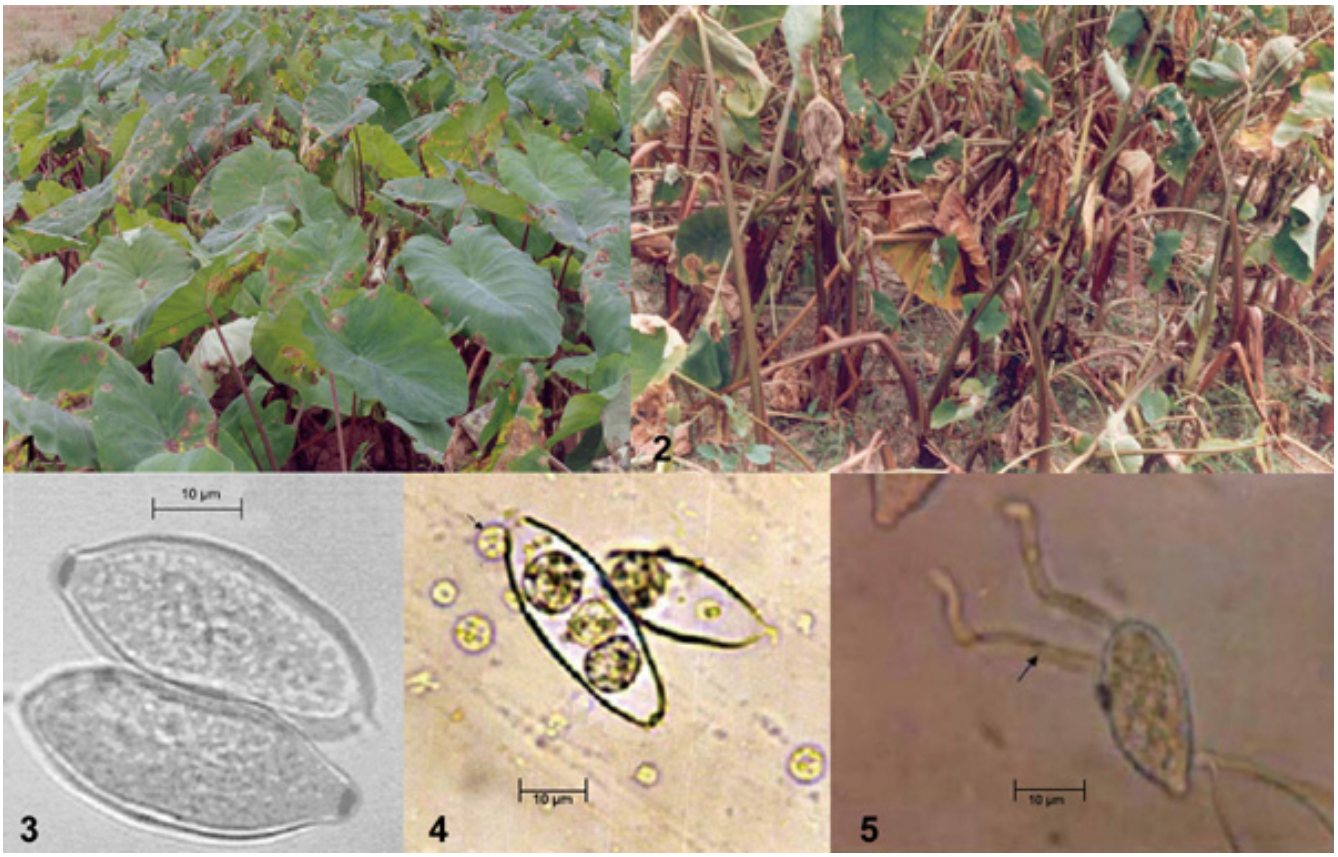

Plate (Figs 1-5). (**1**) Beginning of taro leaf blight disease caused by *Phytophthora colocasiae* in 4-month old taro crop (cv. 'Telia') during rainy (August) season. (**2**) Field view of fully devastated four and half month old taro crop (cv. 'Telia') during rainy (August) season. (**3**) Microscopic view of *Phytophthora colocasiae* sporangia. (**4**) Microscopic view of indirect germination (via zoospores production) of sporangia of *Phytophthora colocasiae* in sterile distilled water at optimum temperature (20-21°C). Arrow indicates the released zoospores. (**5**) Microscopic view of direct germination (via germ tube production) of sporangia of *Phytophthora colocasiae* in sterile distilled water at optimum temperature (20-28°C). Arrow indicates the germ tube.

Butler and Kulkarni (1913) reported leaf blight of taro for the first time in India, which had been observed at various places in India since 1905 causing serious damage. This disease is reported to have destroyed taro plantings in Papua New Guinea (Packard 1975). The disease has severely constrained taro production in American Samoa (Gurr 1996). Initial symptoms of the disease are small brown water-soaked flecks on the leaf that enlarge to form dark brown lesions, often with a yellow margin (**Fig. 1**). Secondary infections lead to rapid destruction of the leaf, which may occur in 10–20 days or less in very susceptible varieties (**Fig. 2**). The normal longevity of a healthy leaf is about 40 days. The disease significantly reduces the number of functional leaves and can lead to yield reductions of the magnitude of 50% (Trujillo and Aragaki 1964; Trujillo 1967; Jackson 1999). Inoculum in the form of spores spread by wind-driven rain and dew to adjacent plants and nearby plantations. The disease can also be spread on taro planting material and the fungus has been reported as remaining alive on planting tops for about three weeks after harvest (Jackson 1999). This is the most likely source of the pathogen in new countries and the means for its rapid spread within a country, once established. Therefore, strict quarantine measures are required as a first line of defense against the disease.

History of taro leaf blight

Leaf blight has become a limiting factor for taro production

Table 2 Occurrence of leaf blight of taro reported from different countries.

Country	Reported by	Year
Indonesia	Raciborski	1900
India, Formosa	Butler and Kulkarni	1913
Sri Lanka	Park	1939
Taiwan	Sawada	1911
Marinas, Carolines and Burma	Anonymous	1943
Philippines	Gomez	1925
Malaysia	Thompson	1939
Hawaii	Parris	1941
Papua New Guinea	Shaw	1963
	Hicks	1967
	Putter	1976
Solomon Islands	Johnston	1960
Trust Territories of Pacific Islands	Trujillo	1971
Indonesia, Malaysia, Sarawak, Africa and Caribbean	Anon	1978

in the Solomon Islands, Ponape, Hawaii and in India causing a 25-30% yield loss (Trujillo and Aragaki 1964; Gollifer and Brown 1974; Bergguist 1974; Jackson *et al*. 1980; Misra 1990, 1999). In addition to leaf blight, *P. colocasiae* causes a serious post harvest decay of corms (Jackson and Gollifer 1975; Jackson *et al*. 1979). The occurrence of leaf blight of taro has been reported from different countries (**Table 2**). In India also, leaf blight is reported to be a serious disease in many areas such as Kangra valley of Punjab which is now in Himachal Pradesh (Luthra 1938), Assam (Chowdhury 1944), Bihar (Anonymous 1950), Himachal Pradesh (Paharia and Mathur 1961) and other states (Prasad 1982; Thankappan 1985; Misra 1999). Leaf blight has also been reported from Fiji (Parham 1953; Graham 1965) and Western Samoa (FAO 1970). The geographic distribution of this disease is probably restricted to South-East Asia and the Pacific Areas (Holliday 1980).

Perhaps, since most taro produced is consumed locally and never reaches the international market, its problems have been relatively neglected, especially taro leaf blight, which is often followed by rhizome rot during storage (Gregory 1983). In this review an attempt has been made to compile information available on leaf blight of taro.

Crop loss

Phytophthora blight of taro appears as small, water-soaked spots that increase in circumference and also spread to healthy plants. The entire leaf area is destroyed within 3-5 days after the initial symptoms depending on the weather conditions. Under cloudy weather conditions with intermittent rains and temperature around 28°C, the disease spreads at tremendous speed and the entire field gives a blighted appearance. This disease is reported to have destroyed taro plantings in Papua New Guinea, both in the islands of Manus and Bougainville (Packard 1975). Yield losses of 25-50% are common in Solomon Islands (Gollifer and Brown 1974; Jackson *et al*. 1980) and in Hawaii (Trujillo and Aragaki 1964; Bergquist 1974) due to infected plants having three functional leaves instead of the more usual number of six or seven. Jackson and Gollifer (1975) found that the infected leaves collapse within 20 days of unfurling compared to 40 days in healthy leaves. They have also found 30-40% loss in tuber yield when the attack was recorded on 40–70-days-old crop. Leaf blight adversely affects dry matter production through destruction of leaf area as expressed in terms of disease severity. A decrease in crop growth in turn reduces tuber yield (Misra 1993). Out of 128 representative fields of *Colocasia* tested during the 1988 monsoon season, 94% of fields were infected by leaf blight with 78.38% of fields having more than 80% incidence. During 1989, out of 164 *Colocasia* fields 92% showed blight infection with 81.75% of fields showing more than 80% incidence. The rainy season crop is damaged during its peak of crop growth. There was a strong positive correlation between disease severity and yield loss in the farmer's field and experimental farm of the Regional Centre of C.T.C.R.I. (Misra 1996a).

In India, Misra (1996) conducted elaborate field trials to assess yield losses caused by taro blight. One set of trials was conducted in the farmer's field at Salepur in Orissa (India) using a local variety and another set was conducted in the Farm of Regional Centre of CTCRI, Bhubaneshwar using two varieties, one tolerant 'Jankhri' and the other susceptible 'Telia'. Spraying with mancozeb (0.2%, one to five sprays) was done to obtain variation in disease severity. One plot with 5 sprayings was considered as a check plot and yield loss was calculated over this. During 1988, yield loss of 45.20% was recorded in the farmer's field while on the farm, a yield loss of 50.46% was recorded in the *Phytophthora* leaf blight susceptible variety and 35.94% in the *Phytophthora* leaf blight resistant cultivar (Misra 1988, 1996a). During 1989, 39.41% yield loss was recorded in a local variety in the farmer's field whereas on the farm, the susceptible variety showed a 55.17% yield loss compared to 29.30% in the tolerant cultivar. Interactions effect between varieties and treatment were highly significant (Misra 1989, 1996a). During 1990, yield loss of 28.75% was recorded in the farmer's field whereas on the Institute Farm, a 46.75% yield loss was recorded in the susceptible variety and 22.75% in the tolerant variety (Misra 1990, 1996a).

It is evident that the yield losses caused by *P. colocasiae* are substantial and adequate attention is required to manage leaf blight before undertaking taro cultivation. Use of tolerant cultivars, in areas known for high blight severity, can alone considerably reduce the damage caused by leaf blight.

Causal organism

Raciborski first described the causal organism of leaf blight of taro as *Phytophthora colocasiae* in 1890 from Indonesia. The mycelium is hyaline, coenocytic and inter- or intra-cellular. The haustoria are slender, long and unbranched. The growth of the fungus is optimum at pH 6.5 and 28°C (Sahu *et al*. 2000). The sporangiophores are very slender, unbranched and extremely narrow at the tip and measure up to 50 µm in length. The sporangia are elongated; lemon- or pear-shaped and measure 38-60 × 18-26 µm (**Fig. 3**). They germinate directly or indirectly depending on the weather conditions. When indirect (20-21°C) as many as 12 remiform, biflagellate zoospores are released (**Fig. 4**), which convert to cysts and germinate after 30 min (Trujillo 1965; Misra 1996b). Indirect germination of zoosporangia occurred in water in less than 2 h at optimum temperature (20-21°C) and zoospores germinated in less than half an hour after release. Direct germination occurred in 5-6 h at 20-28°C. Thick-walled, round, hyaline chlamydospores are also produced, especially in old cultures (Thankappan 1985; Misra 1999).

The zoosporangiophores are slender, unblemished and extremely narrow at the tip and measure up to 50 µm. Misra (1996b) observed that zoosporangial length was over 100 µm and the width was over 50 µm. Depending on the weather conditions, the zoosporangium is capable of producing another zoosporangium. It may germinate directly by producing one or more germ tubes (**Fig. 5**) or by producing zoospores. Zoosporogenesis (indirect zoosporangial germination), like in most other species of *Phytophthora*, starts with the fusion of cleavage vesicles, which occurs almost spontaneously with the release of zoospores. Chilling the zoosporangia at 4°C for 10 min induced zoospore cleavage. Immediately after cleavage, the apical exit pore plug material balloons outwards to form a discharge vesicle that varies in size. The zoospores get expelled from the discharge vesicle and break through the thin plastic wall to escape. Within 20 min of the release, the zoospores encyst having a rather thick cell wall. The cysts germinate within 30 min of their encystment. The cysts are more damaging from a disease point of view as they are produced in large

numbers, are small in size and light in weight compared to zoosporangia. The abundant production of zoosporangia, zoospores and cysts make *P. colocasiae* a devastating pathogen.

The oogonium is spherical and yellowish and the amphigynous antheridium persists at the base of the oogonium for a considerable period after the oospores are formed. The oospores are spherical having a 20-28 µm diameter and lie freely in the oogonium. Ko (1979) screened isolates of *P. colocasiae* from taro fields in Hawaii and found 101 of them as A1 mating type while 5 isolates (3 from Asia) were A2 type. He suggested that the fungus originated in Asia (Zhang *et al*. 1994). Narula and Mehrotra (1980) found A1 mating type of *P. colocasiae* isolated from taro leaves from three North Indian States. Ann *et al*. (1986) found that all 799 isolates from fields of *C. esculenta* in Taiwan infected with blight were similar in colony appearance and behaved as A2 mating types. These results suggest that the fungus is probably not indigenous to Taiwan.

P. colocasiae produces pectolytic enzymes like polygalacturonase, pectin methyl transeliminase and poly methyl galacturonase and these enzymes may play a major role in the pathogenesis on *C. esculenta* (Agarwal and Mehrotra 1986). *Amorphophallus paeonnifolius* and black pepper were also reported to be the host for *P. colocasiae* (Paharia and Mathur 1961).

Besides *P. colocasiae* few other species of *Phytophthora* viz., *P. araceae* (Coleman) Peth., *P. palmivora* Butler, *P. parasitica* Dast. var. *pipernia* Dast., *P. nicotiana* Bredade Ham. var. *parasitica* Dastur (Narasimhan 1927; Umabala and Ramarao 1972), have been reported to infect taro. However, the role of these species in the severity and damage or epidemiological aspects is not known.

Biology and ecology

As compared to other species of *Phytophthora*, very little work has been done on the biology and ecology of *P. colocasiae.* It has survival devices that are less simple than those of *P. infestans. S*porangia are shed in water but not in wind. Spread is by sporangia and zoospores that are carried by splash between plants and plantings. Butler and Kulkarni (1913) found that the fungus survives in rhizomes. Since oospores and chlamydospores are produced, persistence of soil infectivity should not be a mystery. The survival of *P. colocasiae* in the soil in Philippines has been reported perhaps through oospores, in the corm or leaf tissue left in the field after harvest (Gomez 1925). Saprophytic survival of *P. colocasiae* and the role played by alternate host has been studied by Gollifer *et al*. (1980) in Solomon island, where taro is grown all-year round. They found that the inoculum in soil remained viable only for few days. Perennation between crops is effected by short-lived propagules and possibly by mycelium with petiole lesions. Propagating material in the form of decapitated taro tops from infected crops carry the short-lived inoculum to new colocasia plantations. In India, the situation is different where corms are stored and serve as the seed material for next season crop. Narula and Mehrotra (1984) studied the saprophytic survival of *P. colocasiae* in Indian soil. During rainy season, *P. colocasiae* present in naturally infected soil and it can be detected in soils only up to the end of September by leaf baiting technique. Under these conditions, when *P. colocasiae* does not seem to survive much longer freely in the soils or in the infected dead leaf tissues, the corm-borne inoculum of *P. colocasiae* would have much more importance in the recurrence of the disease. *P. colocasiae*, like other foliar *Phytophthora*, seems to have a poor competitive saprophytic ability in soil (Narula and Mehrotra 1984). Another important source of survival is self-sown colocasia plants, which grow as wild plants near ponds or compost pits (Misra and Chowdhury 1997). In Orissa (pers. obs.), it has been observed that the blight appeared invariably on these self-sown taro plants at least 7-15 days before appearing in the field. Besides, the pathogen can also survive on many collateral hosts, which have been found to be natural hosts of *P. colocasiae* (Thankappan 1985).

Epidemiology

Leaf blight is observed in severe form in areas having high relative humidity and frequent rainfall, whereas warmer areas having little rainfall and relative humidity are comparatively free from this disease. Trujillo (1965) found that blight epidemics occur when night and day temperatures ranged between 20-22 and 25-28°C, respectively, with a relative humidity of 65% during the day and 100% at night and accompanied by overcast rainy weather. Under such conditions *Colocasia* leaves could be damaged by blight disease in 5-7 days. According to him, low temperature below 20°C and high temperature above 28°C prevented sporulation of the fungus and reduced severity despite high humidity and rain. The disease out-break could occur when the temperature and relative humidity conditions are optimum for 6-8 h for three consecutive days with light rain or dew in the morning. Minimum temperature and relative humidity had significant positive correlation with disease severity. The occasional sunlight with intermittent rain is more favorable for disease severity compared to prolonged cloudy weather with rainfall (Misra and Chowdhury 1997).

DISEASE MANAGEMENT

Several methods for the management of leaf blight of *Colocasia* have been recommended but the use of tolerant cultivars seems to be the most ideal and economical method. Some of the effective management practices are discussed below.

Use of tolerant cultivars

Many cultivars of taro tolerant to leaf blight have been reported from India. Deshmukh and Chibber (1960) have identified var. 'Ahina' as resistant to blight. On 'Ahina', the number of sporangia produced was less compared to susceptible variety. The size of the infected area increases more slowly in the resistant variety than in susceptible variety. Later, Paharia and Mathur (1964) screened 20 varieties at Simla. They found var. 'Poonam Pat' as immune, 'Sakin V' as resistant and another seven as moderately resistant to blight. Misra (1988, 1989, 1990) screened 43 cultivars of *Colocasia* and cvs. 'Jankhri' and 'Muktakeshi' as highly tolerant to blight. Progress of leaf blight in six selected cultivars showing varying degree of resistance (including these two cultivars) was studied. The appearance of blight was delayed in tolerant cultivars and its subsequent spread was also slow as compared to susceptible cultivars (Misra and Singh 1991; Misra and Chowdhury 1997). Goswami *et al*. (1993) tested 50 lines against taro blight and found that 5 lines were showing resistance to the disease.

In other *Colocasia*-growing countries, varieties having a reasonable degree of resistance to blight have not been found in good number (Parris 1941; Hicks 1967; Gollifer and Brown 1974; Jackson and Gollifer 1975; Dayrit and Phillip 1987; Dey *et al*. 1993; Anonymous 1996; 1999). Trujillo (1967) advocated the development of resistant varieties through breeding and selection, as resistance is already present in the Pacific area within the genus *Colocasia*. Ho and Ramsden (1998) found that proteinase inhibitors were important factors in disease resistance in taro and the increased resistance was associated with the presence of inhibitors in healthy leaves.

Choudhury and Mathura Rai (1988) used wild varieties of *Colocasia* for resistance breeding and selected the resistant lines from them. Out of 20 varieties tested at Arunachal Pradesh, five were immune to blight. The aroid species *Xanthosoma sagittifolium* and *Alocasia macrorrhiza* were presumed to be resistant to *P. colocasiae* (Ho and Ramsden 1998). Attempts were made at CTCRI, Trivandrum, India (Pillai *et al*. 1993) to develop resistant taro lines through

breeding. The maximum proportion of resistant genotypes was obtained from variety 'c-320' self (66%), followed by open pollinated progeny of 'c-12' (33.33%), 'c-78' (30%) and 'Nadia local' (26.31%). Among the crosses, the maximum proportion of resistant genotypes were obtained in '$G_2 \times G_{16}$' (25%) followed by 'Pig × G_6' (23.8%). None of the tolerant parents bred true for resistant genes. The appearance of resistance genotypes in the population resulting from crosses between two partially susceptible genotypes was observed by Ivanicic *et al*. (1995). This indicates that minor genes associated with partial resistance are involved.

Glucan elicitors have been isolated from *P. colocasiae* isolates (Sriram *et al*. 2001). The PC-glucan elicitor could induce a hypersensitive reaction in the field tolerant cultivars like 'Muktakeshi' and 'Jankheri' while the induction of hypersensitive reaction was not induced or delayed in the susceptible variety 'Telia'. A technique for *in vitro* screening of the *Colocasia* varieties for leaf blight resistance using PC-glucan elicitor has been standardized.

Bio-control

Narula and Mehrotra (1981, 1987) studied phylloplane microflora of *C. esculenta* in relation to *P. colocasiae* and found *Myrothecium roridum*, 3 *Streptomyces* spp. and 2 bacterial isolates as antagonistic to *P.colocasiae* in dual culture plates. *In vivo*, the bacteria reduced the disease incidence up to 43%; *Streptomyces albidoflavus* reduced infection by 90-93% and *S. diastaticus* by 76%. Among fungi, *Botrytis cinerea* gave the best control of 33% reduction of plant infection. *Trichoderma viride*, *T. harzianum*, *Gliocladium virens* and one more unidentified sterile fungal culture were found to have potential antagonism against *P. colocasiae in vitro* (Sawant 1995; Pan and Ghosh 1997). The mycoparasitic or hyperparasitic activities of these isolates on *P. colocasiae* were brought about through several morphological changes like coiling of hyphae, formation of haustoria-like structures, disorganization of host cell contents and penetration into host hyphae. *Rhizobacteria* isolated from *Colocasia* rhizosphere soil have been reported to have the ability to completely inhibit the growth of *P. colocasiae in vitro*. *Trichoderma viride* effectively inhibited the population of *P. colocasiae* up to 88.88%, whereas *T. harzianum* and *T. pseudockei* reduced the population of *P. colocasiae* up to 77.77 and 88.88%, respectively. Since our earlier experiments showed that *P. colocasiae* did not survive in soil except during disease season, the findings can be effectively used for exploiting *Trichoderma* in tuber treatment. Apart from *Trichoderma*, other fungi and bacteria isolated from rhizosphere soil from *Colocasia* fields were tested by the dual plate method for their ability to inhibit *P. colocasiae*. Several fungi and bacteria completely inhibited the growth of *P. colocasiae* (Misra *et al*. 2001). Some *Rhizobacteria* formed inhibition zones with *P. colocasiae* in dual plate culture (Anonymous 2000).

Fungicidal control

Copper fungicides have proved very effective in successfully controlling the disease in many places like Fiji (Parham 1949); India (Mundkur 1949); Hawaii (Parris 1941; Trujillo and Aragaki 1964; Bergquist 1972, 1974) and Solomon islands (Jackson *et al*. 1980). Dithane M-45, Polyram, Benlate, Perinox and Dyrene were also found to be very effective in controlling this disease (Anonymous 1950; Bergquist 1972; Maheswari *et al*. 1999). Application of copper oxychloride at 14-day intervals adequately controlled the disease (Jackson and Gollifer 1975). Besides metalaxyl, captafol and chloroneb were also found to be effective in controlling *P. colocasia*e under *in vitro* and *in vivo* conditions (Aggarwal and Mehrotra 1987). Aggarwal and Mehrotra (1988) observed that besides controlling *P. colocasiae* in the field, metalaxyl could inhibit the cellulolytic and pectinolytic enzymes produced by *P. colocasiae*. Results on the chemical control of taro leaf blight with metalaxyl and breeding for disease resistance were reported (Anonymous 1982). The effect of potassium iodide, arsenic oxide on the mycelial growth, sporangial production, pectolytic and cellulolytic enzyme production and control of *P. colocasiae* on taro was reported (Aggrawal *et al*. 1993). Taro leaf blight controls are reported by using a fungicide spray (Forschek, a phosphorous acid-based product) to control the disease (Adams 1999). The effect of fungicides in controlling leaf blight caused by *P. colocasiae* in *C. esculenta* revealed that 0.2% metalaxyl and mancozeb (as Ridomil MZ-72) was the most effective treatment, followed by 0.2% captafol (as Foltaf), bordeaux mixture (1% copper sulfate and lime) and 0.25% mancozeb (as Foltaf) (Bhattacharyya and Saikia 1996). Metalaxyl with copper (as 0.3% Ridomil plus 72 w.p.) gives excellent control of taro leaf blight when applied at 2-week intervals using a knapsack sprayer (Cox and Kasimani 1988). The efficacy of copper oxychloride, mancozeb, metalaxyl, captafol, ziram and Bordeaux mixture against leaf blight disease of taro var. *antiquorum* (Das 1997). Sahu *et al*. (1989) observed that four sprays of zineb at 15-day intervals starting from the end of July to early August reduced the incidence of *P. colocasiae* in *C. esculenta*. Ghosh and Pan (1991) found that spraying with metalaxyl (Ridomil M272WP) at 3 kg/ha at 15-day intervals was highly effective in controlling the disease. Cox and Kasimani (1990) found that 5 applications of metalaxyl at 3-week intervals resulted in an increase of almost 50% in tuber yield. Leaf blight of taro has also been reported to be controlled by spraying 500 ppm of borax. A field experiment involving 10 taro genotypes, spraying of borax (500 ppm) showed a significant reduction in the leaf area damaged per plant by leaf blight and increased the corm/cormel yield (Misra *et al*. 2007).

Cultural practices

Removal and destruction of infected leaves and use of healthy corms and crop rotation have been recommended as control measures (Mundkur 1949). Jackson *et al*. (1980), on the other hand found that removal of infected leaves did not help in reducing the disease incidence; wider than traditional spacing also did not reduce the blight incidence. They observed that the density of the plant could be doubled under conditions of high disease hazards and increased yields could still be obtained. Mulching with paddy straw (pers. obs.) gives better yield, good weed control and slightly lowers disease severity. Other cultural methods that have been recommended include delaying planting on the same land for a minimum of three weeks, avoiding plantings close to older infected ones and preventing the carryover of corms or suckers which can harbour the pathogen from one crop to the next (Jackson 1999). Preliminary findings indicated that fertilizer treatment may have also helped the plant cope with leaf blight (Tililalo *et al*. 1996). Trials in Samoa to investigate the effect of planting time, intercropping, the role of fertilization on the incidence and severity of the disease and the effect of leaf removal were inconclusive (Chan 1997).

Shifting of planting time

Planting time can be shifted in such a way that the crucial stage of plant growth and optimum climatic conditions for disease development do not coincide with each other. In a field trial at the Regional Centre of CTCRI, Bhubaneshwar (India) to study the effect of planting time on the incidence of leaf blight and tuber yield, Misra (1988, 1989, 1990) found that May planting gave highest tuber yield and escaped much of the damage caused by blight (Misra and Chowdhury 1995).

Quarantine measures

Since the disease has been reported in many countries, strict quarantine measures should be observed to prevent further

spread of this disease and movement of taro between countries should be limited to sterile, pathogen tested plantlets growing in tissue culture medium (Zettler *et al*. 1989).

Integrated disease management practices

A farmer-friendly IDM package for the management of the taro blight was developed by Misra *et al*. (2001). The package includes growing short-duration crop with early planting i.e., in March, one protective spray with mancozeb (0.2%) at 45 days after planting followed by one spray with metalaxyl (0.05%) at 60 days after planting, intercropping with non-host crops like okra, use of disease free seed tubers and seed tuber treatment with *Trichoderma viride*. *Phytophthora* leaf blight of taro can be effectively managed by the use of tolerant cv. 'Muktakeshi' with mancozeb (0.25%) spray after the first appearance of the disease symptoms and an another ridomil MZ (0.2%) spray 15 days after the spraying of mancozeb (Misra *et al*. 2007).

The BAP-mediated inhibitory effect of *P. colocasiae* was found *in vitro* and *in planta*. The BAP-mediated growth retardation of *P. colocasiae* provides evidence for its efficacy in a biological control for disease prevention and provides a new strategy to combat taro leaf blight (Mishra *et al*. 2008b).

TARO GENETIC RESOURCES: CONSERVATION AND UTILIZATION

The impact of taro leaf blight, the subsequent loss of taro genetic resources, was the major impetus behind the development of Taro Genetic Resource. In one of our projects, studies were conducted on the collection and conservation of taro germplasm and use of the genetic resources in plant improvement programmes with an overall goal of improving food security and rural incomes (Misra 2008; Mishra *et al*. 2008c).

Genetic variation among taro can be used to solve the potential effects of leaf blight of taro. Different varieties respond differentially to *P. colocasiae* with varying degrees of infection. This has led to several breeding programs being initiated with the aim of broadening the genetic base of breeding populations in India (Lakhanpaul *et al*. 2003) and abroad in taro and other crops (Brummer *et al*. 1995; Wachira *et al*. 1995; Swoboda and Bhalla 1997), in addition to selection for resistance to taro leaf blight. Germplasm characterization and the evolutionary process in viable populations are important links between the conservation and utilization of plant genetic resources. The development of molecular and biochemical techniques help researchers, not only to identify genotypes, but also to assess and exploit genetic variability (Whitkus *et al*. 1994). Insights into the relative genetic diversity among taro cultivars would be useful in plant breeding and *ex situ* conservation of plant genetic resources (Wolff and Peter-van Rijn 1993; Irwin *et al*. 1998; Ochiai *et al*. 2001).

One of the main components of the project is to provide farmers with taro varieties that have improved resistance to taro leaf blight. To achieve this, the project supports breeding programmes in CTCRI, Trivandrum based on durable resistance (Mishra *et al*. 2008a; Sharma *et al*. 2008). Breeding of more resistant varieties together with the introduction of resistant varieties is the most sustainable approach to managing the disease. We plans to make these improved lines, and other resistant varieties, available to farmers in country.

FUTURE PRIORITIES

It is evident that the information available on such an important disease is inadequate to prove conclusively the existence of races, survival of the pathogen, large-scale yield loss, relationship between various weather factors and disease severity, disease management practices etc. Although, A1 and A2 mating types have been reported, there has not been any attempt to study the existence of races, if any of *P. colocasiae.* Nutritional studies on the pathogen are also lacking. Very little information is available on the biology and ecology of the pathogen. Although it is generally believed that the pathogen survives in the tubers during storage but it has not been studied conclusively. The role of collateral hosts and self-sown *Colocasia* crop in harboring the pathogen during off-season and the extent to which these hosts are responsible for the disease build up and perennation of the pathogen needs elaborate studies. Studies on assessment of yield loss due to leaf blight have shown that the pathogen causes extensive damage but there is a need to plan and conduct these studies in order to develop a model to find out the relationship between disease severity and yield loss. Physiology of diseased plant and defence mechanism in tolerant plants needs to be studied. Molecular basis of the disease resistance to the disease has to be elucidated to through more light for the development of the disease resistant varieties. Detailed epidemiological studies are required to establish the correlation between various weather factors, individually and in combination and severity of the disease. The ultimate aim of epidemiological studies is to develop a suitable disease forecasting system. Control of the disease using fungicide alone may not be practical because blight is a rainy season disease and spraying during monsoon season is a problem in *Colocasia* that has characteristic non-sticking leaves. Adjustment of planting time to avoid crucial stage of plant growth from being coincided with optimum weather conditions for disease development can prove to be very effective but it needs extensive study and the recommendations will vary from place to place.

Studies on disease management need priority from a production point of view. Since resistant cultivars are available in India, an attempt should be focused on breeding for disease resistance. Several different lines of evidence demonstrate that the expression of chitinases (particularly when co-expressed with glucanase) enhances plant pathogen resistance (de las Mercedes *et al*. 2006; Frettinger *et al*. 2006; Santos *et al*. 2007). Plants that are characterized by reduced chitinase activity are significantly more vulnerable to attack by unspecific fungi under natural conditions (Heil *et al*. 1999), and plants apparently tend to reduce the activity of these enzymes when they are not required due to the presence of other defense mechanisms (Heil *et al*. 1999, 2000).

The gene(s) conferring resistance against taro leaf blight have been identified (Sharma *et al*. 2008) and need to be incorporated in the accepted varieties to develop transformed plants using molecular techniques so they can respond to infection by expressing a broad-spectrum disease resistance that is active against further pathogen attack. Several aspects of this response are expressed even in non-infected plant parts (i.e., systemically). This systemic acquired resistance (SAR) is characterized by (1) a local hypersensitive response (HR) leading to programmed cell death around the infected cells (Kombrink and Schmelzer 2001), (2) local changes in cell-wall structure and composition preventing the further penetration by pathogens, and (3) the local and systemic expression of pathogenesis-related (PR) proteins (van Loon 1997).

One activator of host defense responses is an elicitor molecule from an invading pathogen. Many elicitors of various structures have been isolated from *Phytophthora* species, among them a cell wall-derived heptaglucan (Sharp *et al*. 1984), extracellular (glyco)-proteins such as a transglutaminase (Brunner *et al*. 2002), elicitins (Ricci *et al*. 1989; Kamoun *et al*. 1997), GP32 (Bailleuil *et al*. 1996), and cellulose binding elicitor lectin (CBEL) (Villalba-Mateos *et al*. 1997). High-affinity binding sites in plants have been described for several general elicitors of bacterial, fungal, and oomycete origin, such as flagellin, chitin fragments, a β-heptaglucoside, and cryptogein (Bourque *et al*. 1999; Gomez-Gomez and Boller 2000; Bradley Day *et al*. 2001). These can trigger a network of signalling pathways

that coordinate the defense responses of the plant, including HR, PR protein, and phytoalexin production (Heath 2000; McDowell and Dangl 2000; Shirasu and Schulze-Lefert 2000).

During the past few years, efforts have been made to generate transgenic plants that express the introduced gene under controlled conditions only. A gene encoding the elicitor cryptogein (a small basic protein, 98 amino acids in length) from the pathogen *Phytophthora cryptogea* was cloned and expressed in transgenic tobacco under control of a pathogen-inducible promoter (Keller *et al*. 1999). Under non induced conditions, the transgene was silent, and no cryptogein could be detected in the transgenic plants. In contrast, infection by the virulent fungus *P. parasitica* var. *nicotianae* stimulated cryptogein production that coincided with the fast induction of several defense genes at and around the infection sites. Induced elicitor production resulted in a localized necrosis that resembled a *P. cryptogea*-induced hypersensitive response and that restricted further growth of the pathogen. The transgenic plants displayed enhanced resistance to fungal pathogens that were unrelated to *Phytophthora* species, such as *Thielaviopsis basicola*, *Erysiphe cichoracearum*, and *Botrytis cinerea*. Another elicitor, INF1, was shown to act as an Avr factor in the tobacco–*Phytophthora infestans* interaction and triggered the onset of the defense reaction (Kamoun *et al*. 1998). Expression of the gene encoding the AVR9 peptide elicitor from *Cladosporium fulvum* in transgenic tomatoes containing the *Cf-9* gene resulted in a necrotic defense response (Hammond-Kosack *et al*. 1994; Honée *et al*. 1995). In transgenic potato, expression of bacterioopsin enhanced resistance to some pathogens but had no effect on others (Abad *et al*. 1997), and further expression of pathogen-inducible *PVS3* promoter and a fused elicitor enhanced the defense response against potato late blight agent without the deleterious consequences of constitutive defense expression and without the constitutive synthesis of a transgenic product. Extensive studied conducted by us led to the identification of elicitor protein and further cloning and characterization of a gene encoding an elicitor protein of *P. colocasiae* (Mishra *et al*. 2008). From a disease resistance perspective of taro plants, it would clearly be advantageous to clone the coding sequence of the elicitor gene in high yielding, diseases susceptible field cultivars of taro. The strategy is predicted on the assumption that the elicitor is recognized by the taro plants' own perception system and that a virulent microorganism thus triggers a hypersensitive reaction. Nevertheless, successful arrest of pathogen growth without damage to the transgenic taro plant requires that the elicitor protein to be expressed rapidly and locally. Because constitutive elicitor production can be lethal to a plant, elicitor activation should occur only at the time of pathogen challenge and not under other circumstances. Thus, the strategy described above requires a gene encoding a highly active protein elicitor and a functional promoter that is specifically inducible by a virulent pathogen *P. colocasiae*. The selected gene promoter will neither be developmentally nor tissue specifically regulated and will not respond to environmental stimuli. The promoter will be activated in taro only during interaction with *P. colocasiae* and other pathogens. Thus resistance response will be appeared timely after the interaction with pathogens and spatially coordinate activation of defense mechanisms. Moreover, this work would provide the basis and framework to other crops infected by different *Phytophthora* species to develop disease resistance engineered crop against their respective *Phytophthora* pathogens and non-specifically to other pathogens.

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