


Review

# Possible Reasons Affecting Different *Phytophthora infestans* Populations in Tomato and Potato Isolates in Thailand

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**Abstract:** Late blight, caused by the oomycete *Phytophthora infestans*, is one of the most important diseases affecting tomato and potato production worldwide. In Thailand, the disease is widespread in the north and northeast, especially in the Chiang-Mai and Tak provinces. The mating type, metalaxyl sensitivity, mitochondrial DNA (mtDNA) haplotype, RG57 fingerprinting, and microsatellite were used to characterize the *P. infestans* populations. The study revealed that the *P. infestans* of tomato isolates in Thailand are of the same lineage as those from 1994 until 2002. The clonal lineages that were found in the potato populations have changed since 1994. The changes in *P. infestans* isolates in the potato populations have likely been the result of the import of seed potatoes to Thailand. Furthermore, the *P. infestans* populations in potatoes show resistance to metalaxyl, whereas those from tomato isolates show sensitivity to fungicides. The reasons for the different responses can be attributed to (i) the use of metalaxyl, (ii) the host preferences of *P. infestans*, and (iii) the migration of new genotypes from infected potato seeds.

**Keywords:** food security; late blight; metalaxyl; population structure; *Solanum lycopersicum*; *Solanum tuberosum*



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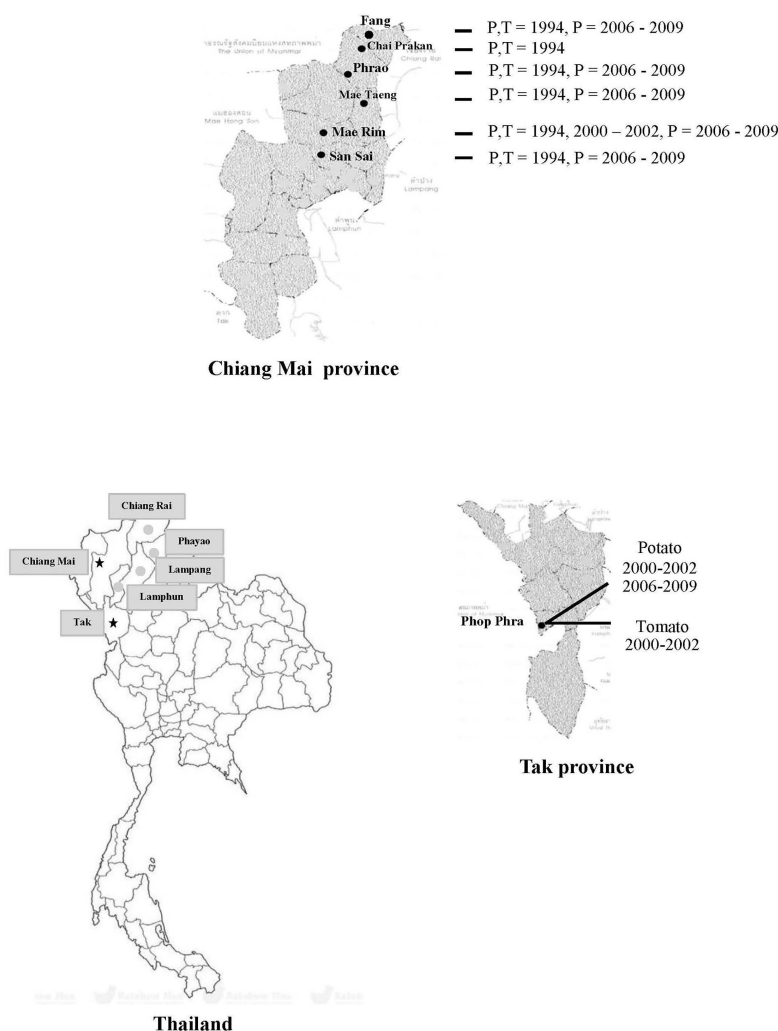
## 1. Background of Late Blight Disease in Thailand

Late blight is a disease that occurs in cultivated tomatoes (*Solanum lycopersicum*) and its close relative, the potato (*Solanum tuberosum*). This disease is caused by the oomycete *Phytophthora infestans* that was responsible for the Irish potato famine of the 1840s [1,2]. In Thailand, tomatoes and potatoes are usually grown in the north and northeast. The cultivation areas for these two crops have generally increased each year because of the increasing demand for fresh and processed food. In 2020, tomato and potato cultivation covered more than 6000 hectares in the north and northeast of Thailand [3]. Specifically, Chiang Mai and Tak provinces are the main areas where both tomatoes and potatoes are being grown. During the period between December and February, which is referred to as the winter season in Thailand, the conditions in the north and northeast of Thailand are high humidity (>90%) and low temperatures (on average 21 °C). Thus, these areas are suitable for the development of the late blight disease. As such, these crops face the risk of infection by this pathogen, which can cause serious damage and subsequently severe economic losses.

Late blight disease is widespread in the north of Thailand, especially in Chiang Mai and Tak provinces. The disease was first reported in 1981 in Chiang Dao district, Chiang Mai province, in both tomatoes and potatoes [4]. After that, the disease became established in both crops, being predominant around Chiang Mai. Tak province has also experienced epidemics of late blight disease, with local reports of *P. infestans* infection.

## 2. Population of *P. infestans* in Tomatoes Isolated in Chiang Mai and Tak Provinces

The first populations of *P. infestans* isolates were characterized in tomatoes in 1994 based on their phenotypes, mating type, metalaxyl sensitivity, and two allozyme genotypes, glucose-6-phosphate-isomerase (*Gpi* 86/100) and peptidase (*Pep* 92/100) [5]. Eighteen samples of late blight tomato isolates were collected from the regions of Mae-Rim, Mae-Tang, San Sai, Praow, Chai Prakran, and Fang, which are located in Chiang Mai (Figure 1). The results demonstrated that all tomato isolates were sensitive to metalaxyl and the A1 mating type. The dilocus allozyme genotype was found for 86/100 of the *Gpi* and 92/100 of *Pep*. Gotoh et al. [6] used the same *P. infestans* population as Nishimura et al. [5] to perform RFLP with an RG57 probe and mitochondrial DNA haplotype analysis. Late blight tomato isolates were found to be of the US-1 and US-1.3 clonal lineages according to the RFLP genotypes and of the Ib mtDNA haplotype according to the mitochondrial genotype (Table 1). Based on the above results, we concluded that the population of *P. infestans* that affects the tomato crops in Thailand is a population of the US-1 clonal lineage, which is distributed in Asia and Europe, as well as North, Central, and South America [7–10].



**Figure 1.** Map of Thailand (<https://www.pinterest.com/pin/580823683215658950/> accessed on 28 October 2023), Chiang Mai and Tak (<https://panteethai.com> accessed on 5 February 2019) show regions of tomato and potato cultivations and the locations in Chiang Mai and Tak provinces of Thailand, where *Phytophthora infestans* isolates were collected during 1994–2009: ★ regions of tomato and potato production where late blight disease has been studied; ● regions of tomato and potato production where late blight disease has not been studied.

**Table 1.** Details of *P. infestans*, including mating type, metalaxyl sensitivity, mitochondrial haplotype, and RG57 fingerprinting in Thailand.

Plant	Province *	District **	Sampling Year	Mating Type	MtDNA ***	Metalaxyl **** Sensitivity	RG57	Reference
Tomato	CM	MR, MT, SS, P, CK, F	1994	A1	Ib	S	US-1, US-1.3	[5]
Tomato	CM	MR, MT, SS, P	2000–2002	A1	Ib	S, I	US-1, US-1.3 US-1.4, TH-2	[11]
Tomato	TAK	Phop Phra	2000–2002	A1	IIa	S	US-1, US-1.3	[11]
Potato	CM	MR, MT, SS, P, CK, F	1994	A1	Ib	S	US-1, US-1.3	[6]
Potato	CM	MR, MT, SS, P	2000–2002	A2	Ia	S	TH-1	
Potato	TAK	Phop Phra	2000–2002	A1	IIa	S, I, R	RF006, RF008	[11]
Potato	TAK	Phop Phra	2000–2002	A1	IIa	R	US-1, RF006, RF008, TH-3	[11]
Potato	CM	SS, P	2006–2009	A1	IIa	S, I, R	-	[12]
Potato	TAK	Phop Phra	2009	A1	IIa	R	-	[12]
Potato	CM	MR, MT, SS, P, F	2006–2009	A1	IIa	S, I	-	[13]
Potato	TAK	Phop Phra	2007–2009	A1	IIa	S, I	-	[13]

\* CM = Chiang Mai. \*\* C = Chaiprakran, F = Fang, MR = Mae-rim, MT = Mae-Tang, P = Praow, SS = San sai. \*\*\* mtDNA: mitochondrial haplotype. \*\*\*\* S, I, and R denote sensitive, intermediate, and resistant to metalaxyl, respectively.

Six years later, in 2000, the populations of *P. infestans* in tomatoes were characterized by Petchaboon et al. [11]. Late blight isolates were collected in Mae-rim during 2000–2002 from the same areas as the Nishimura collection in 1994. The study revealed that the populations of tomatoes were of the US-1, US-1.3, US-1.4, and TH-2 genotypes. All genotypes were the A1 mating type, showing sensitivity to moderate resistance to metalaxyl and Ib mtDNA. Thus, the analyses revealed that the *P. infestans* of the tomato populations in Thailand were from the same lineage that had caused epidemics from 1994 until 2002. Additional data from the RG57 fingerprint demonstrated that the US-1 genotype was predominant in the tomato populations in the Chiang Mai area during 1994–2002.

The first study of *P. infestans* disease in Tak province was conducted from 2000 until 2002 by Petchaboon et al. [11]. Twelve isolates of single-leaf infections were collected and characterized as the US-1 clonal lineage, A1 mating type, sensitive to metalaxyl, and the Ib mtDNA haplotype (Table 1). The study revealed that *P. infestans*, which was widespread in Tak province, was from the same population as that in Chiang-Mai province.

### 3. Populations of *P. infestans* in Potatoes Isolated in Chiang Mai and Tak Provinces

The population structure of late blight disease in Thailand for potatoes was first characterized by Gotoh et al. [6] using the collection of Nishimura et al. [5]. The results of the analysis of phenotypic and genotypic data by Gotoh et al. [6] demonstrated that the *P. infestans* in potatoes had equal proportions of both A1 and A2 mating types, Ia and Ib mitochondrial haplotypes, and US1 and TH1 genotypes. Petchaboon et al. [11] studied the population structure of *P. infestans* in potatoes from 2000 until 2002 at the same locations. During 2000–2002, only the A1 mating type and two common clonal lineages, RF006 and RF008, were found in both Tak and Chiang Mai provinces. These two genotypes were not reported for the collected isolates in 1994 by Gotoh et al. [6]. The latest studies of *P. infestans* in potatoes in Thailand were characterized during 2006–2009 by Jaimasit and Prakop [12] and by Sopee [13]. Jaimasit and Prakop [12] surveyed and collected isolates from 117 late blight samples from a potato field in San Sai and Praow, Chiang Mai province, including the Phob Phra district in Tak province. Sopee [13] isolated 132 *P. infestans* samples from the San Sai, Praow, and Fang districts in Chiang Mai, including Phob Phra district in Tak province. Both studies found that all potato isolates during 2006–2009 were of the A1 mating type, similar to the findings reported by Petchaboon et al. [11]. However, they did not report information on the RG57 fingerprint, so we do not have the genotype data for that period.

To conclude, for the period of 1994 to 2002, the data from the studies of *P. infestans* in potatoes in Thailand showed that the population of late blight has changed from the A1 and A2 to the A1 mating type. The genotype of the RG57 fingerprint showed that the US1 genotype in 1994 was replaced with the RF006 and RF008 genotypes in 2002. The

latest data from 2000 to 2009 also showed that only the A1 mating type was lacking RG57 fingerprint data.

#### 4. Change in *P. infestans* Population Structure in Thailand

Gotoh et al. [6] and Petchaboon et al. [11] found that the *P. infestans* populations in tomatoes in Thailand were of the same lineage as US-1. The *P. Infestans* that infected potatoes in 1994 were also of the US-1 lineage. Importantly, Petchaboon et al. [11] demonstrated that the change in the population structure of *P. infestans* originated from potato isolates. In a study ranging from 2000 to 2002, the researchers found two common genotypes, RF006 and RF008, in the potato isolates. Thus, from the study of late blight disease in Thailand, we can conclude that the *P. infestans* populations have changed in potato isolates but not in tomato isolates (Table 1).

Two hypotheses may explain the changes that have occurred in the *P. infestans* isolates in potatoes.

1. First, the variation could have occurred owing to recombination through sexual reproduction. *P. infestans* is a heterothallic oomycete composed of two mating types, assigned A1 and A2. The oomycete has a coenocytic diploid mycelium and can reproduce both sexually and asexually [14]. When two compatible strains of oomycete interact with two different mating types, for example, A1 and A2, sexual reproduction can occur. The result of this mating system was the formation of thick-walled, resistant oospores [15]. The appearance of self-fertile pathotypes permits the sexual reproduction of *P. infestans* worldwide [16,17]. The mating system is expected to increase the genotypic diversity within the *P. infestans* population due to the rearrangement of existing alleles or the generation of new alleles via genetic recombination. In recent years, in many parts of the world, evidence has shown that *P. infestans* still primarily reproduces asexually, and sexual reproduction is rare [18–21], with the exception of Northern Europe [22].
2. Second, another potential source of change in the population structure is through the migration of new genotypes. The global exacerbation of disease is caused by the migration of new strains [23]. The existing global population structure of *P. infestans* has been created via a series of migrations and displacements of clonal lineages [24–29]. The evidence revealed that the appearance of the original population of *P. infestans* was first dominated by the HERB-1 [30] and later by the US-1 lineage. The *P. infestans* that caused the Irish potato famine was replaced by the US-1 clonal lineage [7]. Genetic data showed that migration was the main factor causing the US-1 clonal lineage to become widespread in the mid-20th century [31]. Historically, the geographic spread of the pathogen primarily occurred via the import of infected plant material, which included potato tubers, tomato fruits, and transplants.

When focusing solely on Thailand, the first hypothesis regarding sexual reproduction is less likely to be evident. This is because the mating of *P. infestans* requires the presence of both A1 and A2 mating types in the same area, the infection of the same leaf, and the formation of oospores for zygote formation [32]. The emergence of a new genotype occurs through the sexual process, resulting in the appearance of different clonal lineages of different mating types. Furthermore, other evidence of sexual reproduction includes several general indicators, such as the presence of both mating types in a 50:50 ratio, readily found oospores in the field, a large number of coexisting clonal lineages, and a large number of genotypes. These pieces of evidence have been consistently observed in Northern Europe [33].

According to the information on the mating type of *P. infestans* in Thailand during the periods of 2000–2002 and 2006–2009, as provided by Petchaboon et al. [11], Jaimasit and Prakob [12], and Sopee [13], only the A1 mating type was identified. Based on this information, we can conclude that the new genotypes of potato isolates in Thailand do not result from sexual reproduction.

Therefore, migration is the most likely explanation for the population change in potato isolates. Considering the historical potato production records in Thailand, two cultivars, ‘Spunta’ and ‘Kennebec’, were used for potato production in 1994. The population analysis of *P. infestans* at that time showed that potato isolates in Chiang-Mai had the TH-1, US-1, and US1.3 genotypes, with equal proportions of the A1 and A2 mating types, and sensitivity to metalaxyl [6]. Petchaboon et al. [11] demonstrated that the genotypes of *P. infestans* during 2000–2002 were RF006 and RF008 and that the main cultivar ‘Atlantic’ was extensively used in Thailand for potato production. In addition, cultivated potato seeds were imported from the U.K. (England, Scotland, and Wales). The results of population structure studies have shown that the RF006 and RF008 genotypes were the most common clonal lineages in Europe during 1995–1998 [34]. The genotypes of *P. infestans* that were endemic in Thailand during 2000–2002 were the same as those in Europe, which was the source of the seed for potato production in Thailand. So, the evidence suggests that the change in the population of *P. infestans* in potatoes in Thailand was caused by the introduction of new genotypes (RF006 and RF008) via infected potato seeds from Europe. This hypothesis corresponds to the most important factor affecting population change in Asia (Japan, South Korea, China, Taiwan, South Asian countries, Nepal, Bangladesh, India, and Pakistan), which is the migration of different genotypes from Europe and the Americas [35].

The main reason for the *P. infestans* population in tomatoes not changing is due to the absence of factors affecting its life cycle, such as the lack of pressure, the absence of migration of new genotypes, and the disappearance of sexual reproduction. This is because tomatoes in Thailand during the 20th and 21st centuries were a minor crop that alternated with the main crop, which was rice. As a result, disease management in tomato crops did not extensively use fungicides, and this lack of intervention did not exert any force on the life cycle of pathogens.

The *P. infestans* genotypes that affect tomatoes are US-1 and US-1.3, which are the most widespread genotypes in tomato and potato production worldwide. Furthermore, experiments attempting cross-infections from potato isolates to inoculated tomatoes did not result in successful infection responses (personal communication). This outcome confirms that the aggressive genotype in potatoes is not exerting pressure to replace the original genotype in tomatoes. In a study by Petchaboon et al. [11], it was found that only the A1 mating type was present, indicating that sexual reproduction had not occurred. Therefore, these factors contribute to the persistence of the original *P. infestans* genotype in the tomato population.

## 5. Factors Affecting Different Responses to Metalaxyl in *P. infestans* Populations in Tomato and Potato Isolates

In Thailand, the results of the population structure analysis of the tomato isolates revealed the dominance of US1. Most isolates from Chiang Mai province showed sensitivity to metalaxyl, except for five isolates collected from Mae Rim, which showed intermediate resistance. Most of the other potato isolates were grouped as intermediate or resistant to metalaxyl (Table 1). We propose the following three possible reasons for the different responses:

### 5.1. The Use of Metalaxyl for Disease Management

The overuse of chemical fungicides has led to an increased degree of pathogen resistance [36]. The management of late blight with the indiscriminate use of metalaxyl has led to the development of resistant strains of the oomycete, which have been found in many countries [37–40]. Potato production in Thailand has rapidly expanded during the 20th and 21st centuries. Potato consumption has also changed from home cooking to potato chips and French fries on an industrial scale. As a result, domestic production changed, providing opportunities for foreign trade [41]. A production system based on contract farming started in 1988 by the United Food company, which used ‘Kennebec’ as the contract cultivar for production in the San Sai district in Chiang Mai province [42]. By



1990, potato production had rapidly expanded, leading to a nearly fivefold increase in production within only 20 years. In addition, the efforts of the Royal Projects to replace opium production in the upland regions of Northern Thailand with other crops were a major cause of the exponential increase in potato production. This large-scale production, in combination with the lack of agronomic knowledge regarding potato cultivation, created difficulties for disease management at that time. The farmers continuously used metalaxyl as the dominant fungicide, which was sprayed approximately 5–20 times per crop cycle. According to Deahl et al. [43], *P. infestans* can easily develop resistance to systemic fungicides such as metalaxyl because these pesticides have only a single mode of action. The continuous increased use of metalaxyl was the main factor that led to the development of fungicide-resistant strains of *P. infestans* [44]. So, this is one pathway through which the pathogen developed resistance to fungicides in the potato population.

During the 20th–21st century, tomato was not among the major crops in Thailand. Tomatoes were only produced on a small scale, usually after rice planting. Disease management was not difficult, and less fungicide was used to decrease the overall cost of tomato production. Consequently, metalaxyl was able to control the disease, as demonstrated by most of the isolates from tomatoes, which showed sensitivity to metalaxyl.

### 5.2. Host Preference of *P. infestans*

*P. infestans* shows host preference (or specificity), which is associated with a particular lineage [45–51]. For example, US-8 is pathogenic mainly on potatoes, whereas US-7, US-11, and US-17 are pathogenic on both potatoes and tomatoes [26,52]. In addition, in Columbia, Uganda, and Kenya, similar data patterns revealed that adapted lineages rarely cause severe disease in other hosts, and the pathogens prefer hosts within a single lineage [51,53]. In Thailand, most clonal lineages in tomatoes are US1, which normally shows sensitivity to metalaxyl. So, we think that US-1 preferentially infects tomato, which shows metalaxyl sensitivity. Conversely, most isolates from potatoes showed resistance to this fungicide. The finding can be explained by the study of Legard et al. [52]. They reported data regarding resistant isolates from potato isolates but not from tomato isolates caused by host preference. Furthermore, additional information provided by Danies et al. [54] proved that each clonal lineage showed reasonably consistent and unique fungicide resistance and host preference. In most cases in Asia, metalaxyl-resistant isolates have been associated with the introduction of or replacement by new *P. infestans* populations [5,48].

### 5.3. Migration of New Genotypes from Infected Potato Seeds

Due to the popularity of potatoes in Thailand, the risk posed by the import of infected potato seeds is higher than that of the import of tomato seeds. Potato production increased by 673% in 2012 in comparison with the production in 1990; however, 353% more land in Northern Thailand was used for potato production at that time [41]. Between 2015 and 2019, the rate of imported potatoes, including both processing and seed potatoes, increased by 15.43% [3]. More specifically, for seed potatoes, the total import of 7099 tons in 2021 originated from the United Kingdom, Australia, the Netherlands, America, and Canada [3].

The two main cultivated potato varieties are ‘Spunta’ and ‘Atlantic’. The ‘Spunta’ variety is mainly imported from the Netherlands to support the fresh market, and the ‘Atlantic’ variety is imported from Scotland and Australia to support the production of potato chips and French fries [41]. Based on the results of the population study reported by Petchaboon et al. [11], the two common clonal lineages, genotypes RF006 and RF008, are predominant in the potato population in Tak and Chiang Mai provinces. These two genotypes, RF006 and RF008, were also found to be the most common clonal lineages in Europe during the same period. Therefore, the original US-1 genotypes from 1994 may have changed to RF006 and RF008 by 2000–2002 in Thailand as a consequence of infected potato seeds imported from Europe. On the contrary, most tomato producers in Thailand use commercial seeds, and *P. infestans* is not transmitted through tomato seeds. Therefore, the migration of new genotypes is less likely to occur through tomato seeds.

## 6. The Importance of *P. infestans* Population Study

*P. infestans* is one of the most aggressive pathogens and has been classified as ‘high risk’, mainly because of its high adaptability to the host [55]. *P. infestans* has a vast genome (240 Mb), consisting of many structures that can develop variable strains and undergo rapid mutations, such as conserved gene sequences with a low number of repeats [56,57]. Additionally, *P. infestans* exhibits high levels of genetic diversity through the sexual process, resulting in high adaptability. For these reasons, controlling the disease using resistant varieties is less likely to be successful due to the pathogen’s rapid adaptation, which outpaces the host’s resistance development [56]. Understanding the dynamics of *P. infestans* populations is an effective strategy for the development of more sustainable disease management.

Currently, potato production in Asia has expanded dramatically and accounts for over 40% of the world’s production [58]. A late blight network for Asia, AsiaBlight, was established following the success of EuroBlight. It is an inclusive network of scientists, farmers, and other stakeholders working on potato late blight disease. The cooperation and data sharing among researchers from across Asia will contribute to the sustainable production of healthy potato crops, thereby improving nutrition and food security for billions of people in Asia. The network’s objective is to generate a coarse-scale map of *P. infestans* populations in Asia, which includes the development of an integrated approach to managing late blight disease [59].

The study of *P. infestans* populations based on mating type, evaluating fungicide effectiveness, and assessing genotypic variation is necessary for understanding the aggressiveness and adaptability of the pathogen. This understanding is crucial for effective late blight disease management. *P. infestans* populations can be identified using standard methods such as metalaxyl sensitivity, allozyme analysis, RG 57 DNA fingerprinting, mtDNA haplotypes, SSRs, and 12-plex SSRs [35]. In Thailand, studies by Petchaboon et al. [11], Jaimasit and Prakob [12], and Sopee [13] have revealed that the majority of damages are attributed to the importation of infected potato seeds, as determined by these standard methods.

A review article on the dynamics of *P. infestans* populations in the major potato production areas of Asia has indicated that the migration of the pathogen from Europe and America also plays a significant role in *P. infestans* population changes in several countries in Asia. These countries include Japan, South Korea, China, Taiwan, South Asian countries, Nepal, Bangladesh, India, and Pakistan [35].

Nowadays, Thailand has increased the amount of imported fresh and seed potatoes, mainly due to consumption demand. Thus, there is a high possibility of new genotypes being present, together with the existence of different mating types, which can promote genotypic variability by sexual reproduction. Thus, the study of *P. infestans* populations should always be monitored and be ongoing research.

In conclusion, the *P. infestans* from the tomato population in Thailand is the same lineage that was endemic from 1994 until 2002. Additionally, the clonal lineage that was found in the potato population changed from US-1 in 1994 to RF006 and RF008 in 2002. This change in *P. infestans* in the potato population was possibly caused by potato seeds imported into Thailand. The *P. infestans* population in potatoes shows resistance to metalaxyl, whereas tomato isolates show sensitivity to the fungicide. The three possible causes of this are (i) the use of metalaxyl, (ii) the host preference of *P. infestans*, and (iii) the migration of new genotypes from infected potato seeds.

Nowadays, the area cultivated for potato production has expanded in many provinces in the north of Thailand, such as Chiang Rai, Lampang, Lamphun, and Phayao. However, no investigations have been conducted on late blight disease in these new cultivation areas (Figure 1). The information regarding the *P. infestans* population structure in Thailand is limited to the areas studied from 1994 until 2002. For this reason, the population structure of *P. infestans* in Thailand needs to be continuously monitored to provide more accurate and updated information, which can be supported by the AsiaBlight network for accurate prediction and forecasting of the late blight disease.

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