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Phytophthora: A Member of the Sixth Kingdom Revisited as a Threat to Food Security in the Twenty-First Century

19

S. Guha Roy

Abstract

This genus *Phytophthora* has a long history in modern science. The re-emergence of *Phytophthora* spp. causing damages in almost all ecological niches along with advancement in molecular technologies and discovery of new species has led to a renewed interest in *Phytophthora* spp. All of which has led to significant changes in the way the taxonomy of *Phytophthora* is now being studied. The genus *Phytophthora* infects an array of spices and plantation crops, and this scenario vis-à-vis *Phytophthora* spp. has been discussed here with special reference to black pepper, onion, garlic, leek, chilli, cocoa, coconut and rubber. Possible approaches for management of these diseases using databases derived from population characterisation through a correlation of their phenotypic and genotypic diversity have been discussed. Molecular tools that can be used for the production of such databases have also been discussed.

19.1 Introduction

The existence of man on Earth is mostly dependent on the ability of plants to harness light and produce oxygen and organic matter. Domestication of plants for agriculture resulted in many great civilizations of the past: Asian civilizations based on rice, Middle Eastern on wheat and barley and American on maize and potato. Like in the past centuries, the staple food of the world population today also depends on only a few major crops: wheat, rice, maize and potato (FAO 2002). However, mankind alone is not in the need to live off plants; a large number and different types of pathogens attack plants and, having 'fine-tuned' their ability to parasitize the living plants throughout evolutionary history, are at considerable advantage in competing to obtain nutrients from this primary food source and therefore are our competitors and enemies too (Strange and Scott 2005)! Worldwide crop loss due to pathogenic diseases, insects and weeds accounts for 31–42 % of the potential crop production capacity; without protective measures, this loss would be greater than 50 % (Agrios 2005).

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Approximately 10,000 fungal species are considered to be plant pathogenic (Farr et al. 1989; Agrios 2005) out of the 72,000–100,000 fungal species identified till date, but, considering that this represents only a small fraction of the fungal kingdom, estimated to include ~1.5 million species (Hawksworth 1991, 2001; Hawksworth and Rossman 1997), the actual number of plant pathogenic fungi is likely to be much greater than 10,000!

Diseases caused by fungi are well established as major constraints of food, fibre and crop production. Equally devastating, if not more, among the fungi is a group of organisms which differ from the 'true fungi' in many characteristics (chitin-less cell wall (Bartnicky-Garcia and Wang 1983), sterol metabolism (Warner and Domas 1987; Wete 1989; Köler 1992; Griffith et al. 1992), other metabolic pathways (Hendrix 1970; Wang and Bartnicky-Garcia 1973; Elliot 1983), storage compounds (Wang and Bartnicky-Garcia 1974; Coulter and Aronson 1977; Bartnicky-Garcia and Wang 1983; Rast and Pfyffer 1989; Pfyffer et al. 1990; Griffith et al. 1992), tubular cristae in mitochondria (Alexopoulos et al. 1996), differential sensitivity to monomeric aluminium (Fichtner et al. 2006) and motile heterokont zoospores (Desjardins et al. 1969)) referred to as 'pseudofungi' by most mycologists and is placed into a new domain of life called Stramenopila (Cavalier-Smith 1987; Leipe et al. 1994; Beakes 1998).

The Stramenopila includes *Oomycetes* such as 'phytophthoras', 'downy mildews' and 'Pythia', which form a unique branch of eukaryotic plant pathogens with an independent evolutionary history (Kamoun et al. 1999) showing a distant evolutionary relationship with true fungi (Gunderson et al. 1987; Förster et al. 1990; Baldauf et al. 2000). The fact that oomycetes are not related to fungi is particularly relevant for heterologous expression of genes and comparative genomics and genetics in general. Still, despite their different evolutionary origins, the morphology of the hyphae, their mycelium-like growth and the airborne spores show remarkable resemblance to fungi. Oömycetes and fungi are probably one of the best examples of convergent evolution.

The *Oomycetes* contain some of the most destructive of plant pathogens; among them, some species of the genera *Phytophthora*, *Pythium* (rots, blights and damping off) and *Peronospora* and *Plasmopara* (downy mildews) stand out; in fact, the name *Phytophthora* means 'plant destroyer'. The genus *Phytophthora* with more than 108 members is presently placed in the kingdom Stramenopila (Belbahri et al. 2006), under the phylum Heterokonta, subphylum Pernosporomycotina, class Pernosporomycetes (Oömycetes), subclass Pernosporomycetidae, order Pythiales and family Pythiaceae. The taxonomy of *Phytophthora* has undergone an evolution in the way it has been studied, from the era of six morphospecies groups (Waterhouse 1963; Newhook et al. 1978; Stamps et al. 1990) to the era of phylogenetic clades (Cooke et al. 2000) and ITS fingerprinting-based keys (Gallegly and Hong 2008) and now to a new era of an integrated morphological and phylogenetic key (Ristaino 2011), and has been reviewed by Guha Roy and Grünwald 2014.

This genus *Phytophthora* has a long history in modern science. The scientific discipline of plant pathology was born in the early 1860s when Anton de Bary recognised *Phytophthora infestans* as the pathogen causing potato late blight responsible for the Irish potato famine in the 1840s (Abad and Abad 2003; Aragaki and Uchida 2001). It also brought about the first formulated use of a fungicide. In addition to this substantial social and historical impact, even considering merely a handful of *Phytophthora* spp. (e.g. *P. sojae*, *P. infestans*) documented to cause significant economic impacts, costs amount to anywhere between two and seven billions of dollars per crop per year worldwide in combined crop losses and management costs not even considering the less quantifiable but equally large impacts to natural ecosystems severely affected by some species (e.g. *P. cinnamomi*, *P. ramorum*).

Phytophthora pathogens also have a large impact on native ecosystems, forests and agricultural crops. The past decade has seen the discov-

ery of a large number of phytophthoras especially from aquatic and forest ecosystems, and a wealth of information is now available on some of the phytophthoras attacking crops and plantations. Only the advances and their possibilities in horticultural and spice crops will be discussed here as exhaustive reviews are already available on the other ecosystem niches (Lamour and Kamoun 2009; Guha Roy 2008; Guha Roy and Grünwald 2014).

Phytophthora is now considered as one of the most important and destructive genera of plant pathogens in temperate and tropical regions, causing annual damages of billions of dollars (Drenth and Guest 2004) due to its high virulence and epidemiological ability to spread rapidly throughout the world.

19.2 The Spice Scenario vis-à-vis Phytophthora

The genus *Phytophthora* infects an array of spices and plantation crops. Some of the important diseases caused by *Phytophthora* are azhukal disease of cardamom, foot rot of black pepper, white tip of leek, leaf blight of onion and garlic, root rot of chilli, bud rot of coconut, abnormal leaf fall of rubber, wilt of *Piper betle*, koleroga of arecanut and some diseases of cocoa. Some of them have been discussed in the following paragraphs:

19.2.1 Phytophthora in Black Pepper

Phytophthora foot rot and leaf rot of black pepper are a serious problem in all black pepper-growing countries like India, Indonesia, Vietnam, Malaysia, Brazil, Thailand, Madagascar, etc. India and Indonesia are the main producers of pepper and account for more than 50 % of the world production. On a global scale, losses due to this disease have been estimated to be US$ 4.5–7.5 million per annum (de Waard 1979). The disease was first reported in 1885 in Lampung, Indonesia and has been called foot rot disease since 1928 (Muller 1936). The disease starts as dark brown spots on tender leaves at the lower region of the bush which enlarge rapidly covering the major area of leaf. These leaf spots have characteristic 'fimbriate margins' and infected leaves drop off prematurely. The fungus also infects green stems and branches causing rotting. In the case of root rot, infection that starts on the fibrous root system reaches the main root and ultimately the collar region or foot region of the bush (http://iisr.agropedia.in/content/phytophthora-disease-black-pepper).

In India, Kerala accounts for over 97 % of the area under pepper cultivation where it is a serious and dreaded disease even affecting coconut, arecanut and rubber plantations in the vicinity (Pruthi 1993; Chowdappa et al. 2003a). Different *Phytophthora* spp. are found to be associated with *Phytophthora* foot rot and leaf rot of black pepper in different geographical regions. In India, the disease was first reported way back in 1902 (Barber 1902; Butler 1906), and currently, *P. capsici* and *P. tropicalis* and isolates having similarity to both have been molecularly identified as being associated with the disease (Chowdappa et al. 2003b; Annual Report IISR 2012–2013); in Indonesia, where it has a long history of cultivation as Hindu migrants probably took pepper to Java between 100 BC and AD 600 (Purseglove et al. 1981), it is affected by *P. capsici* where it causes 52 % yield reduction (Purwantara et al. 2004). In Vietnam, which is now the world's second largest pepper exporter, though the disease was first reported in 1952, the identity of the causal agent was only recently conclusively determined as *P. capsici* (Truong et al. 2008) with low genetic diversity (Truong et al. 2010) but more adapted to black pepper hosts (Truong et al. 2012). Disease losses in Vietnam account to 15–20 % (Drenth and Sendall 2004). In Malaysia, pepper cultivation started with the British organised plantings of pepper in the early nineteenth century (Purseglove et al. 1981). Malaysia is now the fourth largest producer of black pepper in the world (PMB 2001), and currently, 95 % of the pepper produced in Malaysia is grown in Sarawak (PMB 2001) where *P. capsici* is the causal agent and the rest in Johor from where *P. nicotianae* has also been isolated (Lee and Lum 2004). On

the other hand, the causal agents reported from Thailand are *P. palmivora*, *P. nicotianae* and *P. capsici* (Sangchote et al. 2004), while only *P. capsici* has been reported from Turkey on black pepper where it is very destructive and has the greatest economic importance. *P. capsici* is very dangerous for pepper spice and pepper paste production because it causes up to 100 % drying and killing of pepper plants under conditions of poor drainage and incorrect irrigation practices (Biçici and Çinar 1990).

- For the management of *Phytophthora* foot rot in black pepper, crop should be sprayed with 0.25 % Ridomil Gold 68 (WP) or 0.3 % potassium phosphonate during June and August and also drenching the soil with 3 l per vine and 1 kg of neem cake with 50 g of *Trichoderma harzianum* to the root zone of vines twice in a year.
- Biocontrol agent 1 % *Pseudomonas fluorescens* application to the vine as spraying (@ 2 l/vine) and drenching (@ 3 l/vine) during June and the second week of August for management of *Phytophthora* root rot was helpful [http://uhsbagalkot.edu.in/AICRP_sirsi.aspx].

19.2.2 Phytophthora in Onion, Garlic and Leek

(a) *Phytophthora porri* affects different alliums like leek, onion and garlic. White tip is one of the important foliar diseases of leek in Western Europe. The disease has been mainly reported from Europe, Canada and Japan. In Japan, a loss of 70 % or more is found in onion. The disease spreads rapidly on cool, wet weather. On onion and garlic, this pathogen causes water-soaked leaf blight and root rot symptoms. Early symptoms of leek leaves consist of irregularly shaped water-soaked lesions. Older lesions develop a bleached white centre with water-soaked margin which disappears in dry condition.

(b) *Phytophthora nicotianae* causes damping off of green onion seedlings and leaf blight and rot of green onion. On onion leaves, spots begin as small, irregularly shaped, water-soaked lesions on the young and mature leaves. In a few days, these spots expand, girdling the leaf and causing the tissue above the infection point to wither. As the infection progresses, healthy tissue is invaded, eventually killing the entire leaf. Infected plants have a mix of healthy and withered leaves with some leaves showing a characteristic of half-infected, half-healthy symptom. Splashing water from raindrops or irrigation helps to move spores from infected plants to nearby healthy plants. Effective disease control begins with prevention and proper water management to minimise excess moisture on the plants. Ridomil 81 W can be applied to green onion up to 14 days prior to harvest. Also, label directions are to be read carefully and chemicals applied responsibly [http://www.extento.hawaii.edu/kbase/crop/type/p_nicoti.htm].

19.2.3 Phytophthora in Chilli

Phytophthora blight, caused by *Phytophthora capsici*, is a devastating disease on both bell and non-bell peppers. The major symptom is root rot and wilt. However, more precisely, *Phytophthora capsici* infects roots, crowns, stems, leaves and fruit, causing seedling damping off, stem lesion, stem blight, leaf spot and fruit rot. It is a soilborne pathogen which can produce several types of spores, enable it to spread throughout the field and to persist in the field between crops. *P. nicotianae* has also been found to be pathogenic on chilli pepper in Tunisia, NW and Western Spain, but the symptoms described are that of collar and root rot in contrast to fruit rot reported from the Indian subcontinent and those of seedling blight as the isolates were suggested to be different and this *P. nicotianae* is more adapted to their hosts (Andrés et al. 2003; Darinea et al. 2007; Saadoun and Allagui 2008; Rodríguez-Molina et al. 2010).

No single strategy should be used to control Phytophthora blight of pepper. A combination of methods is needed to effectively control this disease. The following practices can help to manage Phytophthora blight in pepper fields:

1. Fields to be selected with no history of Phytophthora blight, if possible.
2. Select fields that did not have peppers, cucurbits, eggplants or tomatoes for at least 3 years.
3. Selected fields are to be well isolated from infested fields with *P. capsici*.
4. Well-drained fields are to be chosen. Low areas or the areas which do not drain well are to be avoided.
5. Excessive irrigation is to be avoided.
6. Seeds should not be saved from a field where Phytophthora blight occurred.
7. Resistant varieties are to be planted, whenever it is possible.
8. Fungicides may be used to reduce Phytophthora infection in pepper fields.

19.2.4 Phytophthora in Cocoa

Phytophthora pathogens are responsible for some of the most serious diseases of cocoa including *Phytophthora* pod rot (PPR) or black pod, stem canker, leaf and seedling blight, chupon wilt and flower cushion infections. PPR causes 10–30 % annual losses in the production of cocoa beans globally and much higher losses locally in particularly wet and humid conditions. The estimated losses in the production in Asia, Africa and Brazil are 450,000 t annually, worth an estimated value of US$ 423 million (Drenth and Sendall 2004). Stem canker causes further losses and also tree deaths. Eight species of *Phytophthora* have been isolated from diseased cocoa, but most losses in the production are caused by *Phytophthora palmivora*, *P. megakarya*, *P. capsici* and *P. citrophthora*, and these vary in both their aggressiveness and the level of crop loss caused (Appiah et al. 2004). *Phytophthora megakarya* is the most aggressive and can cause between 60 and 100 % crop loss (Djiekpor et al. 1981; Dakwa 1988). In contrast, *P. palmivora* is less aggressive and can cause crop losses of 4·9–19 % (Blencowe and Wharton 1961; Dakwa 1984); this species is more aggressive than *P. capsici* (Lawrence et al. 1982). *Phytophthora citrophthora* is more aggressive than *P. palmivora* or *P. capsici* and requires less time for zoospore germination and penetration on unwounded, detached pods (Campêlo et al. 1982). Sequence analysis showed that the four main cocoa-associated species formed two distinct groups, one comprising *P. capsici* and *P. citrophthora* and the other *P. palmivora* and *P. megakarya* (Appiah et al. 2004). Single reports of other *Phytophthora* species causing black pod include *P. botryose* (Chee and Wastie 1970), *P. heveae* (Lozano and Romero 1984) and *P. katsurae* (Liyanage and Wheeler 1989a) and *P. megasperma* (Zentmyer 1988), although these are not considered major problems for cocoa production.

The relative impact of each of these species of *Phytophthora* varies from region to region. In India, both *P. palmivora* and *P. capsici* cause black pod disease, but the *P. palmivora* isolates are of a single clonal lineage also infecting the coconut plantations below which it is cultivated as an understory crop, while on the other hand, the *P. capsici* isolates from cocoa belong to two genetic subgroups (Chowdappa et al. 2003b). A detailed sequence analysis of worldwide collection of *P. capsici* isolates from cocoa as well other hosts and comparison with published literature suggested that *P. capsici* isolates from cocoa may be closely related to *P. tropicalis* (Appiah et al. 2004). In Southeast Asia, *P. palmivora* seems to be the principal pathogen, while *P. megakarya* has only been found in West Africa (Brasier et al. 1981). In Africa, *P. megakarya* tends to be the principal pathogen, while in the Americas, *P. capsici* and *P. citrophthora* are the main causal agents of pod rot (Erwin and Riberio 1996) worldwide. *P. palmivora* is one of the most serious pathogens on cocoa, and in Southeast Asia, this species accounts for almost all of the Phytophthora diseases of cocoa. The most effective control measures are the introduction of resistant cocoa genotypes and farm management practices such as the removal of infected pod husks, proper pruning of the canopy and judicious selection of shade species and associated crops (McMahon and Purwantara 2004).

19.2.5 Phytophthora Diseases of Coconut

Coconut (*Cocos nucifera*) is one of the most valuable plant species in the tropics, providing oil, coconut milk, fibre from the husk, palm wine and timber for furniture and construction with its primary centre of origin in Asia and some secondary centres of origin in Central and South America. Rots caused by *Phytophthora* spp. lead to palm death (by bud rot) and/or yield reduction (by premature nut fall) (Waller and Holderness 1997) and are prevalent in all coconut-growing regions of the world. The disease though sporadic in nature causes severe losses. The earliest visible symptoms are the paling of leaves in the inner whorl followed by collapse of the spear leaf. Bud rot causes a total loss of the palm, since the apical portions are destroyed and will not regenerate further. The principal causal agent in India, Philippines, Indonesia and Malaysia is *P. palmivora*; In Indonesia, *P. arecae* and *P. nicotianae* have also been found in association with these diseases (Thevenin 1994). *Phytophthora nicotianae* is rarely encountered, and it is usually associated with cocoa and infested soil (Waroka and Thevenin 1992).

The economic impact of the disease on a country's economy can be exemplified by what has happened in the Philippines in the recent past. The Philippines was the number one coconut producer in the world during 1976–1986, but the average productivity has declined in the past decade (1991–2000) with an average production of 669 kg/ha. Although *Phytophthora palmivora* was known to cause bud rot and fruit and immature nut fall in the Philippines, the disease losses were relatively low. This changed dramatically after the introduction of highly susceptible MAWA hybrids, which are a cross between Malayan yellow dwarf and West African tall, both of which are known to be susceptible to Phytophthora. The Philippines now lags behind India, which produces, on average, 732 kg/ha, and Indonesia with an average production of 1,041 kg/ha. This lower productivity can be attributed to a number of factors, but all of which are related to disease outbreaks. Bud rot and fruit rot were major causes of the large loss of coconut trees and the significant decrease in the production (Concibido-Manohar 2004).

19.2.6 Phytophthora Diseases of Rubber

The major rubber-grower countries are Indonesia, Thailand, Malaysia, China and India, each with more than a million hectares. There are several different types of symptoms caused by *Phytophthora* spp. on rubber trees: (1) abnormal leaf fall, (2) black stripe of the tapping panel, (3) stem or patch canker and (4) pod rot (Sdoodee 2004). Abnormal leaf fall was recorded from Kerala in India as early as 1910 (McRae 1918) and can reduce 30–50 % of the production (Pillai 1982). Black stripe disease was first noted in Sri Lanka and is widespread in Southeast Asia as well as Africa and America. Other Phytophthora diseases are also common throughout most rubber-growing areas. Black stripe and leaf fall cause serious damage, but economically important outbreaks are confined to areas with long periods of high rainfall. Although patch or stem canker is widespread, recent records of high economic impact are few. At least six species of *Phytophthora* have been reported to be associated with diseases of rubber including *P. botryosa*, *P. heveae*, *P. meadii*, *P. palmivora*, *P. capsici* and *P. nicotianae*. However, *P. palmivora* and *P. meadii* are isolated most frequently as the causal agents (Sdoodee 2004). The identity of the species varies with geographical regions; in India, Myanmar and Sri Lanka, it is predominantly *P. meadii* (Liyanage 1982; Kochuthresiamma et al. 1988; Johnston 1989; Chowdappa et al. 2003a), whereas in Malaysia, Thailand and Vietnam, *P. palmivora* and *P. botryosa* are implicated (Chee 1969; Tsao et al. 1975; Duong et al. 1998). In China, although the main species involved appears to be *P. citrophthora*, other species including *P. palmivora, P. meadii*, *P. nicotianae* and *P. capsici* were also found to infect rubber (Zeng and Ward 1998). There are also reports of *P. citrophthora* infecting rubber in Indonesia (Liyanage and Wheeler 1989a, b). In Brazil, *P. capsici* was reported to be the main species associated with black stripe and

stem canker, but *P. palmivora* and *P. citrophthora* were also isolated from diseased rubber (Dos Santos et al. 1995).

19.3 What Needs to Be Done?

Quality enhancement in spice crops/horticultural crops must necessarily include incorporation of improved control strategies along with those of quality control and agronomical practices. There has been an evolution in the way control strategies were thought of – from the days of chemical to biological to IPM strategies to that of decision support systems (DSS) and databases for specific crops and/or pathogens. Recently, such databases are being increasingly advocated and recommended by extension workers worldwide for timely diagnostic and mitigatory advice to achieve higher productivity (http://iapps2010.wordpress.com/2013/11/07/plant-protection-clinics-in-asia-3/).

For the latter to work, the first prerequisite is an accurate identification and sensitive detection of the pathogen. This is critical for regulatory action and disease management; especially faced with agricultural security concerns, the importance of diagnostic capacity cannot be overemphasised. Traditional culture-based detection and diagnostic methods for *Phytophthora* are inadequate as classical taxonomy of the genus is still based on often inconsistent morphological markers (Duncan and Cooke 2002). Combined with this is the fact that there is display of considerable morphological plasticity within some taxa limits (Brasier and Griffin 1979; Erwin and Riberio 1996; Appiah et al. 2003), and also the need for specialised expertise and time makes species identification based on morphological criteria difficult (Brasier et al. 1981; Erwin and Riberio 1996). This often leads to misidentification (Hall 1998), which, in turn, is detrimental to both practical control and clear scientific communication. Moreover, various reports on molecular identification of the *Phytophthora* pathogen have proved that in the past, new species have been wrongly assigned to current taxa and conversely, morphological variants of the existing taxa incorrectly assigned as new disease threats when the identifications were solely based on morphological criteria (Chowdappa et al. 2003a, b; Mirabolfathy et al. 2001; Guha Roy et al. 2006). Also, several species 'complexes' can be observed in phylogenetic trees showing the presence of potential cryptic species. Presently, powerful molecular techniques combined with morphological characterisation and a renewed interest in probing of the environments have led to discovery of new species, novel variants within species and hybrids and provided a better resolution of species 'complexes' with differentiation of the species therein (Grünwald and Goss 2011).

In the last decade, traditional detection methods have been complemented by various molecular methods for *Phytophthora* (Martin and Tooley 2003, 2004; Schaad et al. 2003; Kong et al. 2003a, c), especially involving PCR amplification of pathogen-specific nucleic acid targets and serological detection of specific pathogen proteins (Benson 1991; Hardham and Cahill 1993). These available diagnostic techniques are effective but can detect only single target pathogen per assay. For parallel detection of multiple phylogenetically diverse organisms simultaneously, as is present in nature, microarray-based diagnostics have been developed (Fessehaie et al. 2003; Bodrossy and Sessitsch 2004; Lievens et al. 2005a, b, 2006). A specific microassay-based diagnostic method using padlock probes (PLP) (Szemes et al. 2005) detects the presence of *Phytophthora* from leaves, roots, soil and stream water and even from air in the multi-institutional Global Phytophthora Network (GPN) project.

While assessment of the diversity, distribution and dynamics of *Phytophthora* in nature requires the deployment of accurate diagnostic methods, implementation of effective control strategies also requires more knowledge about the genetic structure of population of plant pathogens (Wolfe and Caten 1987), as control strategies must target a population instead of an individual if they are to be effective. Defining the genetic structure of a population is a logical first step in studies of fungal population genetics because the genetic structure of a population reflects its evolutionary history and its potential to evolve: aspects important for formulating disease management strategies. 'Genetic structure' refers to the amount and

distribution of genetic variation within and among populations (McDonald 1997).

In fungi that undergo both asexual and sexual reproduction, it is necessary to differentiate between diversity at individual locus, 'gene diversity', and diversity based on the number of genetically distinct individuals in a population, 'genotype diversity'. Taken together, gene and genotype diversity constitute genetic diversity (McDonald 1997). It is, however, important to distinguish between studies of population diversity and population genetics; the former yield the raw data, to which the latter can be applied to answer questions on the fundamental mechanisms and process of genetic change in populations (Cooke and Lees 2004).

Detection of diversity is usually done through the use of phenotypic and genotypic markers that are selectively neutral, highly informative, reproducible and relatively easy and inexpensive to assay. It is clear, however, that no single marker system would be adequate for all aspects of research on the diversity of *Phytophthora* species (Milbourne et al. 1997). The choice of genetic marker can have a substantial impact on the analysis and interpretation of data. As *Phytophthora* reproduce mainly asexually, producing a population structure that is largely composed of clonal lineages, a neutral marker such as a DNA fingerprint, may be used to address both questions relating to roles played by population size, mating systems and gene flow and also for questions relating to effects of selections, for which usually selective markers are used, assuming there is complete correspondence between genotype (DNA fingerprint) and phenotype (e.g. pathotype) (McDonald 1997). However, such assumption may not be valid as variable pathotypes can arise within the same clonal lineages (Drenth et al. 1996; Goodwin et al. 1995; Abu-El Samen et al. 2003).

Though it is best to use a widest practical array of genetic markers, combining a mixture of selected and neutral unlinked markers encompassing the nuclear (and mitochondrial) genome(s) distributed across many chromosomes, the number of marker loci assayed varies with the objective and resources available to the investigator. However, choicest markers are multilocus and have deeper resolving power like those of simple sequence repeats (SSRs) or single nucleotide polymorphisms (SNP). High throughput and massive parallel computing power have allowed multiplexing of these primers in recent times allowing assessment of field level diversity possible in shorter periods of time. Very recently, next-generation sequencing (NGS) has opened up the possibilities of looking at transcriptional polymorphisms of the pathogen population in the field allowing us to detect whether the isolates are under selection pressure and rapidly evolving and also the variability of the pathogen transcribed effectors that are the key in inducing the disease. These information would allow us to make informed choices by predicting about whether a particular fungicide or new host lines/varieties would be effective against the pathogen population.

In the coming decade, these next-generation technologies of sequencing, proteomics and metabolomics will have increased throughput and decreased costs. The upcoming fourth-generation technologies like single molecule real-time sequencing technology (SMRT) which is already available commercially are supposed to bring down the costs to about approx. Rs. 1.50 (3 cents) per Mb, and sequencing of a whole field population of *Phytophthora* spp. will come down to about Rs. 30, 000/- ($500)! Community and population cellular components can then be measured dynamically over space and time.

However, in the Indian scenario while that will be sometime in coming, we can as of now create databases from pathogen population data collected from neutral markers (like SSRs) and associate them with field data like germination temperature, mating type, fungicide sensitivity, morphological phenotypes and others like effector diversity and geographical location. Each cluster formed as a result of use of genetic markers can then be completely characterised. Once such a database is formed, it can be useful as a diagnostic aid to predict the characteristic of the pathogen population and prescribe control measures against that pathogen population. Since Phytophthora populations vary geographically

and devastation times are typically 48–72 h, there is very little time to run series of traditional tests and then prescribe measures. In a typical scenario, once an infected sample is brought to the diagnostic centre/plant health clinic, a single quick molecular marker assay (in a few hours time) would assign the pathogen to a previously characterised pathogen population cluster. Once the match is done, it would become very easy to accurately prescribe control measures. The same information will be very helpful to create DSS specific for crops and their pathosystems.

19.4 Conclusion

The twenty-first century has already seen a major paradigm shift in our understanding of the biology, evolution and genetics of the genus *Phytophthora* as well as the tools and approaches used to develop novel approaches for disease management. The combination of novel tools and approaches provided by the convergence of genome sequencing, computing power and novel genomic/biotechnological tools paints a promising picture of the future of Phytophthora disease management. At the same time, *Phytophthora* pathogens continue to emerge at an accelerated rate due to increased global travel and trade (Guha Roy and Grünwald 2014). Also, selection pressures of random fungicide usage, changing climatic conditions and misdirected (due to little or no knowledge about pathogen populations) control measures have increased coevolutionary rates as evidenced from transcriptional profiling of effectors. The only way we can tackle this menace is if we also 'coevolve' in our approach and adopt novel tools and approaches facilitated by newer technologies to combat it.

References

Abad JG, Abad JA (2003) Advances in the integration of morphological and molecular characterization in the genus *Phytophthora*: the case of *P. niederhauseria* sp. nov. Phytopathology 93:S1

Abu-El Samen FM, Secor GA, Gudmestad NC (2003) Variability in virulence among asexual progenies of *Phytophthora infestans*. Phytopathology 93:293–304

Agrios GN (2005) Plant pathology, 5th edn. Academic, San Diego

Alexopoulos CJ, Mims CW, Blackwell M (1996) Introductory mycology, 4th edn. Wiley, New York, USA

Andrés JL, Rivera A, Fernández J (2003) *Phytophthora nicotianae* pathogenic to pepper in northwest Spain. J Plant Pathol 85(2):91–98

Appiah AA, Flood J, Bridge PD, Archer SA (2003) Inter and intraspecific morphometric variation and characterization of *Phytophthora* isolates from cocoa. Plant Pathol 52:168–180

Appiah AA, Flood J, Archer SA, Bridge PD (2004) Molecular analysis of the major *Phytophthora* species on cocoa. Plant Pathol 53:209–219

Aragaki M, Uchida JY (2001) Morphological distinctions between *P. capsici* and *P. tropicalis* sp. nov. Mycologia 93:137–145

Baldauf SL, Roger AJ, Wenk-Siefert L, Doolittle WF (2000) A kingdom-level phylogeny of eukaryotes based on combined protein data. Science 290:972–977

Barber CA (1902) Annual report for 1901–1902. Department of Agriculture, Madras

Bartnicky-Garcia S, Wang MC (1983) Biochemical aspects of morphogenesis in *Phytophthora*. In: Erwin DC, Bartnicki-Garcia S, Tsao P (eds) *Phytophthora*: its biology, taxonomy, ecology and pathology. American Phytopathological Society Press, St. Paul, pp 121–138

Beakes GW (1998) Evolutionary relationship among protozoa. In: Coombs GH, Vickerman K, Sleigh MA, Warren A (eds) The systematics association special volume series 56. Kluwer Academic Publishers, Dordrecht

Belbahri L, Moralejo E, Calmin G, Oszako T, Garcı'a JA, Descals E, Lefort F (2006) *Phytophthora polonica*, a new species isolated from declining *Alnus glutinosa* stands in Poland. FEMS Microbiol Lett 261:165–174

Benson DM (1991) Detection of *Phytophthora cinnamomi* in azalea with commercial serological assay kits. Plant Dis 75:478

Biçici M, Çinar A (1990) A review of *Phytophthora* diseases of different Mediterranean crops in Turkey. EPPO Bull 20(1):101–105. doi:10.1111/j.1365-2338.1990.tb01185.x. Article first published online: 28 JUNE 2008

Blencowe JW, Wharton AL (1961) Black pod disease in Ghana, incidence of disease in relation to levels of productivity. In: Report of the 6th commonwealth mycology conference. Cocoa, Chocolate and Confectionery Alliance, London. pp 139–147

Bodrossy L, Sessitsch A (2004) Oligonucleotide microarrays in microbial diagnostics. Curr Opin Microbiol 7(3):246–255

Brasier CM, Griffin MJ (1979) Taxonomy of *Phytophthora palmivora* on cocoa. Trans Br Mycol Soc 72:111–143

Brasier CM, Griffin MJ, Maddision AC (1981) Cocoa black pod Phytophthoras. In: Gregory PH, Maddision

AC (eds) Epidemiology of Phytophthora on cocoa in Nigeria, Phytopathological paper no. 25. Commonwealth Mycological Institute, Kew, pp 18–30
Butler EJ (1906) The wilt of pigeon pea and pepper. Agric J India 1:25
Campêlo AMFL, Luz EDMN, de Resnick FCZ (1982) Podridão-parda do cacaueiro, nos Estados da Bahia, Brasil.1 – virulencia das especies de Phytophthora. Revisita Theobroma, CEPEC, Itabuna-Brasil, Ano 12, pp 1–6
Cavalier-Smith T (1987) The origin of fungi and pseudofungi. In: Rayner ADM, Brasier CM, Moore D (eds) Evolutionary biology of the fungi. Cambridge University Press, Cambridge, pp 339–353
Chee KH (1969) Hosts of *Phytophthora palmivora*. Rev Appl Mycol 48:337–344
Chee KH, Wastie RL (1970) Black pod disease of cacao. Planter, Kuala Lumpur 46:294–297
Chowdappa P, Brayford D, Smith J, Flood J (2003a) Identity of *Phytophthora* associated with areacanut and its relationship with rubber and cardamom isolates based on RFLP of PCR-amplified ITS region of rDNA and AFLP fingerprints. Curr Sci 85:585–587
Chowdappa P, Brayford D, Smith J, Flood J (2003b) Molecular discrimination of *Phytophthora* isolates on cocoa and their relationship with coconut, black pepper and bell pepper isolates based on rDNA repeat and AFLP fingerprints. Curr Sci 84:1235–1238
Concibido-Manohar E (2004) Phytophthora diseases of coconut in the Philippines. In: Drenth A, Guest DI (eds) Diversity and management of Phytophthora in Southeast Asia, Monograph no. 114. ACIAR, Canberra, pp 7–9, p 238
Cooke DEL, Lees AK (2004) Markers, old and new, for examining *Phytophthora infestans* diversity. Plant Pathol 53:699–704
Cooke DEL, Drenth A, Duncan JM, Wagels G, Brasier CM (2000) A molecular phylogeny of *Phytophthora* and related oomycetes. Fungal Genet Biol 30:17–32. doi:10.1006/fgbi.2000.1202
Coulter DB, Aronson JM (1977) Glycogen and other soluble glucans from chytridiomycete and oomycete species. Arch Microbiol 15(3):317–322
Dakwa JT (1984) Nation-wide black pod survey. Joint CRIG/Cocoa production division project. In: Annual report of the Cocoa Research Institute, Ghana, 1976/77–1978/79. Tafo (Akim Abuakwa). Cocoa Research Institute, Ghana
Dakwa JT (1988) Changes in the periods for attaining the cocoa black pod disease infection peaks in Ghana. In: Proceedings of the 10th international Cocoa Research Conference, Santo Domingo, Dominican Republic. Cocoa Producers' Alliance, Lagos, pp 427–436
Darinea T, Allaguia MB, Rouaissia M, Boudabbous A (2007) Pathogenicity and RAPD analysis of *Phytophthora nicotianae* pathogenic to pepper in Tunisia. Physiol Mol Plant Pathol 70:142–148
de Liyanage AS (1982) Annual review of the Plant Pathology Department 1980. Rubber Research Institute, Sri Lanka
de Waard PWF (1979) Evaluation of the results of research on eradication of *Phytophthora* foot rot of black pepper (*Piper nigrum*. L) circulated during the first meeting of the pepper community permanent panel on techno-economic studies, 31st Jan–4th Feb 1979, Cochin, pp 1–47
Desjardins PR, Zentmeyer GA, Reynolds DA (1969) Electron microscopic observations of flagellar hairs of *Phytophthora palmivora* zoospores. Can J Bot 47:1077–1079
Djiekpor EK, Goka K, Lucas P, Partiot M (1981) Brown rot of cocoa pod due to *Phytophthora* species in Togo, evaluation and control strategy. Café Cacao Thé 25:263–268
Dos Santos AF, Matsuoka K, Alfenas AC, Maffia LA (1995) Identification of *Phytophthora* species that infect *Hevea* sp. Fitopatol Bras 20:151–159
Drenth A, Guest DI (2004) Introduction. In: Drenth A, Guest DI (eds) Diversity and management of Phytophthora in Southeast Asia. ACIAR, Canberra, pp 7–9. Monograph No. 114, P 238
Drenth A, Sendall B (2004) Economic impact of Phytophthora diseases in Southeast Asia. In: Drenth A, Guest DI (eds) Diversity and management of Phytophthora in Southeast Asia. Australian Centre for International Agricultural Research, Canberra, pp 227–231
Drenth A, Whission SC, Maclean DJ, Irwin JAG, Obstr NR, Ryley MJ (1996) The evolution of races of *Phytophthora sojae* in Australia. Phytopathology 86:163–169
Duncan JM, Cooke DEL (2002) Identifying, diagnosing and detecting *Phytophthora* by molecular methods. Mycologist 16:59–66
Duong N, Thanh HV, Doan T, Yen N, Tam TTM, Dung-Phan T, Phuong LTT, Duong NH, Thanh HN, Yen NT, Dung PT (1998) Diseases and pests of *Hevea brasiliensis* in Vietnam. In: Symposium on natural rubber (*Hevea brasilliensis*), vol 2, Ho Chi Minh City, Vietnam, pp 80–91
Elliot CG (1983) Physiology of sexual reproduction in Phytophthora. In: Erwin DC, Bartnicki-Garcia S, Tsao P (eds) Phytophthora: its biology, taxonomy, ecology and pathology. American Phytopathological Society Press, St. Paul
Erwin DC, Riberio OK (1996) Phytophthora diseases world wide. The American Phytopathological Society, St. Paul
FAO (2002) Statistical databases. http://apps.fao.org
Farr DF, Bills GF, Chamuris GP, Rossman AY (1989) Fungi on plants and plant products in the United States. APS Press, St. Paul
Fessehaie A, De Boer SH, Lévesque CA (2003) An oligonucleotide array for the identification and differentiation of bacteria pathogenic on potato. Phytopathology 93:262–269
Fichtner EJ, Hesterberg DL, Smyth TJ, Shew HD (2006) Differential sensitivity of *Phytophthora parasitica* var. *nicotianae* and *Thielaviopsis basicola* to monomeric aluminum species. Phytopathology 96(6):212–220

Förster H, Coffey M, Elwood H, Sogin ML (1990) Sequence analysis of the small subunit ribosomal RNAs of three zoosporic fungi and implications for fungal evolution. Mycologia 82:306–312

Gallegly ME, Hong CX (2008) *Phytophthora*: identifying species by morphology and DNA fingerprints. APS Press, St Paul, 158p

Goodwin SB, Sujkowski LS, Fry WE (1995) Rapid evolution of pathogenicity within clonal lineages of the potato late blight disease fungus. Phytopathology 85:669–676

Griffith JM, Davis AJ, Grant BR (1992) Target sites of fungicides to control oomycetes. In: Köler W (ed) Target sites of fungicide action. CRC Press, Boca Raton, pp 69–100

Grünwald NJ, Goss EM (2011) Evolutionary and population genetics of exotic and re-emerging pathogens: traditional and novel tools and approaches. Annu Rev Plant Physiol Plant Mol Biol 49:249–267

Guha Roy S, Bhattacharyya S, Mukherjee SK, Mondal N, Khatua DC (2006) *Phytophthora melonis* associated with fruit and vine rot disease of pointed gourd in India as revealed by RFLP and sequencing of ITS region. J Phytopathol 154(10):612–615

Guha Roy S (2008) Progress in *Phytophthora* research: identification, species diversity and population diversity. J Mycopathol Res 46:163–184

Guha Roy S, Grünwald NJ (2014) The plant destroyer genus Phytophthora in the 21st century. Rev Plant Pathol 6:387–412.

Gunderson JH, Elwood HJ, Ingold A, Kindle K, Sogin ML (1987) Phylogenetic relationships between chlorophytes, chrysophytes and oomycetes. Proc Natl Acad Sci U S A 84:5823–5827

Hall GS (1998) Examination of some morphologically unusual cultures of *Phytophthora* species using a mitochondrial DNA miniprep technique and a standardized sporangium caducity assessment. Mycopathologia 140:141–147

Hardham AR, Cahill DM (1993) Detection of motile organisms in a sample. Australian patent no. 48117/93(1 May 1997). US patent no. 5817472 (6 October 1998) European patent under examination. RSBS, Australia's National University

Hawksworth DL (1991) The fungal dimension of biodiversity: magnitude, significance, and conservation. Mycol Res 95:641–655

Hawksworth DL (2001) The magnitude of fungal diversity: the 1.5 million species estimate revisited. Mycol Res 105:1422–1432

Hawksworth DL, Rossman AY (1997) Where are all the undescribed fungi? Phytopathology 87:888–891

Hendrix JW (1970) Sterols in growth and reproduction of fungi. Annu Rev Plant Physiol Plant Mol Biol 8:111–113

Johnston A (1989) Diseases and pests. In: Webster CC, Baulkwil WJI (eds) Rubber. Longman Scientific and Technical, New York, pp 415–458

Kamoun S, Huitema E, Vleeshouwers V (1999) Resistance to oomycetes: a general role for the hypersensitive response? Trends Plant Sci 4:196–200

Kochuthresiamma J, Kothandaraman R, Jacob M (1988) Actinomycetes population of rubber growing soil and its antagonistic activity against *Phytophthora meadii* (McRal). Indian J Nat Rubber Res 1:27–30

Köler W (1992) Antifungal agents with target sites in sterol functions and biosynthesis. In: Köler W (ed) Target sites of fungicide action. CRC Press, Boca Raton, pp 119–206

Kong P, Hong CX, Richardson PA (2003a) Rapid detection of *Phytophthora cinnamomi* using PCR and primers derived from the Lpv storage protein genes. Plant Pathol 52:681–693

Kong P, Hong CX, Richardson PA, Gallegly ME (2003b) Single-strand-conformation polymorphism of ribosomal DNA for rapid species differentiation in genus *Phytophthora*. Fungal Genet Biol 39:238–249

Lamour K, Kamoun S (2009) Oomycete genetics and genomics: diversity, interactions and research tools. Wiley-Blackwell, Hoboken, p 582

Lawrence JS, Luz EDMN, Resnik FCZ (1982) The relative virulence of *Phytophthora palmivora* and *P. capsici* on cacao in Bahia, Brazil. In: Proceedings of the 8th international Cocoa Research Conference, 1981, Cartegena, Colombia. Cocoa Producers' Alliance, Lagos, pp 395–400

Lee BS, Lum KY (2004) *Phytophthora* diseases in Malaysia. In: Drenth A, Guest DI (eds) Diversity and management of Phytophthora in Southeast Asia. Australian Centre for International Agricultural Research, Canberra, pp 227–231

Leipe DD, Wainright PO, Gunderson JH, Porter D, Patterson DJ, Valois F, Himmerich S, Sogin ML (1994) The stramenopiles from a molecular perspective: 16S-like rRNA sequences from *Labyrinthuloides minuta* and *Cafeteria roenbergensis*. Phycologia 33:369–377

Lievens B, Brouwer M, Vanachter A, Levesque CA, Cammue BPA, Thomma B (2005a) Quantitative assessment of phytopathogenic fungi in various substrates using a DNA macroarray. Environ Microbiol 7:1698–1710

Lievens B, Grauwet TJMA, Cammue BPA, Thomma BPHJ (2005b) Recent developments in diagnostics of plant pathogens. In: Recent research developments in microbiology, S.G.S.G. Pandalai, Kerala, India, pp 57–79

Lievens B, Claes L, Vanachter ACRC, Cammue BPA, Thomma BPHJ (2006) Detecting single nucleotide polymorphisms using DNA arrays for plant pathogen diagnosis. FEMS Microbiol Lett 255(1): 129–139

Liyanage A de S (1982) Annual review of the plant pathology department 1980. Rubber Research Institute, Sri Lanka

Liyanage NIS, Wheeler BEJ (1989a) *Phytophthora katsurae* from cocoa. Plant Pathol 38:627–629

Liyanage NIS, Wheeler BEJ (1989b) Comparative morphology of *Phytophthora* species on rubber. Plant Pathol 38:592–597

Lozano TZE, Romero CS (1984) Estudio taxanomico de aislamientos de *Phytophthora* patogenos de cacao. Agrociencia 56:176–182

Martin FN, Tooley PW (2003) Phylogenetic relationships among *Phytophthora* species inferred from sequence analysis of mitochondrially encoded cytochrome oxidase I and II genes. Mycologia 95:269–284. doi:10.2307/3762038

Martin FN, Tooley FW (2004) Identification of *Phytophthora* isolates to a species level using restriction fragment length polymorphism analysis of a polymerase chain reaction-amplified region of mitochondrial DNA. Phytopathology 94:983–991

McDonald BA (1997) The population genetics of fungi: tools and techniques. Phytopathology 87:448–453

McRae H (1918) *Phytophthora meadii* n. sp. on *Hevea brasiliensis*. Mem Dep Agric India Bot Ser 9:219–273

Milbourne D, Meyer R, Bradshaw JE, Baird E, Bonar N, Provan J, Powell W, Waugh R (1997) Comparison of PCR based marker systems for the analysis of genetic relationships in cultivated potato. Mol Breed 3:127–136

Mirabolfathy M, Cooke DEL, Duncan JM, Williams NA, Ershad D, Alizadeh A (2001) *Phytophthora pistacae* sp.nov and *melonis*. The principal cause of pistachio gummosis in Iran. Mycol Res 105:1166–1175

Muller HRA (1936) The Phytophthora foot rot of black pepper (*Piper nigrum* L.) in the Netherlandish Indies. Cited in: Review of Applied Mycology 1937, 16:559

McMahon P, Purwantara A (2004) Phytophthora on cocoa. In: Drenth A, Guest DI (eds) Diversity and management of Phytophthora in Southeast Asia, ACIAR monograph 114 (printed version published in 2004), Canberra, Australia, pp 104–114

Newhook FJ, Waterhouse FM, Stamps DJ (1978) Tabular key to the species of *Phytophthora* de Bary, Mycological paper no. 3. Commonwealth Mycological Institute, Kew, England, p 20

Pfyffer GE, Boraschi-Gaia C, Weber B, Hoesch L, Orpin CG, Rast DM (1990) A further report on the occurrence of acyclic sugar alcohols in fungi. Mycol Res 94:219–222

Pillai PNR (1982) Abnormal leaf fall of rubber caused by Phytophthora spp. In: Nambiar KKN (ed) Proceedings of the workshop on *Phytophthora* diseases of tropical cultivated plants. Central Plantation Crop Research Institute, Kasargod, p 284

PMB (Pepper Marketing Board) (2001) Sarawak black pepper. Official website of the Department of Agriculture, Sarawak. On the Internet: http://www.doa.sarawak.gov.my/modules/web/page.php?id=138. Accessed 24 Mar 2014

Pruthi JS (1993) Major spices of India crop management post-harvest technology. ICAR, New Delhi, p 514

Purseglove JW, Brown EG, Green CL, Robbins SRJ (1981) Pepper. In: Spices, vol 1. Longman Scientific and Technical, London

Purwantara A, Manohara D, Warroka JS (2004) *Phytophthora* diseases in Indonesia. In: Drenth A, Guest DI (eds) Diversity and management of Phytophthora in Southeast Asia. Australian Centre for International Agricultural Research, Canberra, pp 227–231

Rast DM, Pfyffer GE (1989) Acyclic polyols and higher taxa of fungi. Bot J Linn Soc 99:39–57

Ristaino JB (2011) Key for identification of common *Phytophthora* species. APS Press, St. Paul

Rodríguez-Molina MC, Morales-Rodríguez MC, Palo Osorio C, Palo Núñez E, Verdejo Alonso E, Duarte Maya MS, Picón-Toro J (2010) *Phytophthora nicotianae*, the causal agent of root and crown rot (*Tristeza* disease) of red pepper in La Vera region (Cáceres, Spain). Span J Agric Res 8(3):770–744

Saadoun M, Allagui MB (2008) Pathogenic variability of *Phytophthora nicotianae* on pepper in Tunisia. J Plant Pathol 90:351–355

Sangchote S, Poonpolgul S, Sdoodee R, Kanjanamaneesathain M, Baothong T, Lumyong P (2004) Phytophthora diseases in Thailand. In: Drenth A, Guest DI (eds) Diversity and management of Phytophthora in Southeast Asia. Australian Centre for International Agricultural Research, Canberra, pp 227–231

Schaad NW, Frederick RD, Shaw J, Schneider WL, Hickson R, Petrillo MD, Luster DG (2003) Advances in molecular-based diagnostics in meeting crop biosecurity and phytosanitary issues. Annu Rev Plant Physiol Plant Mol Biol 41:305–324

Sdoodee R (2004) Phytophthora diseases of rubber. In: Drenth A, Guest DI (eds) Diversity and management of Phytophthora in Southeast Asia, ACIAR monograph 114 (printed version published in 2004), Canberra, Australia, pp 136–142

Stamps DJ, Waterhouse GM, Newhook FJ, Hall GS (1990) Revised tabular key to the species of Phytophthora, Mycological papers 162. CAB International Mycological Institute, Kew

Strange RN, Scott PR (2005) Plant disease: a threat to global food security. Annu Rev Plant Physiol Plant Mol Biol 43:83–116

Szemes M, Bonants P, de Weerdt M, Baner J, Landegren U, Schoen CD (2005) Diagnostic application of padlock probes—multiplex detection of plant pathogens using universal microarrays. Nucleic Acids Res 33(8):e70

Thevenin JM (1994) Coconut diseases in Indonesia – etiological aspects. Paper presented at the Coconut Phytophthora Workshop, Manado, Indonesia. Cited in: Waller and Holderness (1997)

Truong NV, Burgess LW, Liew ECY (2008) Prevalence and aetiology of *Phytophthora* foot rot of black pepper in Vietnam. Australas Plant Pathol 37:431–442

Truong NV, Liew ECY, Burgess LW (2010) Characterisation of *Phytophthora capsici* isolates from black pepper in Vietnam. Fungal Biol 114:160–170

Truong NV, Burgess LW, Liew ECY (2012) Cross-infectivity and genetic variation of *Phytophthora capsici* isolates from chilli and black pepper in Vietnam. Australasian Plant Pathol 41(4):439–447

Tsao PH, Chew-Chin N, Syamananda R (1975) Occurrence of *Phytophthora palmivora* on *Hevea* rubber in Thailand. Plant Dis Rep 59(12):955–958

Waller JM, Holderness M (1997) Beverage crops and palms. In: Hillocks RJ, Waller JM (eds) Soilborne diseases of tropical crops. CAB International, Wallingford

Wang MC, Bartnicky-Garcia S (1973) Novel phosphoglucans from the cytoplasm of *Phytophthora palmivora* and their selective occurrence in certain life cycle stages. J Biol Chem 248:4112–4118

Wang MC, Bartnicky-Garcia S (1974) Mycolaminarins: storage (1-3)-β-D-glucans from the cytoplasm of the fungus *Phytophthora palmivora*. Carbohydr Res 37:331–338

Warner SA, Domas AJ (1987) Biochemical characterization of zoosporic fungi: the utility of sterol metabolism as an indicator of taxonomic affinity. In: Fuller MS, Jaworski A (eds) Zoosporic fungi in teaching and research. Southeastern Publishing Corporation, Athens, pp 202–208

Waroka JS, Thevenin JM (1992) *Phytophthora* in Indonesian coconut plantations: populations involved. Paper presented at the Coconut *Phytophthora* Workshop, Manado, Indonesia

Waterhouse GM (1963) Key to the species of *Phytophthora* de Bary, Mycological paper no. 92. CMI, Kew, pp 1–22

Wete JD (1989) Structure and function of sterols in Fungi. Adv Lipid Res 23:115–167

Wolfe MS, Caten CE (1987) Populations of plant pathogens: their dynamics and genetics. Blackwell Scientific Publications, Oxford

Zeng FC, Ward E (1998) Variation within and between *Phytophthora* species from rubber and citrus trees in China, determined by polymerase chain reaction using RAPDs. J Phytopathol 146(2–3):103–109

Zentmyer GA (1988) Taxonomic relationships and distribution of *Phytophthora* causing black pod of cocoa. In: Proceedings of the 10th international Cocoa Research Conference, 1987, Santo Domingo, Dominican Republic. Cocoa Producers' Alliance, Lagos, pp 391–405